

REVISION OF VERNONIA (COMPOSITAE),
SUBSECTION PANICULATAE,
SERIES UMBELLIFORMES OF THE
MEXICAN HIGHLANDS

SAMUEL B. JONES, JR.

Vernonia is a large genus of 800 to 1,000 species, particularly abundant in South America, in certain regions of Africa, southeast Asia, and in North America (Willis, 1966). Although relatively uniform in its floral morphology, *Vernonia* exhibits extreme diversity in its vegetative features and includes herbs, shrubs, small trees, and vines. Because of the sheer number of taxa in *Vernonia* and lack of knowledge of most species, natural subdivisions of the genus have only rarely been fully circumscribed.

Subsection *Paniculatae* series *Umbelliformes* of section *Lepidapoa* established by Gleason (1906) seems to be an exception and appears to be a natural grouping. Gleason noted that the branches of the panicle are mostly aggregated or separated by shortened internodes, the peduncles are approximately uniform in length, the heads appear in subumbellate clusters which are in turn united into large pyramidal or hemispheric inflorescences. The plants are herbaceous to suffruticose perennials. The 10 species appear closely related and all are found in the highland regions of Mexico.

Gleason (1906, 1922) recognized nine species and in this paper ten species and seven subspecies are treated with a greatly revised taxonomy. Keys, synonymies, descriptions, typifications, distribution maps and specimen citations are given for the taxa. A new species, *V. cronquistii*, is described from Guerrero and Oaxaca. *Vernonia liatroides* ssp. *gentryi* is described from Durango south to Jalisco. Several changes in rank are made: *V. inuloides* is reduced to *V. karvinskiana* ssp. *inuloides*; *V. ehrenbergiana* is treated as *V. liatroides* ssp. *ehrenbergiana*; and *V. vernonioides* is now *V. seratuloides* ssp. *vernonioides*.

During the past four years, six of the 10 species have been studied in the field and in the greenhouse. Chromosome numbers, sesquiterpene lactones, and flavonoids have been determined for some of the taxa and hybridization experiments have been carried out within the group and with certain other *Vernonias*. The cytogenetical and phytochemical data provided considerable information and insight into the systematics of the group and they are presently being prepared for separate publication and will only be briefly summarized here.

Vernonia alamanii, *V. serratuloides*, and the three subspecies of *V. liatroides* have the sesquiterpene lactone Glaucolide-A (Mabry, et al., 1975). This bitter compound is found in 10 species of the closely related subsection *Paniculatae* series *Verae* from eastern North America; it is found as well in several species from South America. The flavonoid chemistry of *V. alamanii* and *V. liatroides* is similar also to that of series *Verae* with one exception; a compound tentatively identified as 3, 3' -O- dicayl quercetin 7-O-glucoside is present in the series *Umbelliformes* but not in series *Verae* (Mabry, et al., 1975).

Seven of the 10 species are known chromosomally, each having $n = 17$, the same as the 18 species of series *Verae* from eastern North America (Jones, 1974). Experimental hybridizations within and among our accessions of series *Umbelliformes* generally have yielded fertile F_1 hybrids, but crosses between members of series *Umbelliformes* and series *Verae* have yielded vigorous but sterile F_1 hybrids. The phytochemical and cytogenetical data, briefly summarized here, support Gleason's (1923) conclusions that these two series were derived from a common ancestral line.

The taxonomic treatment presented here represents a synthesis of the results of various systematic techniques, but the descriptive and revisionary aspects have been largely drawn from about 900 herbarium specimens borrowed from BM, DUKE, ENCB, F, GA, GH, K, LD, MEX, MINN, MO, NY, P, TEX, UC, UMO, and US.

ACKNOWLEDGEMENTS

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KEY TO THE SPECIES

1. Peduncles multi-bracteate throughout with short bracts 1-2 mm long, similar to the outer phyllaries; heads 3-5 flowered; outer phyllaries glandular-tomentose; rare and local from the state of Tepic. 10. *V. feddemae*
1. Peduncles not bracteate or with only one or two bracts over 2 mm long, not similar to the outer phyllaries; heads (4) 5 or more flowered; outer phyllaries glabrate to glandular or slightly pubescent.
 2. Involucre height 13-24 mm, width 11-18 mm. 1. *V. alamanii*
 2. Involucre height 4-12 (15) mm, width 3-12 mm (14).
 3. Achenes pilose to pilose-hispid or ciliate on the ribs.
 4. Heads with over 50 flowers. . . 9. *V. barclayi*
 4. Heads with less than 20 flowers.
 5. Heads (4) 5-6 (7) flowered; leaf blades 20-30 cm long, 6-15 cm wide; inner phyllaries acuminate. 7. *V. autumnalis*
 5. Heads 10-14 (18) flowered; leaf blades 6-14 (16) cm long, 2-9 cm wide; inner phyllaries acute to cuspidate.

- 6. Leaf blades tomentose to hirsute-vil-
lous beneath; distributed from Oaxaca
to Chiapas. 5. *V. oaxacana*
- 6. Leaf blades glabrate beneath; distrib-
uted from Guerrero to Oaxaca.
. 4. *V. cronquistii*
- 3. Achenes glabrate to glandular or resinous-glan-
dular.
 - 7. Outer phyllaries long-acuminate terminating
gradually in a sharp point, (2) 3-6 mm long,
tips 1-3 mm long. 8. *V. bealliae*
 - 7. Outer phyllaries acute, acute-acuminate, or
apiculate to bitten, not terminating gradually
into a sharp point, 0.8-2.5 mm long, tips less
than 1.5 mm long.
 - 8. Heads 20-60 (70) flowered; inner phyl-
laries emarginate with mucro in notch,
often bitten, sometimes acute-acuminate.
. 2. *V. karvinskiana*
 - 8. Heads 8-20 (25) flowered; inner phylla-
ries acute, sometimes slightly apiculate, or
mucronate.
 - 9. Leaf blades 2-14 cm wide, ovate-lance-
olate to lanceolate, length/width ratio
2-3. 3. *V. liatroides*
 - 9. Leaf blades 1-3 cm wide, oblong to
linear-lanceolate, length/width ratio
(2.2) 3-8. 6. *V. serratuloides*

1. *Vernonia alamanii* DC. Prodr. 5: 61. 1836. TYPE: México: *Alaman* 1831 (Holotype: G-DC, as photo F! US! as IDC microfiche G-DC!).

Cacalia alamanii (DC.) Kuntze, Rev. Gen. Pl. 2: 969. 1891.

Vernonia dictyophlebia Gleas. Bull. New York Bot. Gard. 4: 203. 1906. TYPE: México: Michoacán: Hills of Patzcuaro, *Pringle* 3347 (Holotype: NY! Isotypes: BM! ENCB! F! GH! K! MEX! MINN! MO! NY! P! UC! US!).

Vernonia alamanii DC. var *dictyophlebia* (Gleas.) McVaugh, Contrib. Univ. Michigan Herb. 9: 477. 1972.

Suffruticose, 1-2 m tall; stems floccose, becoming glabrate below. Leaves cauline; leaf blades 8-14 cm long, 3.5-7 cm wide (length/width ratio ca. 2.2), widest below the middle, ovate, ovate-lanceolate, to lanceolate, scabrous above, veiny and either glabrous or pilose-hispid below, apically acute, basally cuneate, margins serrate; petioles 7-33 mm long, floccose. Inflorescences hemispheric or depressed, variable in size. Heads (43) 51-65 (76) flowered; peduncles 2-4 cm long, floccose, aggregated into clusters. Involucres campanulate, 13-24 mm high, 11-18 mm wide; phyllaries glabrous, margins fimbriate, loosely imbricated, outer reflexed, greenish to brownish-purple; inner phyllaries linear to linear-spatulate, 11-19 mm long, 1.5-4 mm wide, tips mucronate-aristate, mucro 0.3-3.5 mm long; outer phyllaries linear to lanceolate or ovate, 4.5-9 (11) mm long, 1.5-3.2 (4) mm wide. Pappus straw-colored; inner bristles (6) 7-11 mm long, outer bristles 0.8-1.7 mm long. Corollas (9.6) 12-19 (21) mm long, reddish-purple. Anthers 3-5 (6.1) mm long. Achenes 3-4.5 mm long, densely white glandular, ca. 10 ribbed, basally terminating in a prominent yellow areola. Chromosome number $n = 17$. Flowering and fruiting occur from November to February (April).

This species is distributed from San Luis Potosí to Jalisco, Michoacán, and Guerrero as shown in Fig. 1. It grows on rocky limestone or volcanic hillsides, fields and roadsides in the oak-pine zone from ca. 1,800 to 2,600 m altitude. This species is centered on the Neo Volcanic Plateau and extends southward into the Sierra Madre del Sur and northward into the Sierra Madre Oriental. Gleason recognized two species but as McVaugh (1972) pointed out, they are not separable on the basis of lower leaf surface. McVaugh's use of the length of the phyllary awns breaks down when one examines a large sample of specimens. The specimens from Michoacán tend to have broader and more pubescent leaves but even this is highly variable.

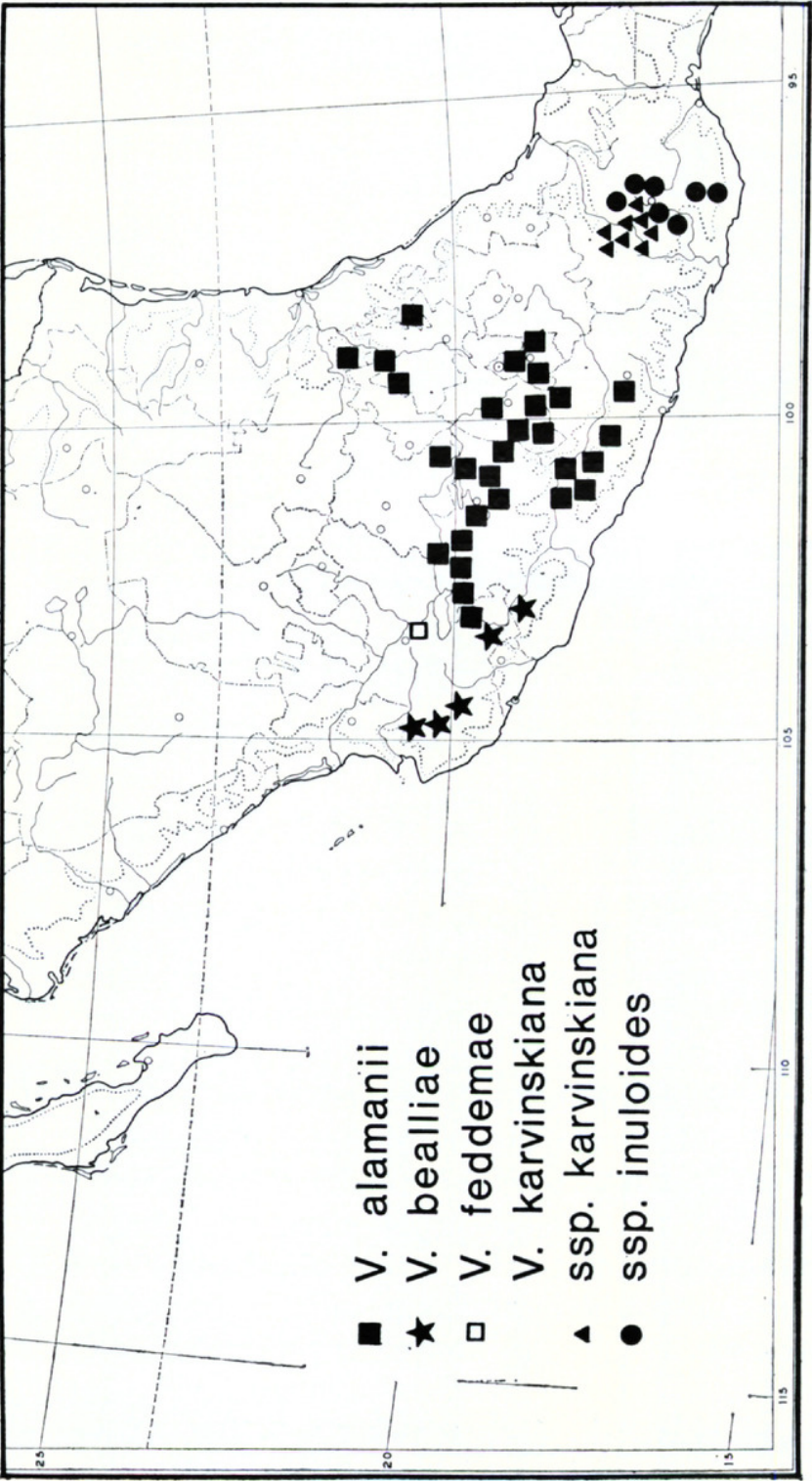


Fig. 1. Distribution of *Vernonia alamanii*, *V. bealliae*, *V. feddemae* and *V. karvinskiana*.

REPRESENTATIVE SPECIMENS: México: San Luis Potosí: ca. 10 mi W Xilitla, hwy 120, *King* 4438 (F, MICH, TEX, UC, US); Hidalgo: 9 mi NE Jacala, hwy 85, *King* 4216 (F, MICH, TEX, UC, US); Veracruz: Huayacocotla, *R. Hdez M. & Vazquez de Hdez* 986 (GH); Guanajuato: Acámbaro, *Rzedowski* 25349 (MICH); Jalisco: Mazamita, *Díaz Luna* 3164 (ENCB); Michoacán: Zitacuraro-Zirahuato, *Hinton* 13541 (GH, MICH, TEX, UC); México: Temascaltepec, *Hinton* 8881 (MICH, TEX, UC, US); DF: Canada of Contreas, *Pringle* 15034 (F, MICH, MIN, MO, TEX); Morelos: Mountain side above Cuernavaca, *Pringle* 8045 (F, GH, MEX, MICH, MIN, UC); Guerrero: San Antonio-Buenos Aires, Montes de Oca, *Hinton* 14071 (GH, MICH, TEX, UC, US).

Natural hybridization occasionally occurs between *Vernonia alamanii* and *V. liatroides* ssp. *ehrenbergiana*. Hybrid specimens examined include: México: México: Pineda, Temascaltepec, *Hinton* 3187 (NY, GH); Nanchititla, Temascaltepec, *Hinton* 7546 (K, US); Michoacán: 12 mi NW of Morelia on hwy 15, *Jones* 20574 (GA).

One putative hybrid between *V. alamanii* and *V. liatroides* ssp. *liatroides* was collected: México: Hidalgo: 0.3 mi N km 150 hwy 85, 11 mi S of State Line, *Chapman* 63 (GA).

2. *Vernonia karvinskiana* DC. Prodr. 5: 62. 1836. TYPE: México: *Karwinski s.n.* (Holotype: G-DC, as IDC microfiche G-DC!; isotypes: P! M, as photo NY! US!).

Ascending, suffruticose perennial, 1-3 m in height; stems glabrate to hispid or floccose. Leaves cauline; upper leaf blades (4.5) 6-10 (11.5) cm long, (0.5) 2-5 (6) cm wide (length/width ratio ca. 2-3), widest at or below the middle, lanceolate to ovate, scabrous above, glabrate to floccose below, apically acute to acuminate, basally cuneate or sometimes rounded-truncate, margins serrate to almost entire; petioles 2-11 mm long, hispid to glabrate or floccose. Inflorescences pyramidal, variable in size but often 1 dm across. Heads 20-60 (70) flowered; peduncles 1-3 cm long, glabrate or pilose to floccose, subumbellate. Involucres vase-shaped, (7) 8-13 (15) mm high, 6-12 (14) mm wide; phyllaries glabrous to resinous, loosely appressed, dark purple to greenish; inner phyllaries lanceolate to linear-

oblong, (6) 7-11 (12) mm long, 1.3-2.6 mm wide, tips emarginate with a mucro in the notch, sometimes bitten or apiculate; outer phyllaries lanceolate, 2.2-6 mm long, 0.7-2.5 mm wide. Pappus straw-colored; inner bristles 5.2-7 mm long, outer bristles 0.5-2 mm long. Corollas (8) 9-12 (13.5) mm long, reddish-purple. Anthers 2.8-4.5 (5) mm long. Achenes 3-4.3 mm long, furrows often glandular, ca. 9 or 10 ribbed. Chromosome number $n = 17$. Flowering and fruiting occur from Sept. to Feb. (Mar.).

This species is restricted to the state of Oaxaca. It grows on rocky hillsides, moist mountain slopes, ridges, or disturbed grassy areas in full sun or partial shade of oak or pine-oak woodlands at an altitude of 1700-2100 m.

Two subspecies are recognized. Their distributions are shown in Fig. 1. They may be characterized and distinguished by the following key:

Inner phyllary tips usually acute; flowers per head 20-30 (34). 2a. ssp. *karvinskiana*
 Inner phyllary tips usually truncate; flowers per head (30) 35-60 (70). 2b. ssp. *inuloides*

2a. *Vernonia karvinskiana* DC. ssp. *karvinskiana*.

Vernonia corymbiformis DC. Prodr. 5: 62. 1836. TYPE: México: *Karwinski s.n.* (Holotype: G-DC, as IDC microfiche G-DC! Isotypes: P! M, as photo NY! US!). (not Gleas. Bull. New York Bot. Gard. 4: 198. 1906).

Cacalia karvinskiana (DC.) Kuntze, Rev. Gen. Pl. 2: 970. 1891.

Cacalia corymbiformis (DC.) Kuntze, Rev. Gen. Pl. 2: 969. 1891.

Vernonia konzattii Robins. Proc. Amer. Acad. 44: 615. 1909. TYPE: México: Oaxaca: Sta. Ines del Monte, Zimatlan, *Konzatti* 1327 (Holotype: GH! Isotype: MEX!).

This subspecies is common in the oak woodlands of the Sierra Madre de Oaxaca. It intergrades with ssp. *inuloides* in the Altiplano de Oaxaca.

REPRESENTATIVE SPECIMENS: México: Oaxaca: Amongst dwarf oaks, dry hills above Las Sedas, 7,000 ft., *Pringle* 6019 (GH, MEX, MICH, MIN, MO, NY, P, UC, US); in oak woodland at summit about 15 km N of Telixtlahuaca on road to Tehuacan, Elev. 2100 m, *Cronquist & Fay* 10914 (NY, TEX, US).

2b. *Vernonia karvinskiana* ssp. *inuloides* (DC.) S. B. Jones, stat. nov.

Vernonia inuloides DC. Prodr. 5: 62. 1836. TYPE: México: *Karwinski s.n.* (Holotype: G-DC, as IDC microfiche G-DC!, as photo NY! US! Isotype: P!).

Cacalia inuloides (DC.) Kuntze, Rev. Gen. Pl. 2: 970. 1891.

This subspecies is common in the oak-pine woodlands of the Altiplano de Coatlan and the Altiplano de Mixtepec northward into the Altiplano de Oaxaca.

REPRESENTATIVE SPECIMENS: México: Oaxaca: 12 miles S of Sola de Vega and 90 miles N of Puerto Escondido, *Cronquist & Sousa* 10504 (GH, MEX, MICH, NY, TEX); 80 miles S of Oaxaca, S of Miahuatlán, *Cronquist & Sousa* 10445 (GH, MEX, MICH, NY).

A splitter perhaps would have recognized two species; however the differences between these two taxa are more apparent than real. Sixteen morphological features were measured or scored on 25 herbarium specimens of each taxon; most were not useful as key characters. The most distinctive features are compared in Fig. 2 where their overlap is readily apparent. The morphological variation of the two subspecies was undoubtedly reinforced by their geographical isolation. Subspecies *karvinskiana* occurs in the mountains to the north of the city of Oaxaca and ssp. *inuloides* is centered in the mountains south of there; in between they intergrade completely. The close relationship of these two taxa is best shown by treatment at the rank of subspecies. If treated as two distinct species this relationship is likely to be obscured.

3. *Vernonia liatroides* DC. Prodr. 5: 34. 1836. TYPE: México: Tamaulipas: Tula to Tampico, *Berlandier* 2139 (Holotype: G-DC, as IDC microfiche G-DC! as photograph US! Isotypes: GH! NY! P!).

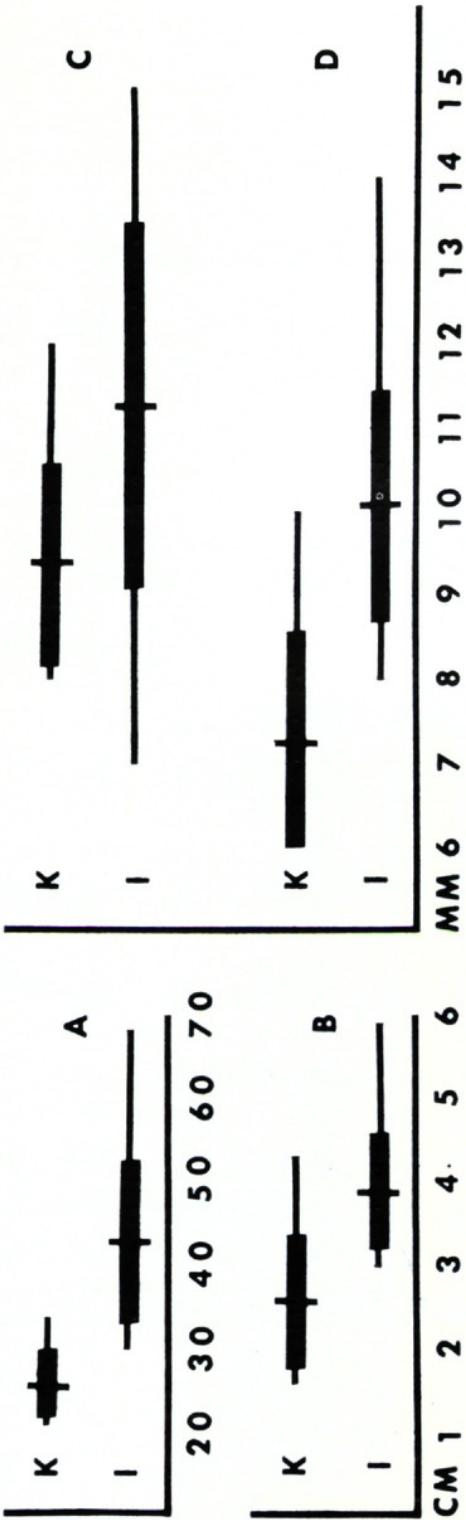


Fig. 2. Ranges, means, and standard deviations of characters of *Vernonia karvinskiana* ssp. *karvinskiana* (K) and ssp. *inuloides* (I). A, number of flowers per head; B, width of the involucre; C, height of the involucre; D, width of the leaf blade.

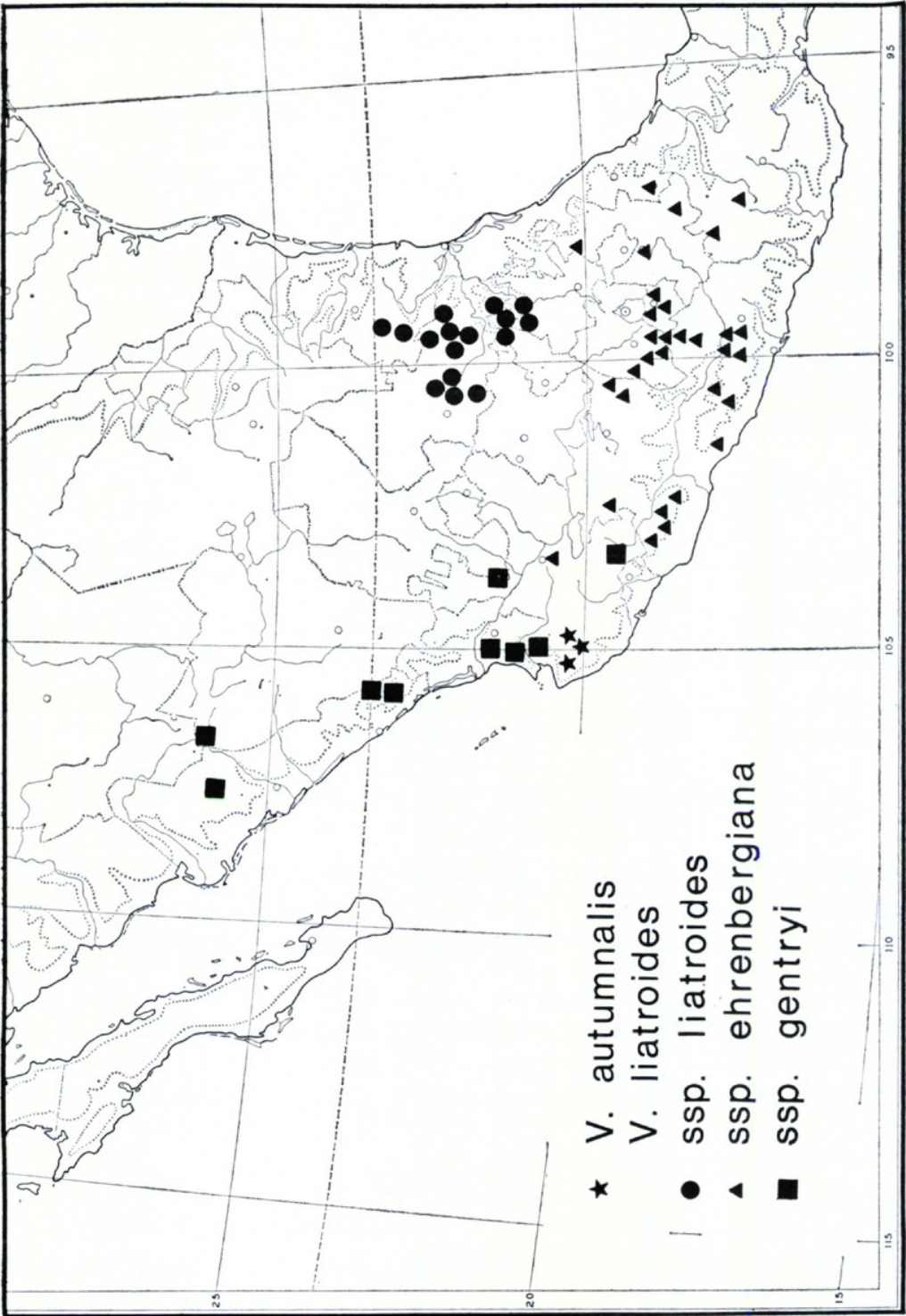
Herbaceous perennial, sometimes becoming frutescent, 1-3 m; stems pilose-hispid or sometimes glabrate. Leaves cauline; leaf blades 4.5-25 cm long, 2-14 cm wide (length/width ratio ca. 2-3), widest at the middle, lanceolate or ovate-lanceolate, slightly scabrous or almost glabrate above, punctate, pilose-hispid, or glabrate below, apically acute, basally cuneate, margins serrate; petioles 0.4 to 3.5 cm long, downy to glabrate. Inflorescences narrowly pyramidal to broadly pyramidal. Heads (8) 9-20 (25) flowered; peduncles 3-5 mm long, downy to glabrate, subumbellate. Involucres campanulate, (3.7) 4.5-6.5 (8) mm high, (2.8) 4-6 (7.5) mm wide; phyllaries ciliate, loosely appressed, greenish-purple sometimes shiny; inner phyllaries oblong-lanceolate, (3.2) 4-5 (6) mm long, (0.8) 1-1.5 (1.7) mm wide, tips acute, slightly apiculate; outer phyllaries lanceolate, (0.8) 1.3-2.3 (2.5) mm long, 0.5-1.2 (1.8) mm wide. Pappus whitish; inner bristles 4.5-6.4 mm long, outer bristles 0.8-1.5 mm long. Corollas (5) 6-10 (11) mm long, reddish-purple to light pink, fading to almost white, glabrous, very fragrant. Anthers 2-4 mm long. Achenes 2-3.2 mm long, resinous glandular or sometimes glabrous, ca 10 ribs. Chromosome number $n = 17$. Flowering and fruiting occur from October to May.

This species is distributed from the Sierra Madre Oriental south and west across the Neo Volcanic Plateau and northward along the Sierra Madre del Sur and the Buried Ranges and Sierra Madre Occidental.

Three subspecies are recognized. Their distributions are shown in Fig. 3. They may be characterized and distinguished by the following key:

Plants normally flowering from October to December, from the Sierra Madre Oriental, or the Neo Volcanic Plateau and the Sierra Madre del Sur; leaf blades (4) 5-11 (13) cm long, 2-5 (7) cm wide, petioles 0.3-1.3 cm long; flowers per head (8) 9-13 (17).

Fig. 3. Distribution of *Vernonia autumnalis* and *V. liatroides*.



Plants from the Sierra Madre Oriental, frutescent herbaceous perennial; corolla lobes (2.2) 2.5-3.5 (4.2) mm long, corolla (5.5) 7-9 mm long. . 3a. ssp. *liatroides*

Plants from the Neo Volcanic Plateau and the Sierra Madre del Sur, herbaceous perennial; corolla lobes 1.8-2.2 (2.7) mm long, corolla 5-7.5 mm long. 3b. ssp. *ehrenbergiana*

Plants normally flowering from late February to April, from the Buried Ranges and the Sierra Madre Occidental; leaf blades (9) 11-20 (25) cm long, (4) 5-11 (15) cm wide, petioles 0.8-3.5 cm long; flowers per head (11) 12-19 (25). 3c. ssp. *gentryi*

3a. *Vernonia liatroides* ssp. *liatroides*.

Eupatorium tulanum Klatt, Abh. Nat. Ges. (Halle) 15: 323. 1882. TYPE: México: Tamaulipas: Tula to Tampico, *Berlandier* 2139 (Holotype GH! Isotypes: G-DC, as IDC microfiche G-DC! P!).

Cacalia liatroides (DC.) Kuntze, Rev. Gen. Pl. 2: 971. 1891.

This subspecies is common on limestone hillsides, in mesic habitats of the Sierra Madre Oriental in the tropical deciduous forest up and into the pine-oak zone. Flowering and fruiting normally occur from October to January. The plants become woody near the base of the stems.

REPRESENTATIVE SPECIMENS: México: Tamaulipas: *Viereck s.n.* (US); San Luis Potosí: 19 mi WSW Xilitla, hwy 120, oak-pine forest, red limestone soil, *Jones* 22376 (GA); Hidalgo: 27 mi S Tamazunchale at Santa Maria, shrub 2 m. tall, rocky hillside, *Jones* 20560 (GA); Queretaro: 5 mi WSW Jalpan, hwy 120, abundant along limestone roadsides, *Jones* 22378 (GA).

3b. *Vernonia liatroides* ssp. *ehrenbergiana* (Sch. Bip.) S. B. Jones, stat. nov.

Vernonia ehrenbergiana Sch. Bip. Linnaea 20: 513. 1847. TYPE: México: Barranco pr. los reyes, *Ehrenberg* 710 (Holotype P!).

Cacalia ehrenbergiana (Sch. Bip.) Kuntze, Rev. Gen. Pl. 2: 971: 1891.

Vernonia capreaefolia Gleas. Bull. N.Y. Bot. Gard. 4: 200. 1906. TYPE: México: Veracruz: Orizaba, *Schaffner* 117 (Holotype: GH!).

This subspecies is commonly found along roadsides and on rocky hillsides in the Neo Volcanic Plateau and the Sierra Madre del Sur. In the latter region it is often associated with limestone. It appears to be a herbaceous perennial, unlike the other two subspecies which become suffrutescent. Subspecies *ehrenbergiana* and ssp. *gentryi* intergrade in western Jalisco. Flowering and fruiting occur from October to January.

REPRESENTATIVE SPECIMENS: México: Jalisco: Guadalajara, *Pringle* 2943 (GH); Michoacán: km 115 hwy 15 between Zitacuaro and Cd. Hidalgo, *Jones* 20572 (GA); Guerrero: 8 km SW Xochipala, *Feddema* 2765 (ENCB, MICH, TEX); México: 2 mi N Ixtapan de Sal hwy 55, *Jones* 20569 (GA); Oaxaca: Huajuapam, *Nelson* 1979 (GH, US); Puebla: by streams near Tehuacan, *Pringle* 6246 (BM, ENCB, F, GH, MEX, MIN, P, UC, US); Veracruz: Orizaba; *Bourgeau* 3339 (F, GH, K, US).

3c. *Vernonia liatroides* ssp. *gentryi* S. B. Jones, ssp. nov. TYPE: México: Durango: 116 mi W of Durango on hwy 40, elev. 2000 m, *Jones* 22527 (Holotype: GA!).

Folia 10-25 cm longa, 5-15 cm lata (ratione longitudinis cum latitudine 1.5-2.5), ovali-lanceolata, vel lanceolata. Capitula (11) 13-18 (25) flora.

This subspecies is abundant at elevations of ca 1,500 to 2,000 m on the mesic west slopes in the pine-oak zone down into the tropical deciduous forests of the Buried Ranges and the Sierra Madre Occidental. It is named in honor of Howard Scott Gentry, whose collections from northwest Mexico have facilitated my studies of this and other species of *Vernonia*. Flowering and fruiting occur from March to May.

REPRESENTATIVE SPECIMENS: México: Durango: San Ramón, *Palmer* 140 (F, GH, MO, NY, US); Sinaloa: 132 mi W Durango near El Batel on hwy 40, *Jones* 22528 (GA); Nayarit: 15 km W Tepic, sobre el camino a Jalcocotán, *Rzedowski* 15614 (ENCB, MEX, MICH). Jalisco: San Sebastian, Hacienda del Ototal, *Mexia* 1681 (BM, F, GH, MICH, MIN, MO, NY, UC, US); Zacatecas: 5 mi SW Mezquital del Oro, *McVaugh* 22135 (ENCB, MICH, NY).

Nineteen morphological features were measured on 25 specimens of each of the three taxa. The measurements in general showed considerable overlap; however, those presented in Fig. 4 are of some diagnostic value. Keeping in mind the many features shared by these three taxa, they are best treated as subspecies.

4. *Vernonia cronquistii* S. B. Jones, sp. nov. TYPE: México: Guerrero: semi-open slopes in pine-oak forest in the mountains along the highway ca. 62 rd miles N of Acapulco, and 20 mi S of Chilpancingo, *Cronquist* 9705 (Holotype: NY! Isotypes: GH! MEX! MICH! MO! NY!).

Herba perennis, erecta, 1.5-metralis; caules purpurei necnon glabri. Folia caulina (6.5) 8-12 (15) cm longa, 1.9-4.5 cm lata (ratione longitudinis cum latitudine ca. 3-4), ad medium dilatata, ovato-lanceolata, supra scabridiuscula, infra glabrescentia, apicibus acuminatis, basibus anguste cuneatis, marginibus serratis; petioli 0.5-1.2 cm longi glabrescentes. Inflorescentiae paniculatae-umbellatae. Capitula 10-14(18)-flora, cum pedunculis 0.5-1.3 cm longis. Involucri anguste campanulata 5.5-8.5 mm longa, 3-7.5 mm lata; phyllaria ciliata, laxe imbricata, purpurea, eis interioribus lineari-lanceolatis, 4.2-7.5 mm longis, 0.9-1.5 mm latis, apicibus acutis vel cuspidatis, eis exterioribus lanceolatis, 1-2 mm longis, 0.6-0.9 mm latis. Pappi setae albae, eis interioribus 5-6.1 mm longis, eis exterioribus 0.6-1.1 mm longis. Corollae (7.3) 9-11 (12.6) mm longae, *Vernonia*-purpureae, glabrae. Antherae 2.7-3.3 mm longae. Achaeinia 2.2-3.1 mm longa, piloso-hispida, ca. 9-11 nervata. Chromosome number $n = 17$. Flowering and fruiting occur from October to December. This species is dis-

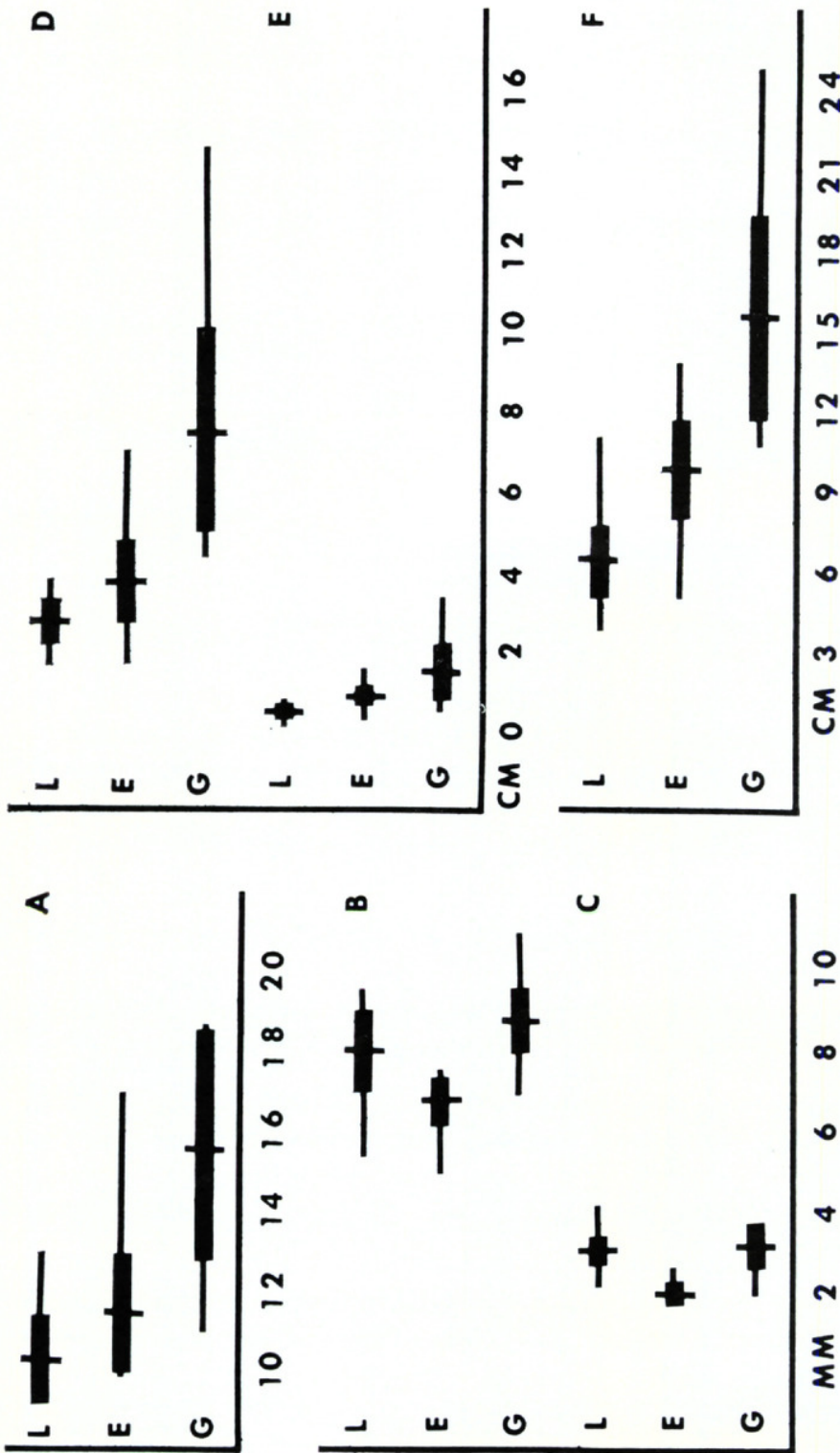


Fig. 4. Ranges, means, and standard deviations of characters of *Vernonia liatroides* ssp. *liatroides* (L); ssp. *gentryi* (G); ssp. *ehrenbergiana* (E); A, number of flowers per head; B, length of the corolla; C, length of the lobes of the corolla; D, width of the leaf blade; E, length of the petiole; F, length of the leaf blade.

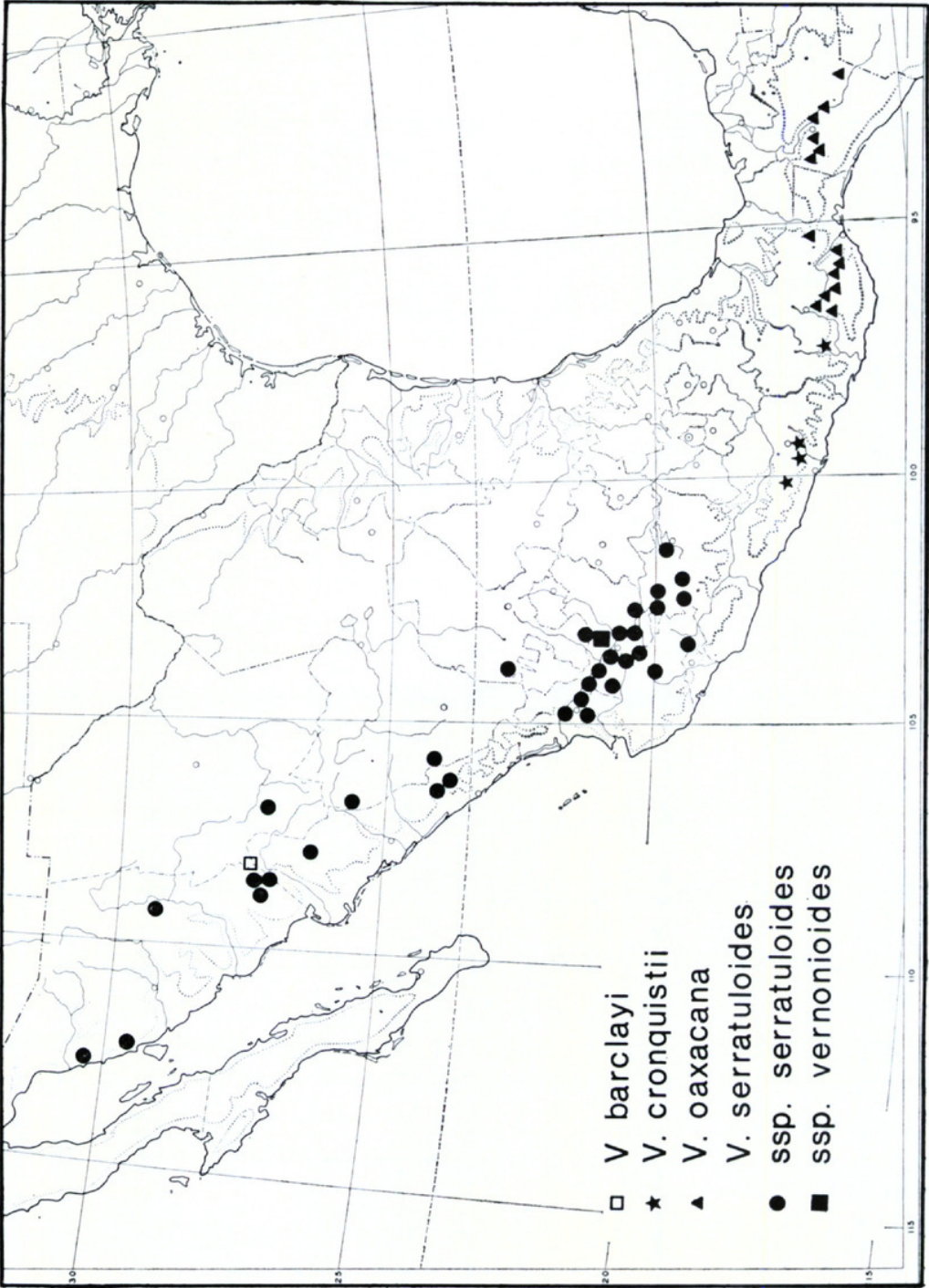
tributed from Guerrero to Oaxaca along the Sierra Madre del Sur as shown in Fig. 5. It occurs on semi-open slopes in pine-oak or pine forests at elevations of 700-950 m. It is named in honor of Dr. Arthur Cronquist who made the type collection and has provided encouragement to me with my studies of *Vernonia*.

Additional specimens examined include: México: Guerrero: Rincón de la Via, *Kruse* 739 (ENCB); Plan de Carrizo, Galeana, *Hinton* 11035 (GH, K, MICH, NY, US); Oaxaca: 5-6 km NE Putla rd to Tlaxiaco, *McVaugh* 22273 (ENCB, MICH).

5. *Vernonia oaxacana* Sch. Bip. ex Klatt, *Leopoldina* 20: 74. 1894. TYPE: México: Chiapas: San Carlos, *Liebmann* 49 (Syntypes: C, as IDC microfiche!, as photo and fragment US!, as photo F! NY! US!, as drawing and fragment GH!, as fragment P!).

Suffruticose, 0.5-2.5 m; stems hirsute-villous to tomentose, becoming glabrate with age. Leaves cauline; upper leaf blades 6.5-14 cm long, 2.4-8.7 cm wide (length/width ratio ca. 2), widest below the middle, elliptic-ovate, pilose-hispid above, tomentose to hirsute-villous below, apically acute, basally oblique to cuneate or rounded, margins serrate; petioles 0.7-2 cm long, villous. Inflorescences pyramidal, large, irregular, highly branched, with many leaves. Heads (10) 11-13 (15) flowered; peduncles 5-10 mm long, hispid, appearing subumbellate. Involucres campanulate, (5.3) 6-7 (8) mm high, 4.2-6.6 mm wide; phyllaries glabrous, loosely appressed, greenish purple; inner phyllaries oblong-lanceolate, 4.2-6.7 mm long, 0.8-1.5 mm wide, tips narrowly cuspidate; outer phyllaries lanceolate, 0.7-2.2 mm long, 0.3-1 mm wide. Pappus white; inner bristles 5-6.5 mm long, outer bristles 0.9-2.2 mm long. Corollas (7) 8-9 (10) mm long, reddish-purple. Anthers 2.5-3.5 mm long.

Fig. 5. Distribution of *Vernonia barclayi*, *V. cronquistii*, *V. oaxacana* and *V. serratuloides*.



Achenes 2-3.2 mm long, sparsely ciliate on ribs, rarely glandular, ca. 10 ribs. Chromosome number $n = 17$. Flowering and fruiting occur from Dec. to Feb.

This species is distributed from Oaxaca to Chiapas as shown in Fig. 5. This species grows in oak woodlands and on rocky roadsides at elevations of 900-1300 m.

REPRESENTATIVE SPECIMENS: México: Oaxaca: Along hwy 190, 67 mi W Tehuantepec, *King* 2476 (MICH, TEX, US); Chiapas: Roadside in low valley with palms, hwy 190, 15 mi S La Trinitaria, *Breedlove & Raven* 8433 (F, MICH).

6. *Vernonia serratuloides* H.B.K. Nov. Gen. Sp. 4: 33. 1818. TYPE: México: Michoacán: "Crescit regione temperata prope urbem Valladolid de Mechoacan, alt. 1000 hex." [Collector?] (Holotype: P, as photo F! as fragment P!).

Herbaceous perennial, ca. 1 m; stems glabrate to pilose-hispid or rarely downy. Leaves cauline, crowded; leaf blades (5.2) 6-12 (13.5) cm long, (0.8) 1-3 (3.8) cm wide (length/width ratio ca. 2.2-8), widest at or below the middle, oblong to linear-lanceolate, scabrous or sometimes glandular-punctate or glabrate above, glandular-punctate or scabrous to pilose-hispid below, apically acute, basally cuneate, margins remotely toothed; petioles 2-5 mm, glabrate to pilose-hispid. Inflorescences narrowly pyramidal. Heads 9-19 flowered; peduncles 3-8 mm long, pilose-hispid to almost downy, subumbellate. Involucres narrowly campanulate, 6-9 mm high, (4) 4.5-9 (10) mm wide; phyllaries ciliate or hirsute to almost glabrate on the margins, tightly appressed, greenish to purple; inner phyllaries oblong-lanceolate, 5-8 mm long, 1-1.5 mm wide, tips acute, sometimes with a small mucro; outer phyllaries lanceolate, 1.3-2.9 mm long, 0.5-1 mm wide. Pappus straw colored; inner bristles 5-6.5 mm long, outer bristles 0.4-1.2 mm long. Corollas 7.4-11 mm long, reddish-purple. Anthers 2.9-3.7 mm long. Achenes 2.5-3.3 mm long, glabrate to resinous-dotted, 9-11 ribs. Chromosome number $n = 17$. Flowering and fruiting occur from Sept. to Dec.

This species is distributed from Sonora southeastward into Jalisco and Michoacán as shown in Fig. 5. It grows on rocky hillsides, dry pastures, oak or oak-pine woodlands, fallow fields, often in sticky clay soil at altitudes of 300-1000 m. The range of this species is associated with the Sierra Madre Occidental and the northwestern part of the Neo Volcanic Plateau.

Two subspecies are recognized. They may be characterized and distinguished by the following key:

Leaf blade length/width ratio 4-8; flowers per head 9-14; corolla length 7.4-9 mm; involucre width 4-7 mm.

..... 6a. ssp. *serratuloides*

Leaf blade length/width ratio 2.2-3.6; flowers per head 15-19; corolla length 9.1-11 mm; involucre width 6.5-10 mm.

..... 6b. ssp. *vernonioides*

6a. *Vernonia serratuloides* ssp. *serratuloides*.

Vernonia sinclairi Benth. Bot. Voy. Sulph. 109. 1845. TYPE: México: Nayarit: San Blas-Tepic, *Sinclair s.n.* (Holotype K!).

Perezia paniculata Gray, Proc. Amer. Acad. Arts 21: 393. 1886. TYPE: México: Chihuahua: Mountains above Batopilas at the Frailes, ca. 7,000 ft, *Palmer* 279 (Holotype: GH! Isotypes: BM! US!).

Cacalia serratuloides (H.B.K.) Kuntze, Rev. Gen. Pl. 2: 970. 1891.

Cacalia sinclairi (Benth.) Kuntze, Rev. Gen. Pl. 2: 970. 1891.

Vernonia umbellifera Gleas. Bull. New York Bot. Gard. 4: 199. 1906. TYPE: México: Jalisco: Plains of Guadalajara, *Pringle* 2316 (Holotype: NY! Isotypes: BM! F! MEX! MO! NY! P! UC! US!).

Vernonia camporum M. E. Jones, Contrib. West. Bot. 18: 69. 1933. TYPE: México: Jalisco: Orendain Nov. 27, 1930, *M. E. Jones s.n.* (Holotype: POM, as photo and fragment US!).

This subspecies is widespread with many collections from the southern part of its range. As to be expected there is some local variability but it is not sufficient to warrant recognition of additional taxa.

REPRESENTATIVE SPECIMENS: México: Sonora: Sierra de Alamos, *Gentry* 4862 (MICH, MO, NY, US); Chihuahua: rd. from Parral to Batopilas, *Goldman* 156 (US); Sinaloa: NW base of Cerro Colorado, *Gentry* 5192 (NY); Durango: Tamazula, *Ortega* 4443 (US); Nayarit: Laguna Santa Maria del Oro, *Windler* 2904 (MICH); Jalisco: Hills near Etzatlan, *Pringle* 11607 (F, MICH, MO, US); Michoacán: ca. 5 mi N Cotija and 22 mi S Jiquilpan, *King & Soderstrom* 4592 (MEX, MICH, NY, TEX, UC, US).

6b. *Vernonia serratuloides* ssp. *vernonioides* (Gray) S. B. Jones, stat. nov.

Perezia vernonioides Gray, Proc. Amer. Acad. Arts 22: 433. 1887. TYPE: México: Rio Blanco, in shady grassy bottoms, *Palmer* 745 (Holotype: GH!).

Vernonia vernonioides (Gray) Bacigal. Contr. Gray Herb. 97: 77. 1931.

Vernonia jaliscana Gleas. Bull. New York Bot. Gard. 4: 198. 1906. TYPE: México: Jalisco: Hills near Guadalajara, 5,000 ft., *Pringle* 9994 (Holotype: GH! Isotypes: F! MO! US!).

Subspecies *vernonioides* is known only from Jalisco near Guadalajara. The one exact location would place it in the dissected canyon country to the NNE of the city.

REPRESENTATIVE SPECIMENS: México: Jalisco: Ixtlahuacán de los Membrillos, oak woodland, *Detling* 8775 (MICH); Rocky hills near Guadalajara, *Pringle* 2884 (F, GH, MEX, NY).

Eighteen morphological features on all nine available specimens of ssp. *vernonioides* and on 25 specimens of ssp. *serratuloides* were measured or scored. The two subspecies share many morphological features indicative of a close relationship. They differ in few characters as shown in Fig. 6. The treatment of these two taxa places emphasis on their similarities rather than on their differences.

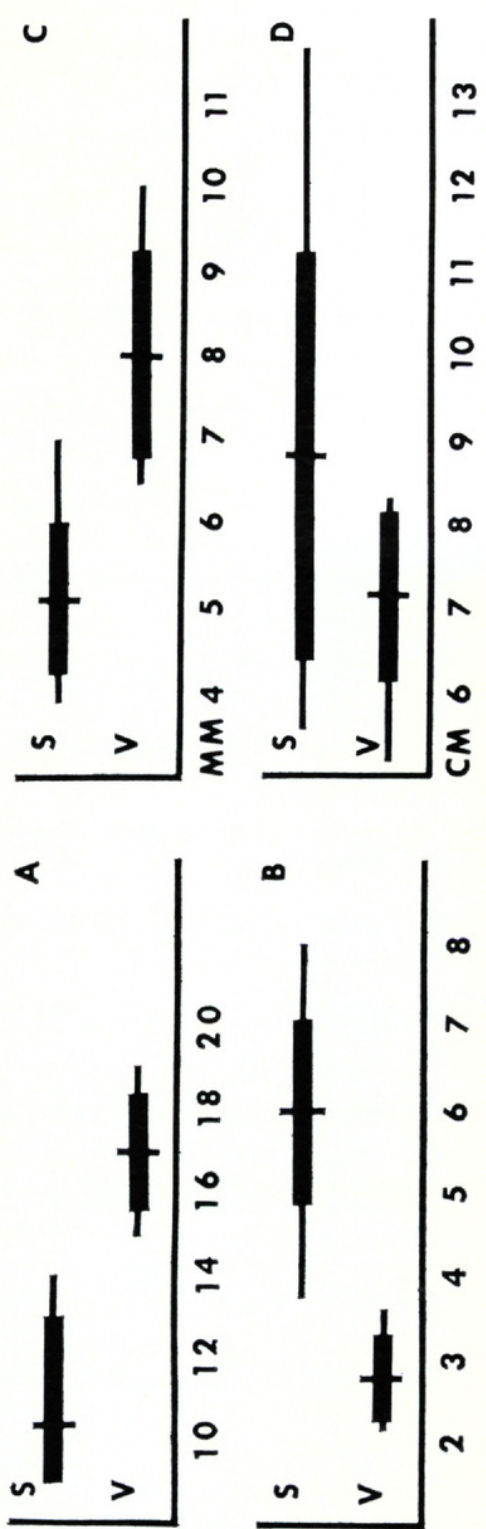


Fig. 6. Ranges, means, and standard deviations of characters of *Vernonia serratuloides* spp. *serratuloides* (S) and ssp. *vernonioides* (V). A, number of flowers per head; B, length/width ratio of the leaf blade; C, width of the involucre; D, length of the leaf blade.

7. *Vernonia autumnalis* McVaugh, Contr. Univ. Mich. Herb. 9: 477. 1972. TYPE: México: Jalisco: 5 km S. of La Huerta, in oak forest, elev. 500-550 m, *McVaugh* 19833 (Holotype: MICH. Isotype: GA!).

Herbaceous perennial, 1-2 m; stems lanate sometimes becoming glabrate, striate. Leaves cauline; leaf blades 20-30 cm long, 6-15 cm wide (length/width ratio ca. 2.5), widest at or above the middle, elliptic-ob lanceolate, glabrous above, lightly resinous to arachnoid below, apically acute, basally cuneate, margins revolute and remotely toothed, sometimes pinnately 4-lobed; petioles 1-2.7 cm long, glabrate to lanate. Inflorescences broadly pyramidal. Heads (4) 5-6 (7) flowered; peduncles ca. 5 mm long, lanate, sub-umbellate. Involucres campanulate (5) 6-9 mm high, (3.5) 4.5-5.2 mm wide; phyllaries arachnoid-ciliate, loosely appressed, purple; inner phyllaries elliptic-oblong, 6.5-8.2 mm long, 1.3-1.9 mm wide, tips acuminate; outer phyllaries lanceolate, 0.9-1.5 mm long, 0.7-0.9 mm wide. Pappus whitish; inner bristles 5.5-6.5 mm long, outer bristles 1-1.2 mm long. Corollas 8.8-10 mm long, reddish-purple, white glandular. Anthers 2.2-3.2 mm long. Achenes 2.7-3.6 mm long, pilose, 6-7 ribbed with 1 main rib on convex side. Chromosome number $n = \text{ca. } 17$. Flowering and fruiting occur from Oct. to Dec.

This species is found in southwestern Jalisco as shown in Fig. 3. It grows in ravines of oak-pine forest and tropical deciduous forest at 650 to 800 m elevation in the Northern Uplands of the Sierra Madre del Sur. *Mexia* 1575 from San Sebastián, Jalisco appears to be a hybrid between *V. autumnalis* and *V. bealliae*.

REPRESENTATIVE SPECIMENS: México: Jalisco: Mountainsides above (north of) La Cuesta, *McVaugh* 20268 (ENCB, MICH); 5 km N El Tuito, Mpio. de Cabo Corrientes, *McVaugh* 25476 (MICH).

8. *Vernonia bealliae* McVaugh, Contr. Univ. Mich. Herb. 9: 479. 1972. TYPE: México: Jalisco: San Sebastián, *Nelson* 4098 (Holotype: GH. Isotype: US!).

Vernonia corymbiformis sensu Gleas. Bull. New York Bot. Gard. 4: 198. 1906, not *V. corymbiformis* DC.

Suffruticose, erect or sometimes arching, 1.5-3 m; stems almost glabrous to lightly floccose. Leaves cauline; leaf blades (7) 9-14 (16) cm long, (2) 3-7 (10) cm wide (length/width ratio ca. 2-3), widest at or slightly below the middle, lanceolate to lanceolate-ovate, glabrous to somewhat scabrous above, reticulate-veined, resinous, with glandular trichomes to almost glabrous below, apically acuminate to almost acute, basally cuneate, margins serrate; petioles (0.7) 1-2 (3.5) cm long, glabrate to pilose-hispid or almost tomentose. Inflorescences pyramidal, usually 1-3 dm wide. Heads 17-29 flowered; peduncles 1-3 cm long, strigose to resinous or glabrate, sub-umbellate in tight clusters. Involucres campanulate, (7.7) 9-11 (11.7) mm high, (5.5) 7-8 (8.3) mm wide; phyllaries glabrous, margins sometimes ciliate, loosely appressed, purple; inner phyllaries lanceolate, 6.3-9 mm long, 1-1.8 mm wide, tips awned, 0.2-1 mm long; outer phyllaries lanceolate, 2-5.6 mm long, 0.6-1.2 mm wide. Pappus white to straw colored; inner bristles 6-7 mm long, outer bristles 0.5-1.5 mm long. Corollas (8.5) 10-11.5 (12) mm long, reddish purple. Anthers (2.5) 3-4 mm long. Achenes ca. 4 mm long, densely white glandular when young, resinous when older. Flowering and fruiting occur from Feb. to May.

This species is distributed from Jalisco south to Michoacán as shown in Fig. 1. It grows in humid pine-oak-fir forests and barrancas on steep slopes and along streams, altitude 1620-2600 m, in the Northern Uplands of the Sierra de Parnaso, the Sierra de Perote, and Sierra de Coalcoman.

REPRESENTATIVE SPECIMENS: México: Jalisco: ca. 15 mi SE Autlán, *McVaugh* 10331 (DUKE, GH, MEX, MICH, NY, TEX); Michoacán: S. Torricillas, Coalcoman, *Hinton* 13674 (F, MO, NY, US).

9. *Vernonia barclayi* H. Robinson & C. F. Reed. *Phytologia* 27: 52. 1973. TYPE: México: Sonora: Sierra Tecuari;

slopes above Rancho El Banco along road between Alamos and Mil Pilas, Chihuahua, A. S. Barclay & J. Arguellas 2018. (Holotype: US! Isotype: REED).

Plants frutescent, ca. 2 m tall; stems striate, whitish tomentose. Leaf blades 4-10 cm long, 1.5-3.5 cm wide (length/width ratio ca. 3) widest below the middle, oblong-elliptic, downy above, tomentose below, apically acute, basally rounded, margins remotely and faintly toothed; petioles 2-3 mm long, whitish tomentose. Inflorescences subumbellate. Heads ca. 60 flowered; peduncles 1.5-2 cm long, whitish tomentose. Involucres campanulate, ca. 8 mm high, 10-12 mm wide; phyllaries arachnoid, tightly appressed in ca. 5 series, greenish with a slight tinge of purple; inner phyllaries lanceolate, ca. 6 mm long, ca. 1.5 mm wide, tips acuminate; outer phyllaries lanceolate, 2.5 mm long, 1 mm wide. Pappus whitish; inner bristles ca. 7 mm long, outer bristles 0.7 mm long. Corollas 12.5 mm long, reddish-purple. Anthers 3.5 mm long. Achenes 3.5 mm long, sparsely pilose-hispid, ca. 10 ribbed. Flowering and fruiting occur from April to May.

This species is known only from the type location in the state of Sonora along the road between Alamos, Sonora and Mil Pilas, Chihuahua (Fig. 5). It is locally abundant along moist ravines in the oak zone of Sierra Tecuari.

10. **Vernonia feddema** McVaugh, Contr. Univ. Mich. Herb. 9(4): 480. 1972. TYPE: México: Tepic: ca. 5 km NE of Puga (ca. 15 km NE of Tepic), pastured lands among large boulders, with trees and shrubs, elev. ca. 1000 m, *Feddema* 846A (Holotype: MICH!).

Perennial herb, 1 m tall; stems striate, slightly pubescent. Leaves cauline, coriaceous; leaf blades 8-12 cm long, 3-5 cm wide (length/width ratio ca. 1.6-1.9), widest at the middle, elliptic, glabrate above, resinous-glandular and slightly downy below, apically acute, basally rounded-cuneate to slightly oblique, margins remotely toothed, revolute; petioles 2-5 mm long, downy. Inflorescences

pyramidal. Heads 3-5 flowered; peduncles ca. 1 cm long, pilose-hispid, multibracteate, almost subumbellate. Involucres cylindric, ca. 8 mm high, ca. 4 mm wide; phyllaries glandular-tomentose, loosely appressed, greenish-purple; inner phyllaries narrowly elliptic, ca. 4 mm long, ca. 1 mm wide, tips apiculate; outer phyllaries ovate, ca. 1.5 mm long, ca. 1 mm wide. Pappus whitish; inner bristles 4.5 mm long, outer bristles 0.9 mm long, scale-like. Corollas ca. 9 mm long, reddish-purple, white glandular. Anthers ca. 2.6 mm long. Achenes ca. 2.5 mm long, pilose, with ca. 9 or 10 ribs. Flowering and fruiting occur from August to September.

This species is known only from the type locality. This collection was made in pastured lands among large boulders, with trees and shrubs, at an elevation of ca. 1,000 m. As McVaugh (1972) noted, this species is related to others in the group by habit, but the repeated forking of the branches of the inflorescence and the long multibracteate peduncles are unique to this group and unique among Mexican *Vernonias*. All things considered, it is probably best placed among this group of *Vernonias* until other evidence suggests otherwise.

EXCLUDED SPECIES

Vernonia bolleana Sch. Bip. ex Seemann, Bot. Voy. Herald 297. 1856. TYPE: México: N. W. México, *Seeman s.n.* (Holotype: K! as photo MICH! Isotypes: P! G!). This species was placed by Gleason (1906) in subsection *Paniculatae* series *Verae* but it does not appear to belong here or in subsection *Paniculatae* series *Umbelliformes*. Most likely it should be placed in the genus *Bolanosa*.

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DEPARTMENT OF BOTANY
THE UNIVERSITY OF GEORGIA
ATHENS, GEORGIA 30602



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