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NEW SUPRAORDINAL NAMES AND RECOGNITION OF FIVE CLASSES IN MAGNOLIOPHYTA

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ABSTRACT

The flowering plants are divided into five rather than two classes, Magnoliopsida, Piperopsida, Liliopsida, Ranunculopsida, and Rosopsida, corresponding to the magnolioides, the paleoherbs, the monocots, the ranunculids, and the eudicots. The subclasses **Piperidae** and **Cornidae**, and the superorders **Piperanae**, **Capparanae**, **Cucurbitanae**, and **Saxifraganae** are proposed as new. A brief linear sequence of the higher taxa (above the rank of superorder) is presented for the flowering plants.

KEY WORDS: Magnoliophyta, Magnoliopsida, Piperopsida, Liliopsida, Ranunculopsida, Rosopsida, Piperidae, Cornidae, Piperanae, Capparanae, Cucurbitanae, Saxifraganae, classification, phylogeny

Ongoing research detailing the relationships among various families of angiospermous plants (Magnoliophyta) is demonstrating the need for changes in the established system of classification (Cronquist 1981, 1988; Takhtajan 1987; Thorne 1992a, b) above the rank of order. Most of these recent efforts (Crane 1985; Chase *et al.* 1993; Doyle & Donoghue 1986, 1992; Donoghue & Doyle 1989; Loconte & Stevenson 1991; Qui *et al.* 1993) have shown that the traditional dicotyledonous group (Magnoliopsida) is not a monophyletic taxon although the monocotyledonous group (Liliopsida) is. To provide a workable nomenclature for a classification reflective of the major higher taxonomic trends within the flowering plants, namely the magnolioides, the paleoherbs, the ranunculids, the eudicots, and the monocots, it is suggested that each be recognized at the rank of class within Magnoliophyta as defined by Cronquist *et al.* (1966).

The use of names at a single rank for nested groups within a single taxon (Magnoliophyta) is a problem because not all members of the nested groups can be distinguished and the loss of phylogenetic information is exacerbated because the relationships of the nesting patterns are not expressed by single-rank names. The limitations of existing nomenclature preclude the recognition of numerous nested groups at different ranks as it is unrealistic to proliferate ranks to account for all the potentially recognizable groups. By using the rank of class for the five groups of flowering plants distinguished here one can at least recognize the major trends within Magnoliophyta, albeit with some still para-monophyletic. As for the formal taxonomic recognition of the unique groups for *Ceratophyllum* (a dicot: Loconte & Stevenson 1991; Chase *et al.* 1993) and for *Acorus* (a monocot: Duvall *et al.* 1993a, b), as distinct from the remainder of the dicots or monocots, I do not consider this worthy for nomenclatural and taxonomic reasons. Much remains to be done to confirm that these genera represent unique groups and that they are the most primitive of our modern dicots and monocots, respectively.

The following linear sequence attempts to outline a system of classification for the flowering plants above the rank of superorder. Several superorders beyond those noted below remain to be published and until those names are available, a more detailed presentation is not appended. It should be noted that while such subclasses as Hamamelididae and Dilleniidae are retained, their definitions differ greatly from the Cronquistian circumscriptions.

Magnoliophyta Cronq., Takht., & Zimmerm., *Taxon* 15:134. 1966.

A. Magnoliopsida Brongn., *Enum. Pl. Mus. Paris* xxvi, 95. 1843.

1. Magnoliidae Novák *ex* Takht., *Syst. Phylog. Magnolioph.* 51. 1967.

B. Piperopsida Bartl., *Ord. Nat. Pl.* 83. 1830.

2. Piperidae Reveal, *Phytologia* 76:3. 1994.

C. Liliopsida Batsch, *Regni Veg.* 108. 1802.

3. Alismatidae Takht., *Syst. Phylog. Magnolioph.* 461. 1967.

4. Triurididae Takht. *ex* Reveal, *Novon* 2:235. 1992.

5. Arecidae Takht., *Syst. Phylog. Magnolioph.* 425. 1967.

6. Liliidae Takht., *Syst. Phylog. Magnolioph.* 473. 1967.

7. Commelinidae Takht., *Syst. Phylog. Magnolioph.* 514. 1967.

8. Zingiberidae Cronq., *Brittonia* 30:505. 1978.

D. Ranunculopsida Brongn., *Enum. Pl. Mus. Paris* xxvi, 96. 1843.

9. Ranunculidae Takht. *ex* Reveal, *Novon* 2:235. 1992.

E. Rosopsida Batsch, *Regni Veg.* 1. 1802.

10. Caryophyllidae Takht., *Syst. Phylog. Magnolioph.* 144. 1967.
11. Hamamelididae Takht., *Syst. Phylog. Magnolioph.* 113. 1967.
12. Dilleniidae Takht. *ex* Reveal & Takht., *Phytologia* 74:171. 1993.
13. Rosidae Takht., *Syst. Phylog. Magnolioph.* 264. 1967.
14. Cornidae Frohne & Jensen *ex* Reveal, *Phytologia* 76:4. 1994.
15. Lamiidae Takht. *ex* Reveal, *Novon* 2:235. 1992.
16. Asteridae Takht., *Syst. Phylog. Magnolioph.* 405. 1967.

The following new names are required within Magnoliophyta.

Piperidae Reveal, *subcl. nov.*, validated by the Latin description associated with Piperopsida Bartl., *Ord. Nat. Pl.* 83. 1830 (as "Piperinae").

Piperanae Reveal, *superord. nov.*, validated by the Latin description associated with Piperopsida Bartl., *Ord. Nat. Pl.* 83. 1830 (as "Piperinae").

By adopting Piperopsida for the paleoherbs it becomes necessary to propose a name at the rank of class, and because the rank of superorder is now widely used (Takhtajan 1987; Dahlgren 1989a, b; Thorne 1992a, b; Reveal 1993)—albeit not recognized formally by the *Code* (Greuter *et al.* 1988), one at the rank of superorder is required as well. As defined here, Piperanae consists of three orders, Aristolochiales, Piperales, and Lactoridales, and four families Aristolochiaceae, Saururaceae, Piperaceae, and Lactoridaceae (Tucker *et al.* 1993). Chloranthaceae is referred to the Chloranthales and placed in Magnoliopsida near Amborellaceae and Trimeniaceae in Illiciales (Endress 1987). The inclusion of Lactoridaceae is supported by their specialized flowers, but their anatropous ovules and follicular fruits are more typical of Magnoliales. The ultimate fate of this family remains to be ascertained.

Capparanae Reveal, *superord. nov.*, validated by the Latin description associated with Order Capnanthema Batsch, *Regni Veg.* 84. 1802, *nom. illeg.*

Takhtajan (1987) and Thorne (1992a, b) include Capparales within Violanae, but evidence presented by Chase *et al.* (1993) shows the Capparales well removed from Violales. By placing Caricaceae in Caricales and associating that order with the Capparales, as suggested by Rodman *et al.* (1993), the two groups become sufficiently distinct to require the recognition of a

new superorder. As here defined, the superorder includes Salvadorales (Salvadoraceae), Moringales (Moringaceae), Caricales (Caricaceae), Limnanthales (Limnanthaceae), Batales (Bataceae), Capparales (Pentadiplandraceae, Toviaceae, Resedaceae, Capparaceae, Brassicaceae) and Elaeocarpaceae (Elaeocarpaceae). The family Gyrostemonaceae is also a member of the taxon, but the ordinal name remains to be validated.

Cucurbitanae Reveal, *superord. nov.*, validated by the Latin description associated with Order Cirrhatae Batsch, *Regni Veg.* 220. 1802, *nom. illeg.*

The placement of Cucurbitales and its relatives is debatable. Cronquist (1981) and Thorne (1992a, b) retain the taxon in Violales while Takhtajan (1987) keeps the order in Violanae. The core membership of the group associated with Cucurbitaceae includes Datisceae and Begoniaceae, and Chase *et al.* (1993) have shown, based on *rbcL* data, that these families are not that closely related to Violales. In addition to the above three families (or four if one accepts Tetramelaceae), I have placed Coriariaceae in Cucurbitanae (in Coriariales), albeit provisionally, but well removed from the Ranunculales where placed by Cronquist (1981) and therefore closer to Rutanae (or Sapindanae) where aligned by Takhtajan and Thorne. The basis for this association is the preliminary data provided by Chase *et al.*

Saxifraganae Reveal, *superord. nov.*, validated by the Latin description associated with Class Corniculatae Endl., *Gen. Pl.* 808. 1839, *nom. illeg.*

The isolation of the Saxifragales from Rosales demonstrated by Morgan & Soltis (1993) also demands recognition of a separate superorder, distinct from Celastranae, well removed from Rosanae, and situated more or less basally in Rosidae. Brexiales and Parnassiales are referred to Celastranae, with Hydrangeales to Cornanae. As here defined, Saxifraganae consists of a series of orders (some not yet validated) which include such families as Greyiaceae, Francoaceae, Crassulaceae, and Grossulariaceae. With the exception of Crossosomataceae, which is here tentatively included in Saxifraganae, all of these families are clearly related to Saxifragaceae.

Cornidae Frohne & Jensen *ex* Reveal, *subcl. nov.*, validated by the Latin description associated with Order Umbraculariae Batsch, *Regni Veg.* 40. 1802, *nom. illeg.*

The work published by Chase *et al.* (1993) and Xiang *et al.* (1993) shows Cornanae to constitute a group distinct from both Rosidae (where Hydrangeales and Cornales have traditionally been placed) and Asteridae (where the Caprifoliales are typically assigned). As here defined, the subclass is composed of two superorders, Cornanae and Araliaanae. The former is composed of four orders (Garryales, Aralidiales, Cornales, and Hydrangeales), the latter of six orders (Toricelliales, Pittosporales, Byblidales, Araliales, Viburnales, and Dip-sacales). Frohne & Jensen (1985, 1992) include Gentiananae in Cornidae, but this taxon is retained in Lamiidae.

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TAXONOMIC REVISION OF *GENIOSTEMON* (GENTIANACEAE)

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ABSTRACT

The genus *Geniostemon*, previously thought to have but two species, is revised as having four species: *G. atarjanum* B.L. Turner, *spec. nov.* (from easternmost Guanajuato, México); *G. coulteri* (from Hidalgo, México); *G. gypsophilum* B.L. Turner, *spec. nov.* (from Nuevo León, México); and *G. schaffneri* (from San Luis Potosí, México). Revised and/or complete descriptions of each of the species are given, along with a key and distributional maps.

KEY WORDS: Gentianaceae, *Geniostemon*, México

Geniostemon was heretofore thought to be a small genus of only two species from northeastern México. It was first proposed by Engelmann & Gray in 1881 to accommodate *G. coulteri* and *G. schaffneri*. The genus is largely distinguished from *Centaurium* by its 4-merous flowers and noncoiled anthers, and was maintained by Gilg (1895), who thought it not especially close to *Centaurium*, placing it between the genera *Bisgoeppertia* and *Cicenda* of his subtribe Erythriinae noting, however, that its pollen was similar to that of *Neurotheca*, a monotypic genus of South America.

Except for its uncoiled anthers and 4-merous flowers, *Geniostemon* might fit comfortably into *Centaurium*, and I suggest here that a more intensive study might show its relationship to be within or near that large genus although, to my knowledge, this has not been suggested by yet other workers.

Geniostemon Engelm. & A. Gray

Erect or prostrate, annual or perennial (?) herbs to 15 cm high. Leaves opposite, small, linear-oblongate to ovate-lanceolate, the margins entire. Flowers terminal, one to a stem, or forming leafy terminal cymes by branching

of the upper stems. Sepals 4, separate or nearly so. Petals 4, the tube somewhat longer than the lobes, the latter pink or white. Stamens 4, inserted on the tube; filaments bearing numerous short glandular hairs at its mid-portion (rarely seemingly absent in *Geniostemon gypsophilum* B.L. Turner); anthers yellow, uncoiled. Pistil glabrous, the style fused throughout or nearly so, often bifid at the apex, the stigmatic portion papillose. Capsule narrowly ovoid, dehiscent into halves, the seeds more or less ovoid or globose with an alveolate-like surface ornamentation. Type species: *Geniostemon coulteri* Engelm. & A. Gray

Key to species

1. Stiffly erect or ascending annual herbs; corollas 4-8 mm long (tube-lobe length); San Luis Potosí and Nuevo León.
 2. Corolla lobes mostly 4-5 mm long; anthers 0.8-1.2 mm long; foliage drying green; San Luis Potosí. *G. schaffneri*
 2. Corolla lobes mostly 2-3 mm long; anthers 0.5-0.7 mm long; foliage drying blackish green; Nuevo León. *G. gypsophilum*
1. Sprawling or mat-forming perennial (?) herbs; corollas 12-14 mm long; Guanajuato, Querétaro?, and Hidalgo.
 3. Foliage and stems markedly beset with minute hair-like papillose enations; corollas 13-14 mm long (tube-lobe length); easternmost Guanajuato and adjacent Querétaro? *G. atarjanum*
 3. Foliage and stems glabrous; corollas ca. 12 mm long; Hidalgo.
 *G. coulteri*

Geniostemon atarjanum B.L. Turner, *spec. nov.* TYPE: MEXICO. Guanajuato: El Charco, 12 km SE of Atarjea, "matorral arbustivo, ladero de cerro, sobre peñas", 1500 m, *E. Ventura & E. López 6361* (HOLOTYPE: TEX!).

Geniostemonem coulteri Engelm. & A. Gray similis sed foliis ac caulibus minute papillatis (vs. glabris) et corollis majoribus (longitudine tubi-lobi 13-14 mm vs. ca. 12 mm).

Prostrate perennial (?) herbs 3-6 cm high. Stems with papillose enations, the leaves about as long as the internodes. Midstem leaves linear-oblongate to ovate, mostly 6-8 mm long, 2-4 mm wide, the margins papillose like the

stems; petioles 2-3 mm long, grading into the blades. Flowers mostly single and terminal on pedicels 5-10 mm long. Sepals ca. 6 mm long, linear lanceolate, glabrous, the apices acicular. Corollas 13-14 mm long, reportedly rose-colored, the lobes 8-10 mm long, 3-4 mm wide. Stamens exerted for ca. 7 mm; filaments 5-6 mm long, glandular-pubescent for ca. 1/2 its length near the middle, the hairs ca. 0.15 mm long; anthers yellow, ca. 1 mm long. Styles ca. as long as the stamens, the apices flabellate and somewhat bilobed. Capsules ellipsoid, 6-7 mm long, ca. 2 mm wide. Seeds immature.

This taxon, known only by type material, is clearly closely related to *Geniostemon coulteri* but is readily distinguished by having foliage with papillose enations (vs. absent) and larger corollas (ca. 12 mm long vs. 13-14 mm). *Atarjea* is located in easternmost Guanajuato along the Querétaro border.

Geniostemon coulteri Engelm. & A. Gray, Proc. Amer. Acad. Arts 16:104. 1881. TYPE: MEXICO. [w/o locality] Hidalgo: Zimapan (?), Feb-Oct 1827, *Thomas Coulter 945* (HOLOTYPE: GH!). According to McVaugh (1943), Coulter resided in Zimapan, Hidalgo during the period indicated, and since the type lacks locality data I assume that he collected the plant in the vicinity of Zimapan. The collection number does not provide a clue as to his collection site since the species were assigned numbers according to their systematic arrangement (McVaugh 1943). Coulter presumably never visited the states of San Luis Potosí or Nuevo León, thus it is likely that the type was collected in Hidalgo, although it is possible that its collection might have been in the states of Querétaro or Guanajuato as he traveled between Zacatecas and Zimapan but, as noted by McVaugh, Coulter only rarely collected plants while "on-the-move".

Perennial (?) sprawling herbs 4-8 cm high. Stems glabrous, mostly unbranched, the leaves about as long as the internodes or somewhat longer. Mid-stem leaves linear-oblancoate, mostly 6-8 mm long, 2-3 mm wide, glabrous; petioles ca. 2 mm long, gradually tapering into the blades. Flowers mostly simple and terminal on glabrous pedicels 4-7 mm long. Sepals ca. 5 mm long, glabrous, acute. Corollas ca. 12 mm long, the lobes 9-10 mm long. Stamens exerted for ca. 6 mm; filaments 4-5 mm long, glandular-pubescent for ca. 1/2 its length near the middle, the hairs ca. 0.15 mm long; anthers yellow, ca. 1 mm long. Styles somewhat longer than the stamens, the apices flabellate. Capsules ellipsoid, 5-6 mm long, ca. 2 mm wide. Seeds globose, ca. 0.3 mm across.

The species is known only by rather fragmentary type material but seems readily distinguishable by habit and flower size as noted in the key to species.

In its seemingly sprawling habit, leaf shape, and corolla size, *Geniostemon coulteri* appears closely related to *G. atarjanum*, but the latter is readily dis-

tinguished by the papillose enations on stems and leaves (vs. enations absent) and larger corollas.

Geniostemon gypsophilum B.L. Turner, *spec. nov.* TYPE: MEXICO. Nuevo León: Mpio. Aramberri, San Francisco, gypsum hillside, 1750 m, large colonies among grasses, 26 Aug 1992, *G.B. Hinton et al. 22354* (HOLOTYPE: TEX).

Geniostemonem schaffneri Engelm. & A. Gray similis sed lobis corollarum minoribus (2-3 mm longis vs. 4-5 mm), antheris minoribus (0.5-0.7 mm longis vs. 0.8-1.2 mm), et foliis in sicco atrovirentibus (vs. viridis).

Annual mostly stiffly erect herbs 3-9 cm high, 2-13 cm across; the internodes as long as or longer than the leaves. Midstem leaves linear-oblongate mostly 4-7 mm long, 1-2 mm wide, glabrous, drying blackish-green. Pedicels mostly 4-6 mm long, glabrous. Sepals 2-3 mm long, glabrous, acute. Corollas mostly 4-6 mm long, purplish in bud, but white or creamy white when open, the lobes 2-3 mm long, ca. 1 mm wide. Stamens weakly exerted for 1-2 mm (the petals only rarely spreading); filaments 1-2 mm long, weakly glandular-pubescent, if at all, the hairs 0.05 mm long; anthers yellow, 0.5-0.7 mm long. Styles somewhat longer than the stamens, the apices weakly flabellate, if at all. Capsules narrowly ellipsoid, 3-4 mm long, ca. 1.5 mm wide. Seeds globose, ca. 0.3 mm across.

ADDITIONAL SPECIMENS EXAMINED: MEXICO. Nuevo León: ca. 30 km ENE of Dr. Arroyo in exposed gypsum, 2.5 km ENE of San Antonio de Peña Nevada, W base of Cerro Peña Nevada, 6600 ft, 3-5 Aug 1981, *Nesom 4266* (TEX); 15.5 mi ENE of junction with the Dr. Arroyo-Aramberri highway, 1940 m, 15 Sep 1988, *Nesom 6701* (TEX); Mpio. Galeana, 5.4 mi SE of junction with Linares-Entranque San Roberto along road S to Dr. Arroyo, gypsum shapes among scattered pines, 1940 m, 16 Oct 1988, *Nesom 6794* (TEX); 4 mi NW of Río San José, gypseous SE-facing slopes, 1490 m, 18 Sep 1993, *Nesom 7621* (TEX); Mpio Galeana, NE lowermost slopes of Cerro Potosí; gypsum soils along road to microwave station, ca. 12 mi NW of Galeana, 20 Aug 1979, *Turner & Davies A-26* (TEX); 1.6 mi N of Galeana on gypsum hillside, 10 Oct 1985, *Turner 15592* (TEX).

This taxon is very closely related to *Geniostemon schaffneri* but is readily distinguished by its smaller flowers which only rarely open (or upon dying tend to close) and foliage which turns blackish-green upon drying, as noted in the key to taxa. *Geniostemon gypsophilum* is found only on gypseous soils and was first collected by Guy Nesom on Cerro Peña Nevada in 1977 and I collected the second known specimen from Cerro Potosí in 1979 (with Frances

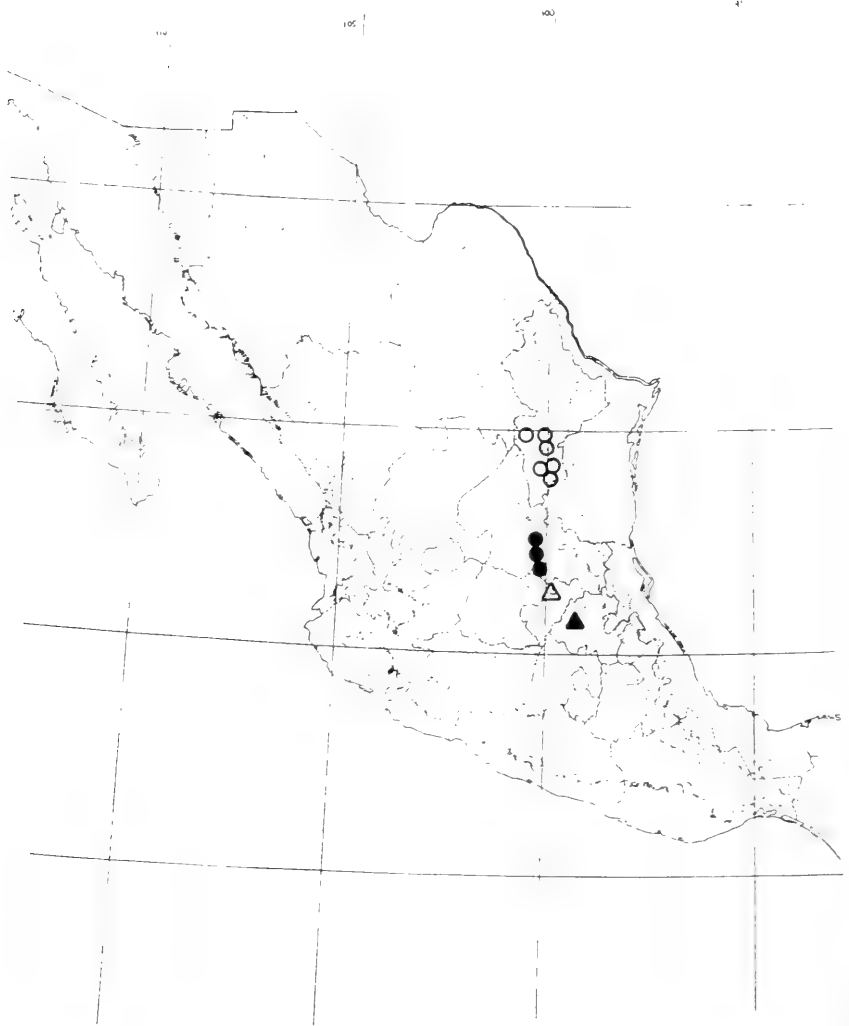


Figure 1. Distribution of *Geniostemon*: *G. atarjanum* (open triangle); *G. coulteri* (closed triangle); *G. gypsophilum* (open circles); *G. schaffneri* (closed circles).

Davies of K). Numerous collections have been made over the last 15 years, all upon rather bare gypseous soils.

Geniostemon schaffneri Engelm. & A. Gray, Proc. Amer. Acad. Arts 16:104 1881. TYPE: MEXICO. San Luis Potosí: mountainous areas in the vicinity of San Luis Potosí, Sep 1876, *J.G. Schaffner 80* (HOLOTYPE: GH!).

Annual divaricately branched herbs 6-10 cm high, 5-15 cm across. Stems glabrous, the internodes as long as or longer than the leaves. Midstem leaves mostly linear-lanceolate to linear-oblongate, mostly 4-6 mm long, 1-2 mm wide, glabrous, drying green. Pedicels mostly 4-15 cm long, glabrous. Sepals ca. 4 mm long, glabrous, acute. Corollas mostly 7-8 mm long, pink in bud, but white or creamy white after the petals spread, the lobes 4-5 mm long, 1.5-2.0 mm wide. Stamens exerted for ca. 3.5 mm; filaments ca. 3 mm long, markedly glandular-pubescent for ca. 1/2 its length near the middle, the hairs ca. 0.1 mm long; anthers yellow, 0.8-1.2 mm long. Styles somewhat longer than the stamens, the apices narrowly flabellate. Capsules narrowly ellipsoid, ca. 4 mm long, 1.5 mm wide. Seeds globose, ca. 0.3 mm across.

ADDITIONAL SPECIMENS EXAMINED: MEXICO. San Luis Potosí: Immediately N of Minas de San Rafael, 1100 m, 30 Jun 1972, *Chiang et al. 8164, 8168* (LL); highest point on gravel road between Villa Juárez and Buena Vista, 1450 m, 21 Jun 1982, *Nee & Diggs 24551* (TEX); San José Pass, 16 Aug 1890, *Pringle 3172* (GH,MO); Villar, 14 Sep 1893, *Pringle 5386* (GH); Minas de San Rafael, Nov 1910, *Purpus 4914* (GH,MO).

Geniostemon schaffneri is closely related to *G. gypsophilum* but differs in having larger flowers on mostly longer pedicels and foliage that tends to dry green (vs. blackish-green). It occurs on both calcareous and gypseous soils (according to label data) and appears to be confined to mountainous regions immediately east of the city of San Luis Potosí (Figure 1).

ACKNOWLEDGMENTS

I am grateful to Guy Nesom for the Latin diagnoses, and to him and T.P. Ramamoorthy for reviewing the paper. Especial thanks to GH and MO for the loan of specimens.

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**NEW SPECIES OF *ADENOSTEMMA*, *AYAPANA*, AND
BRICKELLIASTRUM FROM MEXICO, PANAMA, AND ECUADOR AND A
NEW COMBINATION IN *GROSVENORIA* (EUPATORIEAE: ASTERACEAE)**

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ABSTRACT

Adenostemma harlingii and *A. zakii* are described from Ecuador, having five and six pappus knobs respectively. The alternate-leaved *Ayapana herrerae* is described from eastern Panamá, *Brickelliastrum villarealii* is described from northern México, and a new combination is made in *Grosvenoria*.

KEY WORDS: Asteraceae, Eupatorieae, *Ayapana*, *Adenostemma*, *Brickelliastrum*, *Grosvenoria*, new species, Mesoamerica, Ecuador

The following new species and new combinations are provided for use in floristic studies.

Adenostemma harlingii R.M. King & H. Robinson, *spec. nov.* TYPE: ECUADOR. Napo: Baez, disturbed montane rain forest; ca. 2000 m, 3 Feb. 1980, *Harling & Andersson 16153* (HOLOTYPE: GB).

Herbae perennes decumbentes 0.5-0.7 m altae; caules robusti sparse puberuli. Folia opposita, petiolis 0.5-1.0 cm longis distalter latioribus; laminae herbaceae oblongo-ovatae non angulatae plerumque 4-7 cm longae 2.5-4.5 cm latae base breviter acuminatae margine aliquantum remote serrulatae apice obtuse vel rotundatae supra minute puberulae in nervis pilosulae subtus puberulae plerumque in nervis supra basem trinervatae. Inflorescentiae alterne ramosae multo capitulatae, pedunculis 0.8-15.0 cm long puberulis non glanduliferis. Capitula 6-7 mm alta et lata; bractae

involucri ca. 11 uniseriatae base minime connatae anguste oblongae vel ellipticae ca. 4 mm longae 1.0-1.2 mm latae apice rotundatae vel obtusae extus glabrae. Flores ca. 20 in capitulo; corollae ca. 3.5 mm longae extus puberulae in faucibus rubrescentes anguste infundibulares, lobis brevibus ca. 0.5 mm longis 0.7 mm latis; thecae antherarum ca. 1 mm longae; scapi stylorum superne hirtelli; appendices stylorum distaliter vix lateriores. Achenia ca. 2.5 mm longa, glandulis numerosis sessilibus; clavae pappi plerumque 5 in longitudino 0.5-0.8 mm.

The new species seems most closely related to *Adenostemma platyphyllum* Cass. but usually has five knobs on the achene. The impression of close relationship is reinforced by the presence of one achene in the new species with only three knobs. The species differs from *A. platyphyllum* by the very blunt oblong-ovate leaf blades and the less broadened style appendages in addition to the number of pappus knobs. The new species occurs east of the Andes while *A. platyphyllum* in Ecuador is mostly west of the Andes.

Adenostemma zakii R.M. King & H. Robinson, *spec. nov.* TYPE: ECUADOR. Bolívar: Carretera Chillanes - Bucay, en la hacienda "Tiquibuso" del Sr. Gonzalo Gómez, 0.1°55' S, 79°0.5' W, 2100 m, 1 Sept. 1987, *Zak & Jaramillo 2571* (HOLOTYPE: US; Isotype: MO).

Herbae debilis perennes ad 1 m altae; caules tenues puberuli vel plerumque proxime nodis glandulis stipitatis obsiti glabrescentes. Folia opposita, petiolis ca. 1.5-2.0 cm longis tenuis; laminae membranaceae ovatae non angulatae 4-7 cm longae 2.5-3.5 cm latae base acuminatae in petiolis attenuatae margine remote serrulatae ad mucronato-denticulatae apex breviter acutae supra sparse valide pilosae subtus in venis tenuiter pubescentes supra basem trineratae. Inflorescentiae laxae alterne ramosae ca. tri-capitatae, pedunculis 1.5-3.0 cm longis interdum nutantibus minute stipitate glanduliferis. Capitulae 6-7 mm altae et latae; bractae involucri ca. 10 oblongae vel anguste ellipticae base non connatae ca. 4 mm longae ad 1 mm latae apice obtusae extus glabrae. Flores ca. 10 in capitulo; corollae albae ca. 3.5 mm longae glabrae, faucibus anguste infundibulares, lobis ca. 0.8 mm longis et latis; thecae antherarum ca. 1.5 mm longae; scapi stylorum glabri; appendices stylorum distaliter valide latiores. Achenia ca. 2.5 mm longa, glandulis stipitatis base latis, clavi pappi 6 in longitudino ca. 1.5 mm.

Adenostemma zaku is the only member of the genus having six pappus knobs and it is one of two in the Neotropical region lacking hairs on the style shaft. The other species with a glabrous style shaft is *A. flintii* King & H. Robinson of Nicaragua which has only three knobs on the achene.

Ayapana herrerae R.M. King & H. Robinson, *spec. nov.* TYPE: PANAMA.

Vicinidad de Cordillera SE San Blas, Lado Pacifico y Cabecera del Río Piria (Piriati en el Imapa), 09° 12' N 78° 16' W, 200-400 m, hierba epipétrica a la orilla del Río Piriati, y terrestre; flores blancas y moradas, 28 Feb. 1992, *Herrera, Mojica, & Morris 1148* (HOLOTYPE: US; Isotype: MO).

Plantae herbaceae erectae perennes 3-4 dm altae in rhizomatis ramosae et fibroso-radicatae; caules brunnescentes sparse pilosi vel subhirsuti in parte glabrescentes non fistulosi base breviter decumbentes. Folia alterna, petiolis 2-5 mm longis distaliter indistincte demarcatis; laminae lineares vel lineari-oblancoelatae plerumque 3-6 cm longae 2-6 mm latae base anguste cuneatae margine superne pauce remote serrulatae apice acutae supra glabrae laeves subtus leniter pallidiores in epidermis tenuibus glandulo-punctatae, nervis secundariis tenuibus paucis sublongitudinalibus. Inflorescentiae terminales alterne ramosae laxae cymosae, ramis dense hirtellis, pilis stipitate glanduliferis, pedunculis plerumque 5-17 mm longis. Capitula late campanulata 5-6 mm alta et 4-5 mm lata; bractae involucri virides, chartaceae ca. 20 ca. 3-seriatae oblongo-ellipticae 1.5-3.0 mm longae 0.6-0.9 mm latae apice pauce laciniatae dentatae extus dense vel sparse stipitato-glanduliferae. Flores ca. 20 in capitulo; corollae albae et rubrescentes ca. 3 mm longae extus glabrae, tubis angustis ca. 1.5 mm longis, faucibus campanulatis ca. 0.8 mm longis, lobis oblongis ca. 0.8 mm longis basi 0.5-0.6 mm latis apice obtusis; filamenta in partibus superioribus ca. 0.35 mm longa; thecae antherarum ca. 0.7 mm longae; appendices antherarum oblongae vel late ovatae ca. 0.25 mm longae 0.18 mm latae; basi stylosum nodati glabri; rami stylosum distincte papillosae, papillis apice rotundatis. Achenia subfusiformia 1.8-2.0 mm longa setulifera, setulis in costis aliquantum densioribus; carpodia late obturaculiformia, cellulis basilaribus mediocriter majoribus; setae pappi ca. 20 non contiguae ca. 2.5 mm longae apice non latiores. Grana pollinis in diametro ca. 25 μ m.

The new species is unique in the genus by the spirally inserted leaves, the peduncles and involucre bracts hirtellous with stipitate glands, and by

**NEW SPECIES OF *FERREYRANTHUS* AND *MUNNOZIA* FROM PERU
(LIABEAE: ASTERACEAE)**

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ABSTRACT

Ferreyranthus gentryi*, *Munnozia chachapoyensis*, *M. luyensis*, and *M. smithii from Perú are described as new.

KEY WORDS: Asteraceae, Liabeae, *Ferreyranthus*, *Munnozia*, new species, Perú

The following four species are described as new. These include an eighth species of *Ferreyranthus* and three species of *Munnozia* raising the total recognized in that genus from 40 (Robinson 1983) to 43.

Ferreyranthus gentryi H. Robinson, *spec. nov.* TYPE: PERU. Amazonas: 20 km E of Balsas on road to Leimebamba, Marañón Valley, 2000 m, dry roadside, 17 June 1978, A. Gentry, M. Dillon, J. Aronson, & C. Díaz 23126 (HOLOTYPE: US; Isotype: MO). PARATYPE: PERU. Amazonas: Chachapoyas, Marañón River Valley, Celendín - Chachapoyas road, ca. 15 km from Puente Chocanto, 1600-1920 m, dry shrubland with patches of dry forest, 24 May 1984, D.N. Smith & J. Cabanillas 7061 (MO,US).

Plantae suffrutescentes vel frutescentes 0.5-1.8 m altae; caules atro-brunnescentes teretes vel subhexagonales evanescentiter albotomentelli. Folia opposita, petiolis 2-7 mm longis; laminae oblongae 1.5-3.2 cm longae 0.7-1.5 cm latae base et apice obtusae margine vix reflexae minute undulatae supra rugulosae evanescentiter sparse tomentellae subtus dense albo-tomentosae, nervis secundariis ascendititer pinnatis utrinque 4-6 in binis basilaribus ascenditioribus. Inflorescentiae in ramis foliosis terminales dense

corymbosae, ramis et ramulis dense albo-tomentellis, pedunculis 1-2 mm longis. Capitula heterogama anguste campanulata 8-9 mm alta 2-3 mm lata; bracteae involucri flavo-brunnescentes ca. 25 subimbricatae in seriebus 4-5 ovatae vel lanceolatae 1-5 mm longae ca. 1 mm latae apice acutae extus inferne sparse tomentellae in medio longitudinaliter brunneo-vittatae. Flores radii 4 vel 5; corollae flavae ca. 5 mm longae extus multo minute glanduliferis inferne sparsius, tubis angustis ca. 2.5 mm longis, limbis ellipticis ca. 2.5 mm longis 0.8 mm latis apice trilobatis. Flores disci 5; corollae flavae ca. 5.5 mm longae extus multo minute glanduliferae inferne sparsius; tubis ca. 2 mm longis, faucibus ca. 2 mm longis, lobis anguste oblongo-lanceolatae ca. 1.5 mm longis, ca. 0.35 mm latis; thecae antherarum pallidae 1.8 mm longae base dentatae; appendices apicales antherarum oblongo-ovatae ca. 0.4 mm longae 0.17 mm latae; basi stylorum abrupte distincte nodulosi. Achenia cylindrica ca. 1.8 mm longa 8-10-costata dense setulifera et multo minute glandulifera, raphidis elongatis; setae pappi albae ca. 5.5 mm longae distaliter leniter latiores; squamae exteriores lineares 1.0-1.5 mm longae. Grana pollinis in diametro ca. 37 μ m.

The new species is named for the late Al Gentry, the first listed collector of the holotype specimen.

The species is distinct in its small size. The size difference includes the small leaves, up to 3 cm long, and the narrowly campanulate heads with only about 10 florets.

Munnozia chachapoyensis H. Robinson, *spec. nov.* TYPE: PERU. Amazonas: Chachapoyas, 27 kms NE of Florida, off road up a logging trail, 1200 m, 30 December 1979, James Aronson 1021 (HOLOTYPE: US; Isotype: MO).

Plantae herbaceae 0.3 m altae; caules teretes appresse pallide lanulati, internodis 0.3-2.0 cm longis. Folia opposita sessilia anguste elliptica vel lanceolata 3.0-4.5 cm longa 1.0-1.4 cm lata base breviter subpetioliformia breviter amplexicaulia et anguste perfoliata margine grosse regulariter lobulata apice breviter acuta supra valide alte bullata vix evanescentiter arachnoideo-puberula in nervis primariis persistentiter albo-lanulata subtus dense sordide tomentosa in nervis et nervulis prominentia, nervis secundariis pinnatis utrinque ca. 7. Inflorescentiae scaposae uni- vel tri-capitatae; scapi 9-12 cm longi tenuiter arachnoideo-tomentelli. Capitula heterogama campanulata in involucrio ca. 12 mm alta

et lata; bractee involucri ca. 40 subimbricatae in seriebus ca. 5 plerumque oblongae vel oblongo-lanceolatae 1.5-9.0 mm longae 1.0-1.8 mm latae apice rotundatae vel obtusae; bractee paucae interiores lineari-lanceolatae ca. 9 mm longae anguste acutae; receptacula squamulifera vel lobulifera. Flores radii ca. 20; corollae flavae 18-19 mm longae extus persparse pilosulae, pilis attenuatis biseriatis, tubis ca. 4 mm longis, limbis 14-15 mm longis ca. 1 mm latis extus sparse minute glanduliferis. Flores disci ca. 10; corollae flavae ca. 9 mm longae, tubis ca. 4 mm longis, faucibus ca. 2 mm longis, lobis anguste lanceolatae ca. 3 mm longis et 0.5 mm latis extus distaliter minute glanduliferis et minute biseriatis puberulis apice minute papillosis; thecae antherarum leniter nigrescentes 2.8 mm longae base integrae; appendices apices antherarum oblongo-ovatae ca. 0.45 mm longae 0.2 mm latae. Achenia ca. 1.7 mm longa 10-costata superne dense setulifera, raphidis subquadratis; setae pappi sordido-flavae 4.5-6.5 mm longae apice tenues; squamae pappi exteriores paucae lineares 0.7-1.0 mm longae. Grana pollinis in diametro ca. 32 μ m.

The new species is named for the Province of Chachapoyas in Depto. Amazonas, Perú where it was collected.

Munnozia chachapoyensis is a small but beautiful member of the genus. The crowded leaves are remarkable in the dark, sharply bullate upper surface, the densely tomentose lower surface, and pinnately lobulate margins. The scapose inflorescences end in single heads or cymes of three heads. The new species seems closest to *M. perfoliata* (S.F. Blake) H. Robinson & Brettell of Colombia (Cauca, Chocó Nariño, Putumayo) and recently collected in Ecuador, Carchi, *Panero & Clark 3038* (TEX,US). The latter species differs by the much broader leaf blades with longer secondary veins that appear darker below. The upper surfaces of the leaves of the latter have comparatively numerous small bullations that are not higher than wide, and the leaves are spreading from the bases without any obvious vagination. The material seen of the new species does not show rhizomes like those of *M. perfoliata*, but such rhizomes may be found in better material.

Munnozia luyensis H. Robinson, *spec. nov.* TYPE: PERU. Amazonas: Luya Province, Ocallí, anexo Ouispe, propeidad de San Esteban Fernández entraudo por "Galera," 1920-2300 m, 19 June 1991, C. Díaz, José Campos, y Luis Campos 4405 (HOLOTYPE: US; Isotype: MO).

Plantae volubiles flexuosae indefinite elongatae; caules subhexagonales minute appresse puberuli et in parte evanescentiter tenuiter arachnoideo-lanati, internodis 5-7 cm longis. Folia opposita,

petiolis 5.5-7.5 cm longis tenuibus glabris vel subglabris; laminae triangulares 9.5-16.0 cm longae 5.3-8.5 cm latae base hastatae in sinu subacutae in angulis argute acutae margine remote denticulatae apice acutae vel breviter acuminatae supra planae minute puberulae subtus vix pallidiores sparse evanescentiter arachnoideolanulatae minute glandulo-punctatae, nervis secundariis base late patentiter trinervatis aliter patentiter pinnatis. Inflorescentiae late pyramidaliter paniculatae multo capitatae, ramis pyramidaliter paniculatis, ramulis plerumque tricapitatis, pedunculis 3.5-5.5 cm longis minute puberulis et evanescentiter arachnoideo-lanulatis. Capitula heterogama late campanulata in involucri 5 mm alta et 10 mm lata; bractee involucri ca. 22 plerumque oblongo-ovatae subaequales 3-5 mm longae ca. 2 mm latae apice breviter acutae extus glabrae et 5 aut 7 lineatae; bractee involucri interiores paucae anguste lanceolatae ca. 4 mm longae anguste acutae vel acuminatae; receptacula squamulifera vel lobulifera. Flores radii 25-30?; corollae flavae ca. 16 mm longae, tubis ca. 4 mm longis sparse hirtellis, limbis ca. 12 mm longis 1.2 mm latis sparse pilosulis et persparse glandulo-punctatae, pilis biseriatis. Flores disci ca. 20; corollae flavae 7-8 mm longae, tubis 4.0-4.5 mm longis hirtellis, faucibus abrupte campanulatis ca. 1.5 mm longis base dense pilosulis, lobis ca. 2 mm longis 0.3 mm latis extus mediocriter pilosulis et glandulo-punctatis, pilis biseriatis; thecae antherarum leniter nigrescentes ca. 1.7 mm longae base integrae; appendices apicales antherarum oblongae 0.35 mm longae 0.17 mm latae. Achenia ca. 1.2 mm longa 10-costata dense setulifera, raphidis subquadratis; setae pappi sordide flavae 5.0-5.5 mm longae apice attenuatae; setae exteriores paucae minores 0.25-0.45 mm longae. Grana pollinis in diametro ca. 27 μm .

The new species is named for the Luya Province in Depto. Amazonas, Perú where it was collected.

Munnozia luyensis seems closely related to the widely distributed *M. senecionidis* Benth., but differs by the subglabrous stems and leaf undersurfaces. The broadly triangular rather than lanceolate leaves also differ in the widely spreading, almost horizontal veins of the basal trination in the short part before they branch. The greenish undersurfaces of the leaves somewhat resemble those of *M. subviridis* (S.F. Blake) H. Robins. & Brett., but the latter is a relative of the distinctive *M. hastifolia* (Poepp. & Endl.) H. Robins. & Brett. of southern Perú and adjacent Bolivia with leaves glabrous below and the trination of the leaves usually not at the bases of the blades.

Munnozia smithii H. Robinson, *spec. nov.* TYPE: PERU. Pasco: Oxa-

pampa Prov., Cerro Pajonal, 29 km from Oxapampa, "Pajonal", 2650 m, low vegetation (shrubs & grass 2503) with abundant bryophytes, mostly terrestrial, forming a thick organic layer (1+ m) over mineral soil, 6 Oct. 1982, *D.N. Smith & Robin Foster 2517* (HOLOTYPE: US; Isotype: MO).

Plantae herbaceae prostratae indefinite elongatae; caules teretes in sicco plicatae glabri, internodis plerumque 1-2 cm longis. Folia opposita patentiter decussata sessilia oblongo-ovata plerumque 1.5-2.5 cm longa 0.7-1.4 cm lata base obtusa ascendenter trinervata margine subintegra vel paucè remote denticulata apice obtusa vel breviter acuta supra atro-virides plana glabra subtus pallide appresse tomentosa in nervis primariis variabiliter subglabra. Inflorescentiae scaposae unicapitulatae; scapi 10-12 cm longis evanescentiter albo-lanulati et minute hirtelli, bracteis minutis binis in nodis 1 vel 2 anguste ellipticis 5-8 mm longis 1.0-2.5 mm latis. Capitula late campanulata vel hemisphaerica sine radiis ca. 1 cm alta et 1.5 cm latis; bractee involucri ca. 32 leniter gradatim 3-4 seriatæ 5-7 mm longae 1.0-1.5 mm latae distaliter brunnescentes vel subrubrescentes extus glabrae obscure 5-lineatae distaliter evanescentiter albo-lanulatae; bractee exteriores oblongae apice obtusae vel breviter acutae; bractee interiores lanceolatae anguste acutae vel breviter acuminatae; receptacula squamifera vel lobulifera. Flores ca. 30; corollae ignotae. Achenia leniter rubrescentes obovata ca. 2 mm longa ca. 1 mm lata 10-costata supra medio setulifera in zonis distinctis apicalibus constricta et glabra, raphidis subquadratis vel subrhombiformibus; setae pappi sordide flavae 4.0-4.5 mm longae apice attenuatae; setae exteriores paucae 0.3-0.5 mm longae.

The new species is named for the late David Smith, first listed collector of the type collection.

Munnozia smithii is unusually distinct in its appearance. It is described on the label as a prostrate herb, and the specimen shows close-set, spreading, decussate, sessile leaves that are dark and glabrous above and densely pale-tomentose below. The heads resemble typical *Munnozia* in their involucre and mature pappus, but their solitary, scapose condition is distinctive. The material has mature achenes, but all corollas have been lost.

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**A NEW SPECIES OF *OBLIVIA* AND A NEW COMBINATION IN
ELAPHANDRA FROM ECUADOR (ECLIPTINAE: HELIANTHEAE:
ASTERACEAE)**

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ABSTRACT

Oblivia ceronii is described as new from the Department of Napo in Ecuador, and *Aspilia retrofleza* is transferred to *Elaphandra*.

KEY WORDS: Asteraceae, Heliantheae, Ecliptinae, *Oblivia*, *Elaphandra*, new species, new combinations

A continuing review of the Heliantheae for treatment of the Flora of Ecuador has shown the need to describe the following new species.

Oblivia ceronii H. Robinson, *spec. nov.* TYPE: ECUADOR. Napo: Canton Tena, Estación Biológica Jatun Sacha, Río Napo, 8 km al E de Misahuallí 1°04' S 77°36' W, 400 m, 11-14 abril 1989, C. Cerón 6411 (HOLOTYPE: US; Isotype: MO).

Plantae frutescentes volubiles indefinite elongatae; caules leniter costati strigillosi vel scabridi et minute puberuli in angulis ca. 90° ramulosi. Folia opposita, petiolis 0.4-2.2 cm longis; laminae chartaceae ovatae vel oblongo-ovatae plerumque 6-12 cm longae 2.0-4.5 cm latae base rotundatae vel obtusae margine subintegrae vel remote serrulatae apice acuminatae supra aliquantum nitidae sparse vel dense scabridulae in nervis majoribus densius subtus hebes scabrae non glandulo-punctatae, nervis subpinnatae vel leniter trinervatis, nervis secundariis validioribus vix vel non mediis foliorum attingentibus. Inflorescentiae anguste thyrsoidae, bracteis primariis foliiformibus, ramis lateralibus breviter pyramidalibus 5-7-capitulatis bracteis primariis brevioribus, pedunculis

1.5-7.0 mm longis scabridulis 1-3 bracteoliferis. Capitula heterogama; involucri late campanulata ca. 8 mm alta et lata; bractee involucri chartaceae ca. 35 ca. 4-seriatae ovatae vel lanceolatae 3-7 mm longae 1.2-1.5 mm latae, bracteis exterioribus 3-4 in apicem herbaceis breviter oblongis vel spathulatis 1.0-1.5 mm longis, bracteis interioribus viride-brunnescentibus margine pallidis apice acutis et sinuatis extus appresse puberulis; paleae bracteis interioribus similes ca. 7 mm longae. Flores radii fertiles ca. 9; corollae flavae ca. 6 mm longae, tubis ca. 2 mm longis glabris, laminae oblongae ca. 4 mm longae 1.2 mm latae breviter bilobatis subtus plerumque glabris apice penicillate pilosis, pilis strictis ad 0.5 mm longis. Flores disci bisexualis 40-45; corollae ca. 5.5 mm longae, tubis basilaribus ca. 1.5 mm longis glabris, faucibus ca. 3 mm longis glabris, lobis ca. 1 mm longis extus strigosis, pilis argutis usque ad 0.5 mm longis; thecae antherarum nigrae ca. 2 mm longae, appendices antherarum apicales pallidis ovatae ca. 0.3 mm longae non glanduliferae; rami styliorum extus non glanduliferi. Achenia obconica 4-5 mm longa glabra, alis ad 0.25 mm latis, aristae pappi in acheniis radii plerumque 3 interioribus ad 4 mm longae in acheniis disci 2 subaequales ca. 3 mm longae, squamis pappi lateralibus in acheniis disci connatis. Grana pollinis in diametro ca. 25 μm .

The species was collected in a moist, tropical forest at 400 m elevation. The species is evidently related to *Oblivia simplex* (Badillo) H. Robinson (1990) of Venezuela in the comparatively weakly trinervate leaves, the presence of basal tubes on the ray corollas, and the larger numbers of disk florets. The present Ecuadorian species differs from *O. simplex* and is more like the widely distributed generic type *O. mikanioides* (Britton) Strother (1989) in the narrower thryoid, less shortly corymbiform inflorescence, the shorter and less leafy lateral branches that do not exceed the subtending leaves in length, and the smaller herbaceous appendages on the outer involucrial bracts. The new species is distinct from both the other species of the genus by the long, stiff hairs on the tips of the corolla lobes.

The genus now has three acknowledged species of which only the type species, *Oblivia mikanioides* has the ray corolla limb mounted directly on the top of the ray achene.

A further new combination is needed in the genus *Elaphandra* for the treatment of the Flora of Ecuador. Eleven species have previously been placed in the genus (Strother 1991; Robinson 1992).

Elaphandra retroflexa (S.F. Blake) H. Robinson, *comb. nov.* BASIONYM:
Aspilia retroflexa S.F. Blake, *Contrib. U.S. Nat. Herb.* 22:618. 1924.

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NEW COMBINATIONS IN AMERICAN VERNONIEAE (ASTERACEAE)

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ABSTRACT

Combinations are validated for *Joseanthus sparrei* and *J. trichotomus*, and additional combinations are made in *Critoniopsis*, *Lepidaploa*, *Lessingianthus*, and *Vernonanthura*.

KEY WORDS: Asteraceae, Vernonieae, *Critoniopsis*, *Joseanthus*, *Lepidaploa*, *Lessingianthus*, *Vernonanthura*, new combinations

In the publication establishing the new genus *Joseanthus* (Robinson 1989), basionyms of two of the species were incomplete. These are properly validated here.

Joseanthus sparrei (H. Robinson) H. Robinson, *comb. nov.* BASIONYM:
Vernonia sparrei H. Robinson, *Phytologia* 34:302. 1976.

Joseanthus trichotomus (Gleason) H. Robinson, *comb. nov.* BASIONYM:
Vernonia trichotoma Gleason, *Bull. Torrey Bot. Club* 52:190. 1925.

The following additional combinations are made in *Critoniopsis*, *Lepidaploa*, *Lessingianthus*, and *Vernonanthura*.

Critoniopsis aristeguietae (Cuatrec.) H. Robinson, *comb. nov.* BASIONYM:
Vernonia aristeguietae Cuatrec., *Bol. Soc. Venez. Cienc. Nat.* 21:304.
1960.

Lepidaploa balansae (Hieron.) H. Robinson, *comb. nov.* BASIONYM:
Vernonia balansae Hieron., *Bot. Jahrb. Syst.* 22:690. 1897.

The species was not placed in the genus earlier because of the presence of type A pollen (Robinson 1992) in the first specimens examined. Lophate grains have now been seen in other material, and reversion to type A apparently occurs in the present species. The raphids of the achene wall are elongate but smaller than usual for *Lepidaploa*.

Lepidaploa marguana (Cuatrec.) H. Robinson, *comb. nov.* BASIONYM: *Vernonia marguana* Cuatrec., Bot. Jahrb. Syst. 77:57. 1956.

The failure to list this species in the earlier paper on *Lepidaploa* (Robinson 1990) was called to my attention by John Pruski. The pollen is type C.

Lepidaploa paraensis (H. Robinson) H. Robinson, *comb. nov.* BASIONYM: *Vernonia paraensis* H. Robinson, Phytologia 46:111. 1980.

The single available specimen has type A pollen, but this is considered a reversion within the genus. Other characters such as the habit, the long hairs on the outside of the corolla, and the elongate raphids of the achene wall place the species in *Lepidaploa*.

Lepidaploa pellita (H.B.K.) H. Robinson, *comb. nov.* BASIONYM: *Vernonia pellita* H.B.K., *Nov. Gen. et Sp.*, ed. folio 4:28. 1818.

The species is known only from the type, but a photograph shows clear characters of *Lepidaploa*. The combination is made to facilitate use in floristic treatments.

Lepidaploa spixiana (Mart. ex DC.) H. Robinson, *comb. nov.* BASIONYM: *Vernonia spixiana* Mart. ex DC., *Prodr.* 5:53. 1836.

Vernonia subcordata Gardn., Lond. J. Bot. 5:226. 1846.

The species is very similar in superficial aspect to *Lessingianthus regis* (H. Robinson) H. Robinson, and the latter is anomalous in *Lessingianthus*, in having a sclerified enlargement at the base of the style. Nevertheless, *Lepidaploa spixiana* is distinct in the critical characters of type G versus type B pollen and elongate versus short raphids in the achene wall. This *Lepidaploa* is also distinct in the thicker walled, shorter, less dense setulae of the achene, the presence of blister-like idioblasts on the achene surface, and the stiff straight hairs rather than numerous small glands on the outside of the corolla lobes.

Lessingianthus scabrifolius (Hieron.) H. Robinson, *comb. nov.* BAsIONYM: *Vernonia scabrifoliata* Hieron., Bot. Jahrb. Syst. 22:677. 1897.

The species was described from a Kuntze collection from Mato Grosso, Brazil, and additional material has been seen from Mato Grosso: Serra Ricardo Franco (15° S 60° W), May 1978, *Windisch 1995* (HB), *Marinon Barres s.n.* (HB); and Amazonas: Mun. de Humaitá, estrada Humaitá - Porto Velho, km 38, 8° S, 63° W, *Teixeira et al. 104.004* (NY,US) det. Pruski. The herbarium name *Vernonia velascens* Hieron. based on a Kuntze specimen from Dpto. Santa Cruz, Prov. Velasco, Bolivia is evidently the same species. Additional specimens seen from Prov. Velasco, Bolivia are *Seidel 594* (BOL,US) and *Nee 41145* (NY,US). The Teixeira specimen from Amazonas was compared with type material by Pruski.

Vernonanthura santacruzensis (Hieron.) H. Robinson, *comb. nov.* BAsIONYM: *Vernonia santacruzensis* Hieron., 22:699. 1897.

The species is more robust than the related *Vernonanthura patens* (H.B.K.) H. Robinson, and has broader, short-petiolate leaves with broadly rounded blade bases. A specimen, BOLIVIA: Depto. Santa Cruz, *Nee & Coimbra 35235* (NY,US) has been compared with type material by John Pruski.

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COMPARATIVE STUDIES ON THE POLLINATION BIOLOGY OF
DARWINIOTHAMNUS TENUIFOLIUS (ASTERACEAE) AND *PLUMBAGO*
SCANDENS (PLUMBAGINACEAE) ON PINTA ISLAND AND SANTA CRUZ
ISLAND, GALAPAGOS

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ABSTRACT

Fruit set and flower visitors of *Darwiniothamnus tenuifolius* (Asteraceae) and *Plumbago scandens* (Plumbaginaceae) were compared on Pinta Island and Santa Cruz Island, Galapagos, Ecuador. Results suggest that autogamy was favored during the initial colonization by these species. This mode of reproduction may now be supplemented by nonautomatic selfing and cross-pollination due to the presence of various flower visitors.

KEY WORDS: Pollination, Galapagos Islands, Ecuador, Asteraceae, *Darwiniothamnus tenuifolius*, Plumbaginaceae, *Plumbago scandens*

INTRODUCTION

In 1964, an unprecedented event in the history of Galapagos Islands research took place. This was the Galapagos International Scientific Project. For several weeks, the combined talents of botanists, zoologists, geologists, and many others were brought together in an attempt to more intimately know

the natural history of these Islands. Robert L. Usinger was among the entomologists who attended. Afterwards, he wrote of the "challenge to discover how the various animals and plants have worked out their destinies together" (Usinger 1972:249). Toward this end, E. Gorton Linsley (1966) compiled the first list of pollinating insects in the Galapagos Islands. This was followed by a detailed study of the pollination behavior of the endemic carpenter bee, *Xylocopa darwini* Cockerell (Hymenoptera: Apidae) (Linsley *et al.* 1966).

Other studies on the pollination of Galapagos angiosperms have followed (Rick 1966; Grant & Grant 1981; Aide 1986; McMullen 1985, 1986, 1987, 1989, 1990; Elisens 1989; McMullen & Close 1993). Most recently, a list of flower-visiting insects of the Galapagos Islands was compiled by McMullen (1993). This list was obtained from records in the scientific literature, as well as from personal observations conducted in the field during the summer of 1990. However, the relative importance of each visitor was not discussed. As the author suggested, details should be sought among the literature cited, or in future publications. The present paper will provide these details for two of the angiosperms mentioned in McMullen (1993).

METHODS

The two species treated here are *Darwiniothamnus tenuifolius* (Hook. f.) Harling (Asteraceae), an endemic shrub; and *Plumbago scandens* L. (Plumbaginaceae), a nonendemic native herb. The corymbiform inflorescences of *D. tenuifolius* are composed of heads with both disc and ray flowers. The yellow disc flowers are perfect and fertile, while the white ray flowers are pistillate and fertile. These inflorescences possess a mildly sweet odor. The white perfect flowers of *P. scandens* are arranged in paniculate spikes. They have little apparent scent.

Field work for the first part of this research was conducted on the southeastern slope of Pinta Island from 23 Jun - 26 Jul 1990. The study site for *Darwiniothamnus tenuifolius* was located at ca. 518 m altitude. Two sites were chosen for *Plumbago scandens*. One was located at 213 m, the other at 533 m.

Bagging experiments were conducted to determine if the species are autogamous (automatic self-pollinators). Fruit yields were compared for inflorescences completely isolated from insects (bagged), and others that were exposed to potential pollinators before being covered (open-pollinated).

Observations were made to determine what insects are visitors to the flowers of each species and might act as pollinators. *Darwiniothamnus tenuifolius* observations lasted 36 hours over four days. Those of *Plumbago scandens* lasted 40 hours during five days. Information such as how many visits were made and how long each visit lasted was obtained. The maximum time allowed for observing an insect during any one visit was 15 minutes. After this, the insect

was either captured, or another observation was begun so as not to spend an excessive amount of time watching one individual.

Similar studies were undertaken on the southern slope of Santa Cruz Island from 31 Jul - 10 Aug 1990. The study site for *Darwiniothamnus tenuifolius* was located at 632 m altitude near the craters known as "Los Gemelos." *Plumbago scandens* sites were located at 5 m altitude near Hotel Galapagos, and at 91 m altitude ca. 4 km north of Puerto Ayora on the road to Bella Vista. No bagging experiments were conducted as this information was available from previous studies performed in 1983-84 (McMullen 1987). All other observations and measurements were performed. However, the time spent observing visitors on this island was less than on Pinta (six hours during one day for both *D. tenuifolius* and *P. scandens*). Once again, this was due to the fact that research had previously been performed on Santa Cruz.

Voucher specimens of the plants were collected and deposited in the Charles Darwin Research Station herbarium (CDS). Specimens of each insect visitor were also collected and the majority of these are now part of the station's reference collection. Some duplicate specimens are housed at the Systematic Entomology Laboratory, United States Department of Agriculture in Beltsville, Maryland, and at Carleton University, Ottawa, Ontario.

RESULTS

Bagged inflorescences produced fruits for *Darwiniothamnus tenuifolius* and *Plumbago scandens* on Pinta and Santa Cruz (Table 1). Open-pollinated flowers of *P. scandens* produced a higher percentage fruit set than bagged flowers on both islands. The opposite was true for *D. tenuifolius* on Pinta.

Several flower visitors were recorded during this study and the insects visiting a particular plant on Pinta were often quite different from those visiting the same species on Santa Cruz (Table 2). *Darwiniothamnus tenuifolius* was visited most frequently on Pinta by a species of *Goniozus* (Hymenoptera: Bethyliidae) (127 visits, 22,722 seconds). Pollen was seen on the abdomen of one such individual. A species of *Olcella* (Diptera: Chloropidae) made slightly fewer visits (112), but for a total of 28,422 seconds. *Atteva hysginiella* Wallengren (Lepidoptera: Yponomeutidae), an *Orthoperus* species (Coleoptera: Corylophidae), and *Lepidanthrax tinctus* Thomas (Diptera: Bombyliidae) also made visits to this plant. Of the twelve *A. hysginiella* individuals, one was seen with pollen on its antennae. *Goniozus* and *Olcella* individuals were the only visitors to stay on an inflorescence for longer than 15 minutes.

On Santa Cruz, *Darwiniothamnus tenuifolius* was visited most often by an unidentified moth (Lepidoptera: Tortricidae) (22 visits, 4,090 seconds). It was also visited by *Toxomerus crockeri* Curran (Diptera: Syrphidae), *Darwinysius marginalis* Dallas (Hemiptera: Lygaeidae), *Urbanus dorantes galapagensis* Williams (Lepidoptera: Hesperiiidae), *Xylocopa darwini*, and another

Table 1. Bagging experiment results. Those for Santa Cruz are based on studies performed in 1983-84 (McMullen 1987).

<i>Darwiniothamnus tenuifolius</i>			
	# Heads Tested	# Fruits Set	# Fruits per Head
Bagged			
Pinta	998	32,810	32.88
Santa Cruz	36	250	-
Open-Pollinated			
Pinta	990	24,799	25.05
Santa Cruz	47	250	-
<i>Plumbago scandens</i>			
	# Flowers Tested	# Fruits Set	% Fruits Set
Bagged			
Pinta	554	70	12.64
Santa Cruz	57	30	52.63
Open-Pollinated			
Pinta	742	313	42.18
Santa Cruz	95	58	61.05

Table 2. Insect visitors. Visitation times are in seconds. Total refers to the time of all visits combined. N refers to the number of visits.

	Total	Mean	SD	N
<i>Darwiniothamnus tenuifolius</i> ^{1,2}				
Pinta				
<i>Olcella</i> sp. ³ (Diptera)	28,422	253.77	277.12	112
<i>Goniozus</i> sp. ³ (Hymenoptera)	22,722	178.91	198.36	127
<i>Atteva hysginiella</i> ¹ (Lepidoptera)	1,664	138.67	134.33	12
<i>Orthoperus</i> sp. ³ (Coleoptera)	188	94.00	19.80	2
<i>Lepidanthrax tinctus</i> ³ (Diptera)	160	20.00	27.37	8
Santa Cruz				
Moth ³ (Lepidoptera: Tortricidae)	4,090	185.91	177.64	22
<i>Tozomerus crockeri</i> ¹ (Diptera)	1,062	88.50	86.88	12
<i>Darwinysius marginalis</i> ³ (Hemiptera)	791	87.89	85.91	9
Moth ³ (Lepidoptera: Gelechioidea)	90	-	-	1
<i>Urbanus dorantes galapagensis</i> ³ (Lepidoptera)	23	3.29	2.14	7
<i>Xylocopa darwini</i> ¹ (Hymenoptera)	2	-	-	1
<i>Plumbago scandens</i> ^{2,5}				
Pinta				
<i>Leptotes parrhasioides</i> ⁶ (Lepidoptera)	543	9.53	13.13	57
<i>Cardiocondyla nuda</i> ³ (Hymenoptera)	491	81.83	51.58	6
<i>Lepidanthrax tinctus</i> ³ (Diptera)	10	2.50	1.91	4
<i>Naucles</i> sp. ³ (Coleoptera)	Not Timed, Night Visitor			
<i>Ornebius erraticus</i> ³ (Orthoptera)	Not Timed, Night Visitor			
<i>Paratrechina</i> sp. ¹ (Hymenoptera)	Not Timed, Night Visitor			
Santa Cruz				
<i>Phoebis sennae</i> (Lepidoptera)	641	3.08	2.31	208
<i>Leptotes parrhasioides</i> (Lepidoptera)	143	15.89	25.06	9
<i>Urbanus dorantes galapagensis</i> ³ (Lepidoptera)	13	-	-	1
<i>Xylocopa darwini</i> ¹ (Hymenoptera)	1	-	-	1
<i>Wasmannia auropunctata</i> ¹ (Hymenoptera)	Not Timed			

¹ Flowers recorded for the first time as visited by insects in the Galapagos Islands.² Flowers recorded for the first time as visited by *X. darwini*.³ Insect recorded for the first time as a flower visitor in the Galapagos Islands.⁴ Insect recorded for the first time as a flower visitor to this plant species.⁵ Flowers recorded for the first time as visited by insects on Pinta Island.⁶ Insect recorded for the first time as a flower visitor on Pinta Island.

moth (Lepidoptera: Gelechioidea). There were actually many more Tortricidae moths, *T. crockeri*, and *D. marginalis* present than could be accurately timed, so only a fraction of the activity that took place is recorded.

Leptotes parrhasioides Wallengren (Lepidoptera: Lycaenidae) was the most common visitor to flowers of *Plumbago scandens* on Pinta (57 visits, 543 seconds). Other visitors included *Cardiocondyla nuda* Mayr (Hymenoptera: Formicidae), *Lepidanthrax tinctus*, a species of *Naucles* (Coleoptera: Scaptiidae), *Ornebius erraticus* Schudder (Orthoptera: Gryllidae), and a species of *Paratrechina* (Hymenoptera: Formicidae). The latter three were night visitors, and were not timed.

On Santa Cruz, *Plumbago scandens* was visited most frequently by *Phoebis sennae* (Lepidoptera: Pieridae) (208 visits, 641 seconds). Also making visits were *Leptotes parrhasioides*, *Urbanus dorantes galapagensis*, *Xylocopa darwini*, and *Wasmannia auropunctata* (Hymenoptera: Formicidae). Flowers of this species were previously recorded as being visited on Santa Cruz by *L. parrhasioides* and *P. sennae* (McMullen 1986, 1990).

DISCUSSION

Darwiniothamnus tenuifolius is at least facultatively autogamous on both Pinta and Santa Cruz. With the level of insect activity observed at these plants, the open-pollinated inflorescences might be expected to produce more fruits than the bagged inflorescences. This was not the case, probably because the open-pollinated flowers were exposed to predation before being isolated with pollination bags. Finches were observed on several occasions feeding on the flowers and fruits of this species. In addition, due to differing rates of maturation within a corymbiform inflorescence, the fruits of some heads fell before the flowers of others had reached anthesis. Thus, some fruits were lost before the entire inflorescence could be bagged.

From the timed observations, a species of *Ocella* and a species of *Goniozus* appear to be most important as pollinators of *Darwiniothamnus tenuifolius* on Pinta Island. However, it should be noted that *Atteva hyzginiella* seemed to be much more common during casual observations than during the timed periods. Perhaps this insect was more aware of the observers, and avoided the plants at these times. Of the two visitors, *Ocella* and *Goniozus*, the latter may be more important in promoting cross-pollination since it spends less time on any one inflorescence. Three insect species may be important pollinators of *D. tenuifolius* on Santa Cruz. These are a Tortricidae moth, *Toxomerus crockeri*, and *Darwinysius marginalis*. Based on the above logic, the latter two may be more useful as cross-pollinators.

Plumbago scandens also produced fruits autogamously on both islands. Open-pollinated inflorescences showed a greater fruit set than bagged inflorescences. This would be expected given the insect activity during the timed

observations, and suggests that the insect visitors may be important pollen vectors. However, crosses on Santa Cruz did not produce any fruits (McMullen 1987). Perhaps these insects are more important in effecting maximum selfing, while outcrossing is negligible.

Darwiniothamnus tenuifolius was newly reported as having its flowers visited by insects in the Galapagos Islands. *Plumbago scandens* was recorded for the first time as having its flowers visited by insects on Pinta Island. In addition, *D. tenuifolius* and *P. scandens*, were newly reported as having their blossoms visited by *Xylocopa darwini*.

Eleven of the insects in Table 2 were recorded for the first time as visiting flowers in the Galapagos Islands, while one was newly recorded as visiting flowers on Pinta Island. Two insects were newly reported as flower visitors to *Darwiniothamnus tenuifolius*, and three were newly reported as flower visitors to *Plumbago scandens*. Although pollen was not observed on all of the visitors, the high level of activity within flowers for many of them suggests that they may be functioning as pollinators to some extent. The fact that many of the visitors were lepidopterans is significant since these insects are common pollinators on the mainland. This adds support to their possible role as pollen vectors in the Galapagos Islands.

In summary, the results of this study support the hypothesis that autogamous angiosperms were favored in the initial colonization of the Galapagos Islands (Rick 1966; McMullen 1987). This mode of reproduction may now be supplemented by nonautomatic selfing and cross-pollination due to the presence of various flower visitors. One of the more revealing discoveries of this research is the fact that, although few when compared to mainland standards, more insects visit flowers in this archipelago than previously believed.

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**TAXONOMIC STUDY OF THE GENUS *SYNEDRELLA* (ASTERACEAE,
HELIANTHEAE)**

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ABSTRACT

A taxonomic study of the monotypic genus *Synedrella* is rendered. It is represented by a single, highly variable, weedy species, *S. nodiflora*. Originally native to the New World tropics, it is now widely distributed in the tropical regions of the Old World and various island in between. An account is given of its taxonomic history, chromosome numbers, generic position, and worldwide distribution, including maps.

KEY WORDS: Asteraceae, Heliantheae, *Synedrella*, tropical weed

The genus *Synedrella* was established in 1791 by Gaertner, based upon *Verbesina nodiflora* L., which is typified by material collected in the West Indies (Jamaica) by Browne (Adams 1972; Howard 1989). According to most workers it is native to tropical America (perhaps the Caribbean Islands) but is now pantropical in distribution.

Some authors (e.g., Adams 1972) have noted that the genus contains two species because of a second named taxon, *Synedrella peduncularis* Benth. from Ecuador, the latter transferred to the genus *Schizoptera* Turcz. in 1916 by Blake, where it is properly positioned.

Because of its weedy nature and pantropical distribution, *Synedrella nodiflora* (L.) Gaertn. is accounted for in numerous regional or local floras. Nevertheless, to my knowledge, infraspecific taxa within the species have not been proposed, nor would I suggest that such exist, there being considerable variation of nearly all characters, both within and between populations.

CHROMOSOME NUMBERS

There have been over 20 published articles in which chromosome counts for *Synedrella* are reported (cf. standard indices through 1989). It was first counted by Banerji & Pal (1959) as diploid with $2n = 40$. Most subsequent workers have corroborated this number, except for a few workers who report counts of $2n = 32$ (1 count), $2n = 36$ (2 counts), and $2n = 38$ (2 counts). Nirmala & Rao (1981, 1986) have reported the most recent anomalous counts for *Synedrella* ($2n = 36$ and 38 , respectively), both counts from populations in India. Other workers, however, have reported yet other Indian populations as $2n = 40$. In summary, the preponderance of counts suggest that the prevalent number in *Synedrella* is $2n = 40$, suggesting an ancestral base number of $x = 10$.

GENERIC RELATIONSHIPS

Synedrella belongs to the tribe Heliantheae where it relates to a group of genera centering about the large pantropical genus *Wedelia*. Both Stuessy (1977) and Robinson (1981) positioned *Synedrella* in the subtribe Ecliptinae, the latter taxon mostly characterized by their compressed, often winged, carbonized achenes; disk florets mostly hermaphroditic, having blackened anther thecae, and corollas with well-defined fiber sheaths. As treated by Robinson (1981) the subtribe contains 65 or more genera. Amongst these *Synedrella* seems closest to the poorly known South American genus *Synedrellopsis* Hieron. & Kuntze, with which it might comfortably be combined; at least I can find no significant characters to distinguish between them (the achenes of both *Synedrella* and *Synedrellopsis* are pictured in Robinson [1981]). Aside from *Synedrellopsis*, *Synedrella* appears closely related to *Calyptocarpus* Less. (cf. McVaugh & Smith 1967). According to restriction site analysis of chloroplast DNA (Kim, K.-J., unpubl.), *Calyptocarpus* is clearly related to the genus *Lasianthaea*, a largely Mexican genus of the subtribe Ecliptinae.

SYNEDRELLA Gaertn., *nom. cons.*

Erect tap-rooted herbs. Leaves simple, opposite. Heads arranged 2-10 to a node, sessile or rarely pedunculate. Involucral bracts 2, herbaceous, tubes slender, as long or longer than the ligules; style branches slender and filiform with acute apices. Disk florets 4-merous; anther appendages plicate, wider than long; style branches linear-lanceolate, gradually acuminate. Achenes heterocarpic, those of the ray tangentially flattened with stiff erose margins and erect pappus scales, those of the disk oblanceolate to clavate and somewhat



Figure 1. North American distribution of *Synedrella nodiflora*.

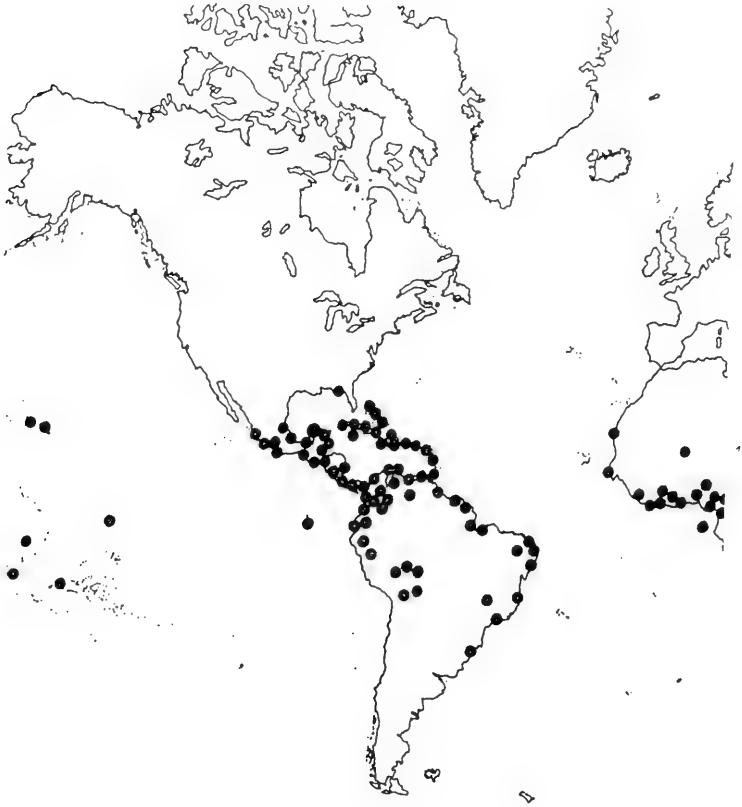
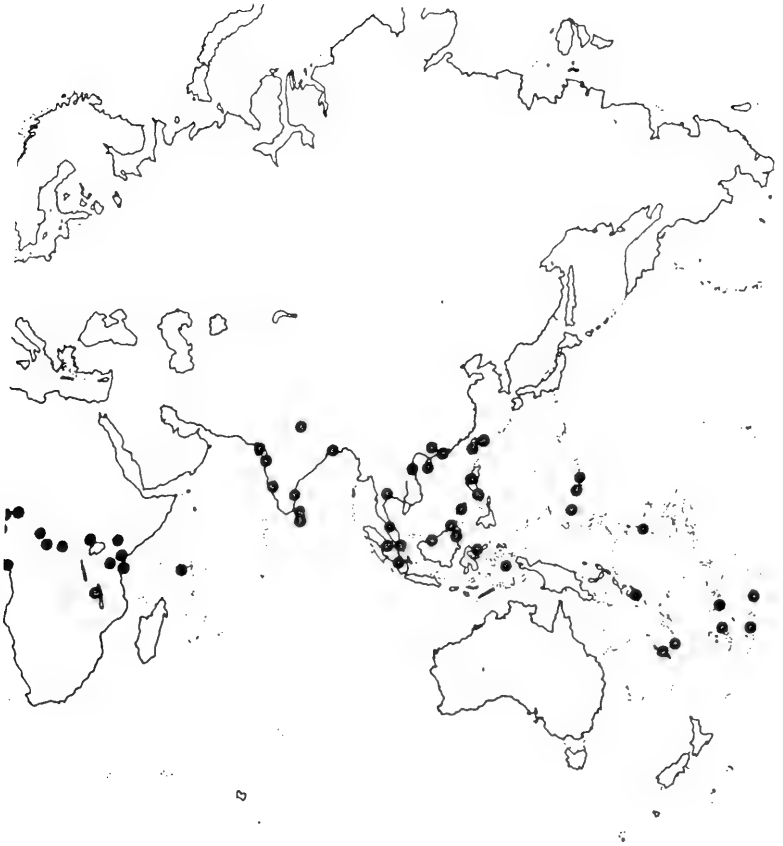


Figure 2. World distribution of *Synedrella nodiflora*.



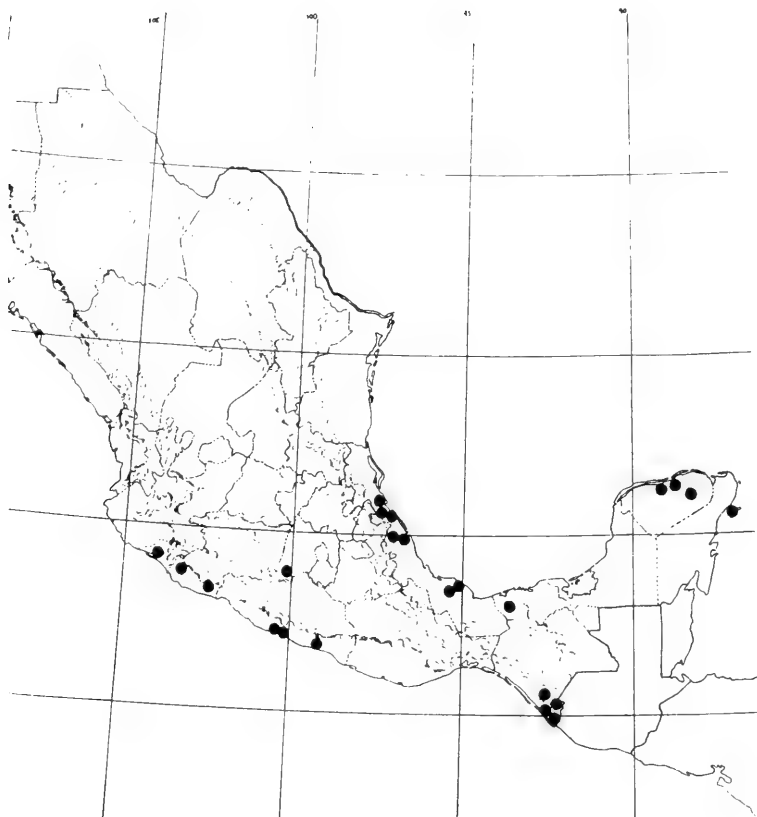


Figure 3. Mexican distribution of *Synedrella nodiflora*.

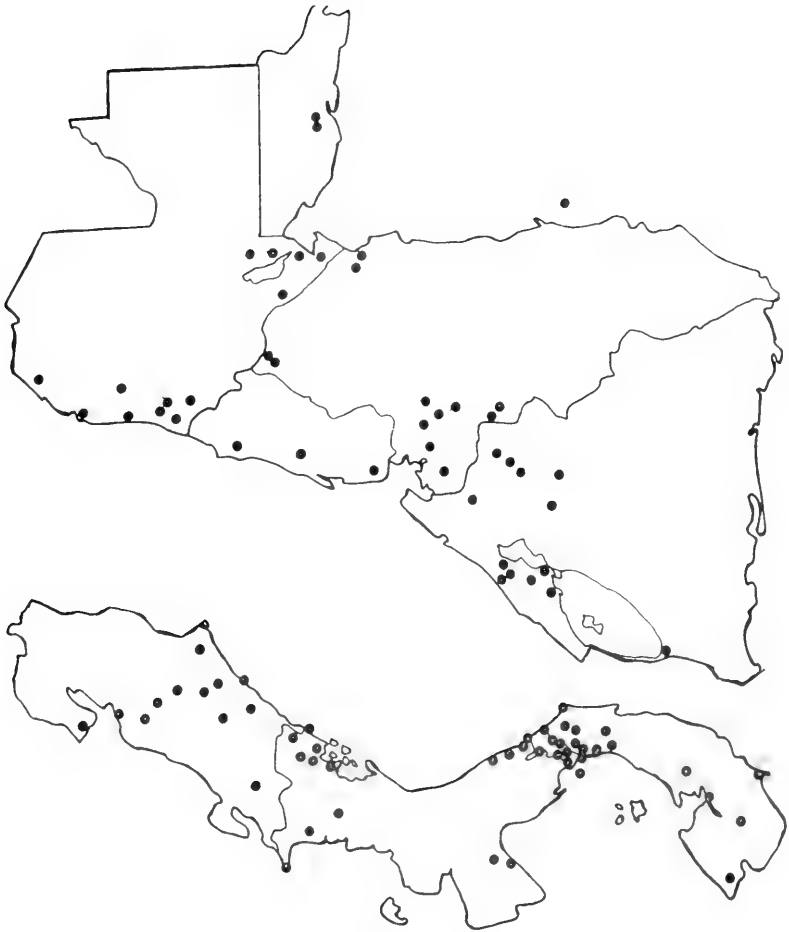


Figure 4. Central American distribution of *Synedrella nodiflora* (Guatemala to Panamá).

4-sided, tangentially compressed, the pappus of 2-3 stiff divaricate awns. Base chromosome number, $x = 20$.

Synedrella nodiflora (L.) Gaertn., *Fruct.* 2:456. pl. 171. 1791. BASIONYM: *Verbesina nodiflora* L., *Cent. Pl.* 1:28. 1755. *Ucacou nodiflorum* (L.) Hitchc., *Rep. Missouri Bot. Gard.* 4:100. 1893. According to Adams (1972), this name is typified by material collected in Jamaica by Browne. The illustration accompanying the original description and that of Adams (1972) leaves little doubt as to its correct application.

Since the genus is monotypic the generic description provided here, as well as McVaugh's excellent description and illustrations (1984) suffice to circumscribe the species. As would be anticipated in a pantropical weedy species (Figure 2) the taxon is exceedingly variable as to habit, foliage shape, and vestiture, but the floral characters are remarkable uniform throughout its range, except that the achenes are quite variable, especially as regards shape and degree of surface ornamentation of the disk achenes, these varying from tangentially flattened and without corky enations, to subquadrate and markedly corky, the 2-3 awns of the pappus varying from either stiffly erect to widely divergent.

DISTRIBUTION - *Synedrella nodiflora*, as already noted, is a pantropical weed. It is likely that it was originally native to tropical America and subsequently distributed elsewhere by modern man. The species is largely restricted to lowland regions from sea level to ca. 500 meters and is clearly weedy, most often found in disturbed habits, usually fallow fields. It flowers in all seasons, depending on rains and should be readily disseminated considering its small readily detached achenes with their lateral hooking devices.

Because the plant is abundant in herbaria, and the fact that only a simple clearcut species is involved, I will let the distributional maps (Figures 1-4) document its occurrence as determined from sheets personally examined. I do provide below a brief listing of selected collections showing the location of appropriate voucher material and the earliest date of collection (shown in parentheses) within a region.

NORTH AMERICA

UNITED STATES. Hawaii: Honolulu, *Degener 18308*, NY (1925). Florida: Apalachicola, *Chapman 6095*, MO (1898; not collected since).

MEXICO. Chiapas: *Matuda 17229*, NY (1947). Colima: *McVaugh 24970*, LL (1970). Guerrero: *Hinton 10969*, LL (1937). México: *Hinton 5362*, NY (1933). Michoacán: *Hinton 7581*, LL (1935). Quintana Roo: *Lewis 6378* (1967). Tabasco: *Cowan 1758*, TEX (1978). Veracruz: *Orcutt 3129*, MO (1910). Yucatán: *Millsbaugh 185*, F (1895).

CENTRAL AMERICA

GUATEMALA. Escuintla: *Standley 64086*, F (1939). Izabal: *Ortiz 3555*, F (1908). Jutiapa: *Standley 75028*, F (1940). Quezaltenango: *Croat 32775*, MO (1976). Retalhuleu: *Molina 26967*, F (1907). Santa Rosa: *Standley 37907*, F (1892).

BELIZE. *Gentle 108*, F (1933).

EL SALVADOR. Morazán: *Tucker 493*, F, NY (1941).

HONDURAS. Choluteca: *Standley 27758*, F (1949). El Paraiso: *Standley 16536*, F (1949). Islas de la Bahía: *Molina 20742*, F (1967). Morazán: *Standley 11658*, F (1947). Ocotepeque: *Molina 22540*, F (1968). Yoro: *Standley 53920*, F (1927).

NICARAGUA. Boaco: *Stevens 14571*, NY (1979). Chinandega: *Grijalva 537*, F (1979). Estelí: *Nelson 7704*, NY (1968). Granada: *Sandino 1281*, F (1981). Jinotega: *Stevens 15434*, MO, NY (1979). Managua: *Stevens 3431*, F (1969). Masaya: *Stevens 4244*, F (1977). Nuevo Segovia: *Moreno 13623*, MO (1981). Río San Juan: *Sandino 1744*, F, NY (1981). Zelaya: *Ipoly 3546*, MO (1979).

COSTA RICA. Heredia: *Hammel 7883*, MO (1980). Limón: *Davidson 6908*, MO (1978). Puntarenas: *Kernan 53* (1988).

PANAMA. Bocas del Toro: *Dunlap 314*, F (1924). Chiriquí: *Croat 21922*, MO (1973). Coclé: *Rodriguez 1173*, MO (1947). Darién: *Duke 4143*, MO (1961). Herrera: *Tyson 3136*, MO (1966). Los Santos: *Burch 1265*, MO (1966). Panamá: *Macbride 2795*, F (1923). San Blas: *Croat 16964*, MO (1971). Veraguas: *Tyson 5170*, MO (1968). W/O Locality: "Colón" *O. Kuntze s.n.*, NY (1841).

WEST INDIES

BAHAMA ISLANDS. Abaco: *Brace 1959*, NY (1904). Crooked Island: *Brace 1906*, F, NY (1906). Eleuthra: *Correll 48937*, NY (1977). Great Exuma: *Correll 44089*, NY (1975). New Providence: *Hitchcock s.n.*, F (1890).

GREATER ANTILLES: CUBA. Camaguey: *Shafer 120*, NY (1909); Havana: *Rugel 1849*, NY (1849); Matanzas: *Britton 370*, NY (1903). Oriente: *Shafer 1581*, F, NY (1909); Pinar del Río: *Alain 425*, NY (1943); Santa Clara: *Combs 478*, F, NY (1895); Cuba: *Wright s.n.*, NY (1856-57). DOMINICAN REPUBLIC. *Taylor 764*, F, NY (1909). GRAND CAYMAN. *Armour 1276*, F (1859). HAITI. *Nash 1037*, NY (1905). JAMAICA. *Lloyd 1121*, F, MO (1890). PUERTO RICO. *Garber 27*, NY (1880). TRINIDAD. *Skousted 33*, MO (1935). VIRGIN ISLANDS. *Acevedo 1888*, NY (1987); *D'Arcy 5106*, MO (1971); Saint Croix, *Ricksecker 31*, F, NY (1895); Saint Thomas, *Kuntze 102*, NY (1874).

LESSER ANTILLES: ANTIGUA. *Boz 936*, F (1937). BARBADOS. *Bovell 380* (1901). DOMINICA. *Lloyd 465*, NY (1903). GRENADA. *Broadway s.n.*, MO (1904); w/o data, F (1904). GUADELOUPE. *Duss 2496*, NY (1902). MARTINIQUE. *Hahn 390*, NY (1871). MONTSERRAT. *Shafer 27*, F, NY (1907). SAINT BARTHELEMY *Forsstrom 7227*, F (w/o date). SAINT KITTS. *Britton 136*, NY (1901). SAINT VINCINT. *Smith 723*, NY (w/o date). TOBAGO: *Eggers 5527*, NY (1889). CURAÇAO. *Boldingh s.n.*, NY (1913).

SOUTH AMERICA

BOLIVIA. *Gentry 44241*, MO (1984). Beni: *Solomon 6273*, MO, NY (1981). Nor-Yungas: *Solomon 7372*, F, MO, NY (1982). Pando: *Nee 31596*, MO, NY (1980).

COLOMBIA. Bolívar: *Killip 14286*, NY (1926). Caldas: *Cuatrecasas 23104*, F (1946). Chocó: *Gentry 17257*, MO (1976). Cundinamarca: *King 5888*, F, NY (1965). Los Llanos: *Cuatrecasas 1975*, F (1938). Magdalena: *Andre s.n.*, F (1875). Norte de Santander: *Fabrega 850*, F (1944). Tolima: *Pennell 3376*, MO (1917). Valle: *Cuatrecasas 22596*, F (1946).

ECUADOR. Chimborazo: *Camp E-3043*, NY (1945). El Oro: *Daly 114*, NY (1978). Esmeraldas: *Asplund 16443*, NY (1955). Galapagos Islands: *Snow 346*, NY (1963). Guayas: *Mille 1006*, F (1937). Los Rios: *Dodson 7051*, F, MO (1978). Morona-Santiago: *Brandbyge 32238*, NY (1980). Napo: *Bowbray 69927*, MO (1969). Pichincha: *Harling 9288*, F, MO, NY (1968). w/o locality: *Andre 483*, NY (1975).

PERU. Junín: *Woytkowski 7362*, MO (1962). Loreto: *Croat 17989*, MO (1972). Ucayali: *MacRae 15*, F (1981).

VENEZUELA. Aragua: *Pittier 148*, MO (1927). Bolívar: *Boom 6271*, MO (1985). Delta Amacuro: *Steyermack 115217*, MO (1977). Fed. Distr.: *Bailey 206*, MO (1921). Guarico: *Davidse 4189*, MO (1976). Isla Margarita: *Miller 131*, F, MO (1901). Miranda: *Croat 21685*, MO (1973). Monagas: *Trujillo 9467*, F (1969). Portuguesa: *Smith 892*, MO (1982). Sucre: *Fernández 3751*, NY (1980). Tachira: *Croat 54960*, MO (1982). Zulia: *Bunting 11339*, NY (1982).

BRITISH GUIANA. *Persand 150*, F (1923).

FRENCH GUIANA. *Feuillet 1695*, F, MO (1985).

SURINAM. *Coulen 331*, MO (1841).

BRAZIL. Bahia: *Chase 7879*, MO (1924). Ceara: *Drovet 2234*, F (1935). Minas Geraes: *Chase 9261*, MO (1925). Para: *Dahlgren 451*, F (1929). Pernambuco: *Pickel 19*, F (1930). w/o locality: *Rusby 233*, F, MO (1895).

ASIA

- AMBOINA. *Robinson 1835*, NY (1913).
BANGLADESH. *Khan 4312*, MO (1976).
CELEBES. *Kauderns 258*, NY (1917).
CEYLON. *Millspaugh 2498*, F (1912).
CHINA. Hainan: *Chow 78475*, MO, NY (1978). Kwong Tung: *Levine 1899*, MO (1917).
HONG KONG. *Millspaugh 2735*, F (1911).
INDIA. Madras, *Pres. Madras Coll. s.n.*, NY (1929).
JAPAN. *Iwatsuki 682*, MO (1976).
MALAYSIA. *Elmer 20709*, MO (1922).
PHILIPPINES. *Merrill 36*, NY (1902).
SINGAPORE. w/o collector, MO (1904).
SUMATRA. *Toroës 3649*, NY (1933).
TAIWAN. *Gressitt 485*, NY (1934).
THAILAND. *King 5562*, F (1963).
VIETNAM. *Squires 28*, NY (1927).

AFRICA

- BURUNDI. *Lambinon 78/133*, MO (1978).
CAMEROON. *Gandoger s.n.*, MO (1906).
GAMBIER. *Chapin 935*, NY (1934).
GHANA. *Enti 69*, NY (1971).
HAUTE-VOLTA. *Georges 15403*, MO (1958).
IVORY COAST. *Amshoff 637*, MO (1972).
KENYA. *Robertson 3319*, MO (1982).
KIVU. *Alcool 8961*, MO (1958).
LIBERIA. *Baldwin 6949*, MO (1947).
MALAWI. *Pawek 8267*, MO (1974).
NIGERIA. *Ekwuno 63767*, MO (1971).
REP. CENTRAFRICAINE. *Leeuwenberg 6252*, MO (1965).
S. TOME. *Viegas s.n.*, NY (1948).
SENEGAL. *Georges 582*, MO (1948).
SIERRA LEONE. *Thomas 2955*, MO (1914).
TANZANIA. *Tanner 1917*, NY (1955).
UGANDA. *Dummer 3264*, MO (1917).
ZAIRE. *Louis 11542*, NY (1938).
PACIFIC ISLANDS: CAROLINES. *Carr 11093*, NY (1935). COOK. *Yuncker 9867*, NY (1940). ELLICE. *Chambers 46*, MO (1974). FIJI. *De-gener 13518*, F (1940). FRENCH POLYNESIA. *Florence 1982*, NY (1952).

MARIANAS. *Kanehira* 2215, NY (1933). MARQUESAS. *Chapin* 762, NY (1934). NEW CALEDONIA. *Baumann-B.* 13744, NY (1951). SAMOA. *Vaupel* 2, MO (1905). SEYCHELLES. *Jeffrey* 437, NY (1961). SOCIETY. *Moore* 36, MO (1926). SOLOMON. *Riley* 23, NY (1945). TONGA. *Hurlimann* 522, NY (1926).

EXCLUDED NAMES

Synedrella peduncularis Benth., *Pl. Hartw.* 119. 1843. Blake (1916, in Hook. Ic. Pl. t. 3058) correctly positioned this name in the genus *Schizoptera*, *S. peduncularis* (Turez.) S.F. Blake, where it replaced the later name *S. trichotoma* Turez. (1851).

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TAXONOMIC OVERVIEW OF *GILIA*, SECT. *GILIASTRUM*
(POLEMONIACEAE) IN TEXAS AND MEXICO

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ABSTRACT

A taxonomic treatment of *Gilia* sect. *Giliastrum* is rendered for Texas and México. Five species are recognized as occurring within Texas: *G. incisa*, *G. insignis*, *G. ludens*, *G. rigidula*, and *G. stewartii*; and seven species occur in México: *G. gypsophila*, *G. incisa*, *G. insignis*, *G. palmeri*, *G. purpusii* (including *G. platyloba*), *G. rigidula*, and *G. stewartii*. One new species, *G. gypsophila* B.L. Turner *sp. nov.*, is described and illustrated. Chromosomal data are reviewed for the sect. *Giliastrum* as a whole, and distribution maps of the Texas and Mexican taxa are provided. Complete synonymy is given for all of the taxa concerned, along with appropriate taxonomic comments.

KEY WORDS: Polemoniaceae, *Gilia*, *Giliastrum*, México, Texas

The sect. *Giliastrum* of *Gilia* was first erected by Brand (1907) to accommodate *Gilia rigidula* Benth. in DC. and its allies. He placed the section in his subgenus *Benthamiophila*, which in today's nomenclature must be called subgenus *Gilia* since it contains the type element of *Gilia*. Brand recognized five species under his concept of *Giliastrum*: *G. incisa* Benth. in DC., *G. foetida* Gill. ex Benth., *G. palmeri* S. Wats., *G. purpusii* K. Brandege (not to be confused with *G. leptantha* Parish subsp. *purpusii* [Mkkn.] A. & V. Grant) and *G. rigidula*, the latter divided into two subspecies (*rigidula* and *insignis* Brand), one of these (*rigidula*) further divided into two varieties (*acerosa* A. Gray and *rigidula*).

Grant & Grant (1956) provided a conspectus of the subgenus *Gilia* in which they recognized four sections: *Arachnion*, *Gilia*, *Gilmania*, and *Saltugilia*. The sect. *Giliastrum* was not included in the subgenus at that time, but Grant (1959) subsequently modified their 1957 infrageneric treatment of *Gilia* to include five sections: *Gilia*, *Giliandra*, *Arachnion*, *Saltugilia*, and *Giliastrum*

(which included the sect. *Gilmania* of Grant & Grant 1957). So construed, *Giliastrum* was said to contain eleven North American species and at least one, and possibly more, South American species.

Following Grant's (1959) broad overview of sect. *Giliastrum*, two new species were added to the section by Shinnery (1963), *Gilia perennans* Shinnery, which I treat as synonymous with *G. incisa*, and *G. ludens* Shinnery, which is recognized. Two Mexican taxa, *G. insignis* (Brand) Cory & Parks and *G. stewartii* I.M. Johnston., both of which occur in Texas, are recognized here as specifically distinct and *G. platyloba* I.M. Johnston. is treated as synonymous with the Mexican species, *G. purpusii*. I have also added a newly described species *G. gypsophila*.

Five species of the sect. *Giliastrum* are now recognized as occurring in Texas, and seven in México. Altogether, the sect. *Giliastrum* currently contains approximately seventeen species, most of these native to North America, but at least a few are confined to South America, as noted in the chromosomal account that follows.

CHROMOSOME NUMBERS

Chromosome numbers are available for only eight of the approximately seventeen species of the sect. *Giliastrum*, as noted in Table 1. Most of the species have chromosome numbers on a base of $x = 9$, with the exception of *Gilia insignis* ($2n = 12$) which apparently has an extant base number of $x = 6$. Indeed, if the latter were thought to be the ancestral base number for the section, one might view the remainder of the taxa as being either hexaploids ($2n = 18$) or dodecaploids ($2n = 36$).

Grant (1959), because of the frequency and phyletic distribution of species having numbers on a base of $x = 8$ and 9, inferred that the base number of the family as a whole was $x = 9$; the relatively few taxa with $x = 6$ were thought to be derived via aneuploid reduction. This might be the case for *Gilia insignis* because, except for the anomalous count of $2n = 20$ for *G. rigidula* var. *acerosa*, all of the taxa counted to date appear to be on a base of $x = 9$. Regardless, the base number of $x = 6$ found in *G. insignis* strongly suggests that it is best treated as a distinct species, the rank accorded the taxon by Shinnery (1963), Wherry (1966) and yet others (Henrickson, in prep.) than as a subsp. of *G. rigidula* as originally proposed by Brand.

KEY TO TEXAS AND MEXICAN SPECIES OF *GILIA* SECT.

GILIASTRUM

1. Corollas mostly 4-7(-8) mm long; basal-most leaves frequently simple or deeply serrate. *G. incisa*

1. Corollas mostly (7-)8-20 mm long; basal-most leaves variously dissected or pinnately lobed. (2)
 2. Calyx lobes united for 1/3 their length or less. (3)
 2. Calyx lobes united for 1/3 their length or more. (4)
3. Corollas mostly (7-)8-9 mm long. *G. stewartii*
3. Corollas mostly 10-13 mm long. *G. purpusii*
 4. Leaves simple or merely 3-parted, the blades or their divisions linear, when 3-parted the terminal lobe 3-5 times as long as the lateral lobes; Baja California. *G. palmeri*
 4. Leaves not as described in the above; not in Baja California. .. (5)
5. Corollas mostly 18-22 mm long, at anthesis broadly flaring, 22-32 mm across the expanded lobes. *G. insignis*
5. Corollas mostly 10-18 mm long, at anthesis 15-20 mm across the expanded lobes. (6)
 6. Perennial, stiffly erect much-branched suffruticose herbs, the basal leaves scarcely persisting, the stem leaves numerous and usually acerose or pungently pointed. *G. rigidula*
 6. Annual or weakly perennial sparsely branched herbs, the basal leaves usually persisting, the stem leaves not especially acerose or pungent. (7)
7. Plants with primary stems stiffly erect and somewhat zigzag; basal leaves coriaceous with deeply incised simple lobes, their apices acute; gypseous soils of Nuevo León, México. *G. gypsophila*
7. Plants not as described in the above; basal leaves mostly pinnately lobed or dissected, the ultimate units mostly broadly ovate to oblanceolate in outline; southcentral Texas. *G. ludens*

Gilia gypsophila B.L. Turner, *sp. nov.*, Figure 1. TYPE: MEXICO. Nuevo León: 14 km N of Rancho las Estacas, on road to Rancho Lechuguillal (26° 28' 30" N, 100° 50' W), gypsum flat, 680 m, 16 Mar 1973, *M.C. Johnston, T.L. Wendt, & F. Chiang 10222* (HOLOTYPE: LL!).

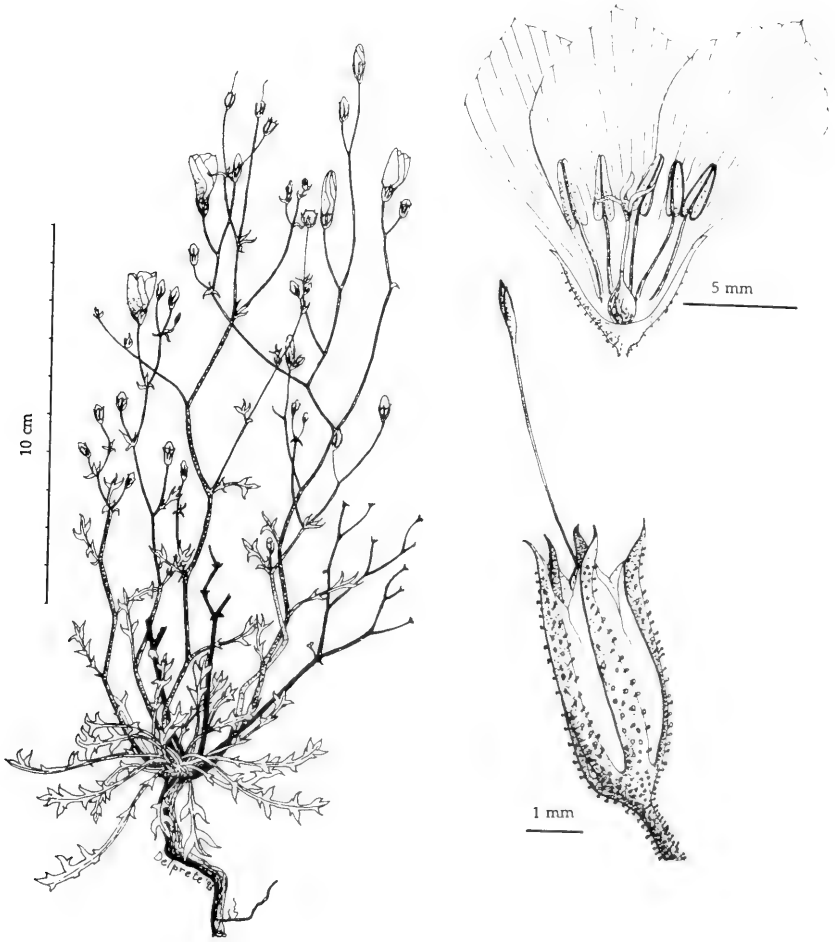


Figure 1. *Gilia gypsophila*, from holotype.

Giliae rigidulae Benth. in DC. var. *acerosae* A. Gray similis sed plantis majoribus strictisque rosulas persistentes basales parietibus, foliis midcaulis vix acerosis secus caules separatis internodiis plerumque 1-2 cm longis (vs. 0.3-1.0 cm) differt.

Stiffly erect perennial herbs 15-25 cm high. Stems 2-10 arising from a ligneous tap root, prominently glandular-pubescent throughout, the hairs 0.2 mm long or less. Basal leaves persistent as a well-defined rosette of coriaceous laciniately lobed leaves 3-5 cm long, 0.6-1.6 cm wide, minutely pubescent like the stems, the petioles 1.5-2.5 cm long; blades oblanceolate in outline, the lobes acute with callous apices. Stem leaves sessile or shortly petiolate, not at all acerose, well-spaced along the somewhat zig-zag stem, the internodes mostly 1-2 cm long. Flowers 3-10 per stem, arranged in terminal open cymes; the pedicels mostly 5-20 mm long. Flowering calyces ca. 5 mm long, the lobes linear-lanceolate, united for 1/2-3/5 their length, minutely glandular-pubescent dorsally. Corollas apparently lavender or bluish, rotate, ca. 16 mm long with lobes extended, the lobes ca. 12 mm long, apices broadly rounded. Anthers yellow, ca. 2 mm long. Capsule decidedly globoid, ca. 4-5 mm high, ca. 4.1 mm wide. Seeds (immature) oval, ca. 2 mm long.

ADDITIONAL SPECIMEN EXAMINED: MEXICO. Nuevo León: Minas Manto Blanco y Sabana Blanca, just N of the Cañon de Potrerillos (26° 04' N, 100° 45' W), gypsiferous clay loam, 950-1000 m, 17 Mar 1973, *Johnston et al.* 10250c (LL).

This taxon is clearly related to *Gilia rigidula* but differs in having a persistent rosette of coriaceous leaves, numerous, rather zig-zag stems with elongate midstem internodes. It appears to stand somewhat between *G. rigidula* var. *acerosa* and *G. ludens*, as noted by J. Henrickson on the paratype. As shown in Figure 1, *G. gypsophila* occurs within the southern range of *G. rigidula* var. *acerosa*, but these apparently do not co-occur at a given site.

Gilia incisa Benth. in DC., *Prodr.* 9:312. 1845. *Navarretia incisa* (Benth.) Kuntze, *Rev. Gen. Pl.* 2:433. 1891. *Polemonium incisum* (Benth.) Kuntze, *Rev. Gen.* 3:203. 1898. TYPE: U.S.A. Texas: Central Texas, 1835, *T. Drummond 463* (HOLOTYPE: K; Isotypes: GH, TEX!).

Gilia lindheimeriana Scheele, *Linnaea* 21:753. 1848. TYPE: U.S.A. Texas: Comal Co., vicinity of New Braunfels, 1844-1850, *F. Lindheimer* (holotype not located).

Gilia perennans Shinnery, *Sida* 1:174. 1963. TYPE: U.S.A. Texas: Culberson Co., Guadalupe Mts., McKittrick Canyon, 18 Aug 1946, *D.S. Correll 13958* (HOLOTYPE: SMU).

This is a widespread variable species but readily distinguished by its mostly simple unbranched stems, relatively weakly dissected thin leaves, and small corollas. It is sympatric with most of the Texas and Mexican taxa, except for *Gilia ludens* (Figure 2), preferring relatively moist shady habitats.

Gilia insignis (Brand) Cory & Parks, Texas Agr. Exptl. Sta. Bull. 550:85. 1938. *Gilia rigidula* Benth. in DC. subsp. *insignis* Brand in Engler, *Pflanzenr.* IV. 250:147. 1907. TYPE: MEXICO. Coahuila: Jimulco Station, ca. 25° 07' N, 103° 20' W, 16 May 1885, C.G. Pringle 248 (LECTOTYPE [selected here]: B, destroyed; Isolectotypes: GH!, UC!, VT!).

This is a well-marked relatively widespread species, readily distinguished by its wiry stems, large corollas on elongate peduncles, and chromosome numbers on a base of $x = 6$ (Table 1). Nevertheless, Wherry (1966) retained it as a subspecies of *Gilia rigidula*.

Gilia ludens Shinnery, Sida 1:174. 1963. TYPE: U.S.A. Texas: Jim Wells Co.: 4 mi W of Alice, 10 Apr 1955, L.H. Shinnery 19581 (HOLOTYPE: SMU).

This is a relatively well-marked taxon what with its somewhat sprawling or recumbent habit with persistent basal leaves. It is superficially similar to *Gilia rigidula* var. *rigidula*, but as indicated in figures 4 and 6, the two do not normally co-occur.

Gilia palmeri S. Wats., Proc. Amer. Acad. Arts 24:61. 1889. TYPE: MEXICO. Baja Calif. Norte: Stony ridges near Los Angeles Bay, 1887, E. Palmer 593 (HOLOTYPE: GH; Photoholotype: CAS!).

Gilia palmeri S. Wats. subsp. *spectabilis* A. Day in Shreve & Wiggins, *Veg. & Fl. Sonoran Desert* 2:1164. 1964. TYPE: MEXICO. Baja Calif. Norte: Hills of Sierra del Volcán, 4 mi E of El Marmol, 13 Feb 1935, I. Wiggins 7570 (HOLOTYPE: DS!).

A very distinct member of the sect. *Giliastrum*, not likely to be confused with another. Very large-flowered populations have been recognized as subsp. *spectabilis*, but there appears to be much variation in corolla size both within and among populations, to judge from collections at CAS.

Gilia purpusii K. Brandegees, Zoe 5:179. 1904. TYPE: MEXICO. Coahuila: Viesca, ca. 25° 20' N, 102° 26' W, Mar 1904, C.A. Purpus 533 (HOLOTYPE: CAS!).



Figure 2. Distribution of *Gilia gypsophila* (triangles), and *G. ludens* (circles).

Table 1. Chromosome numbers in *Gilia* sect. *Giliastrum*.**

Species	Source, reference, and/or voucher	2n number
<i>G. campanulata</i> A. Gray	U.S.A. Nevada: Esmeralda Co. (Grant 1959)	18*
<i>G. filiformis</i> Parry	U.S.A. California: Inyo Co. (Grant 1959)	18*
<i>G. foetida</i> Gill. ex Benth.	ARGENTINA. Mendoza: Las Heras (Covas & Schnack 1946)	18*
<i>G. incisa</i>	MEXICO. San Luis Potosí: San Luis Potosí (Grant 1959)	18*
<i>G. incisa</i>	MEXICO. San Luis Potosí: Río Verde (Grant 1959)	18*
<i>G. incisa</i>	U.S.A. Texas: Travis Co. (Grant 1959)	18*
<i>G. incisa</i>	U.S.A. Texas: Uvalde Co. (Grant 1959)	18*
<i>G. insignis</i>	MEXICO. Chihuahua: 20 mi NE Carmago (Weedin & Powell 1978)	6 prs
<i>G. insignis</i>	MEXICO. Nuevo León: 5 mi N of Espinoza (Weedin & Powell 1978)	12 prs
<i>G. latifolia</i> S. Wats.	U.S.A. California: Riverside Co. (Grant 1959)	36*
<i>G. rigidula</i> var. <i>rigidula</i>	Flory 1937; seed source unknown.	18*
<i>G. rigidula</i> var. <i>rigidula</i>	U.S.A. Texas: Edwards Co. (Grant 1959)	36*
<i>G. rigidula</i> var. <i>rigidula</i>	U.S.A. Texas: Hayes Co., (Grant 1959)	36*

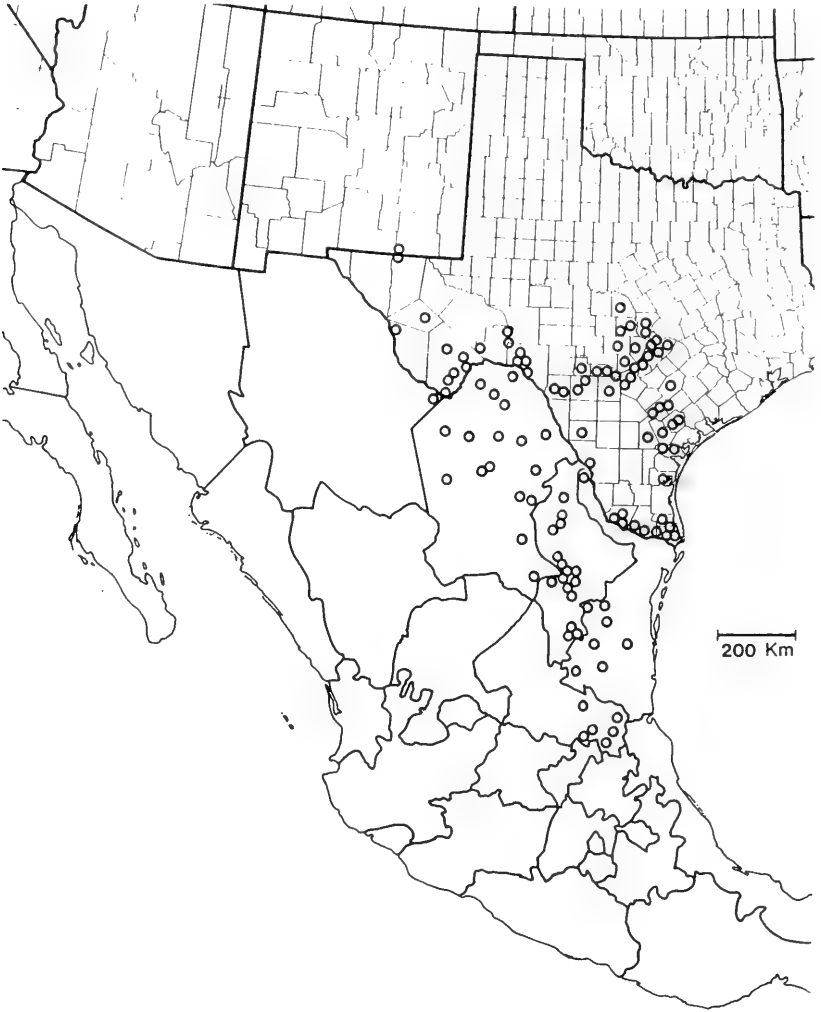


Figure 3. Distribution of *Gilia incisa*.



Figure 4. Distribution of *Gilia insignis* (open circles) and *G. palmeri* (closed circles).

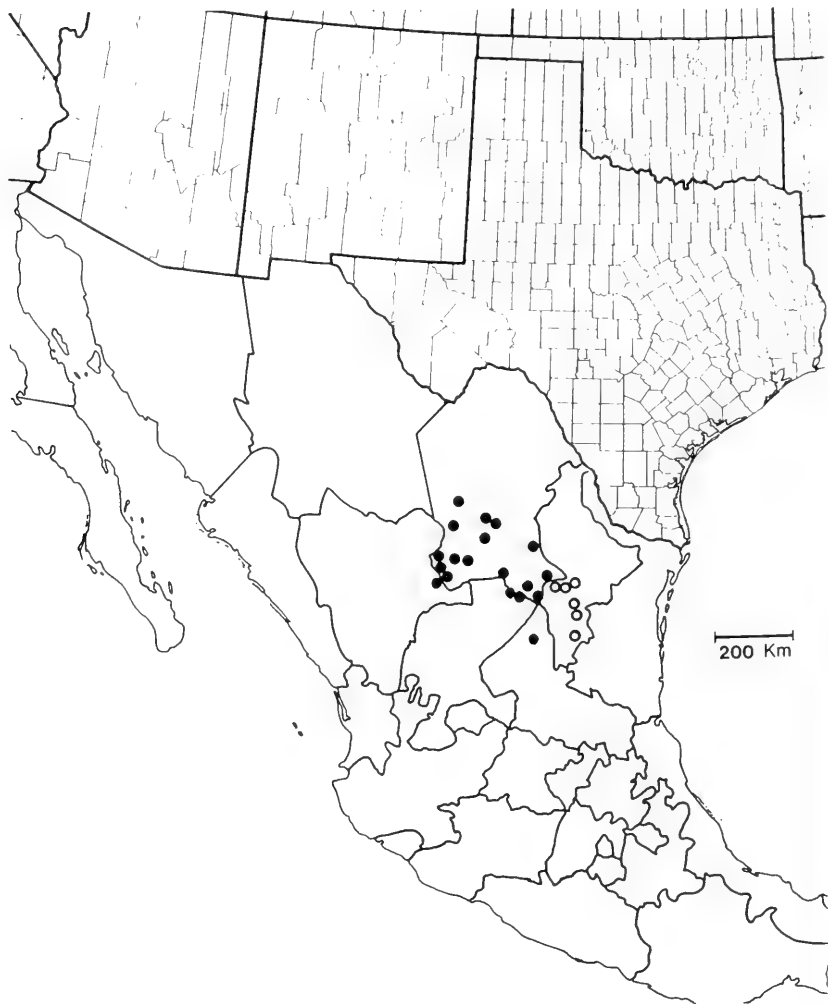


Figure 5. Distribution of *Gilia purpusii*. Typical collections from calcareous soils at lower elevations shown as closed circles; atypical collections from pine forests in gypseous soils at higher elevations shown as open circles.

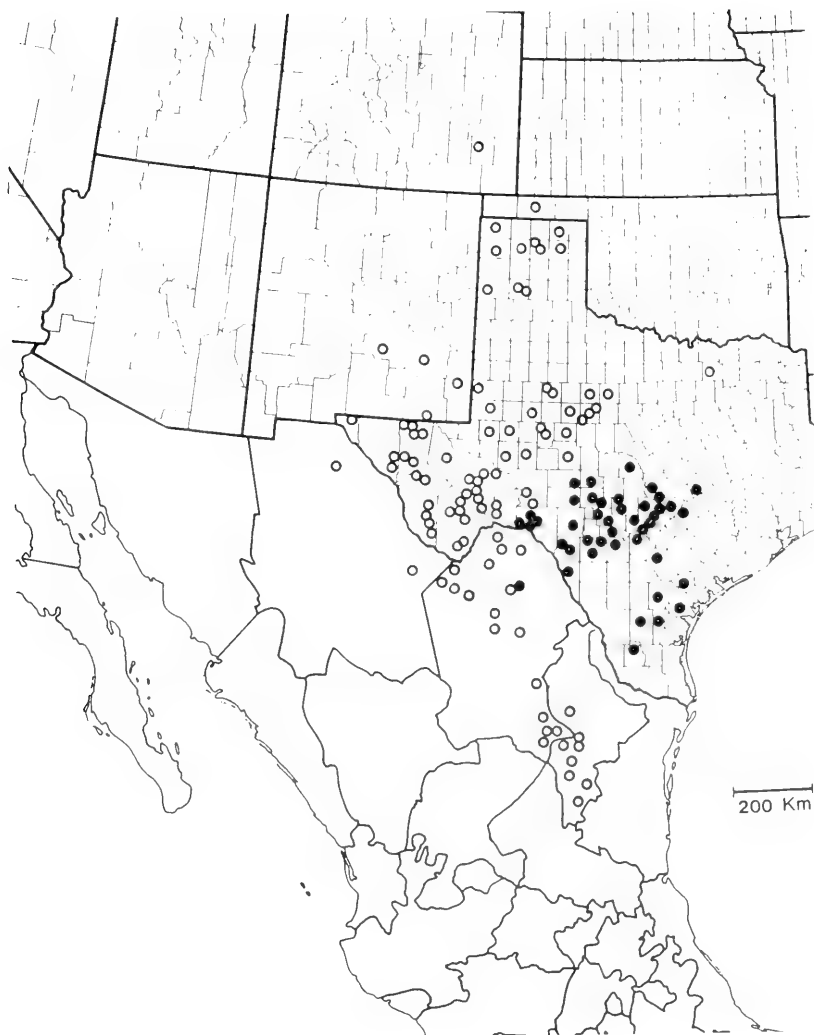


Figure 6. Distribution of *Gilia rigidula* var. *acerosa* (open disks); and var. *rigidula* (closed disks).

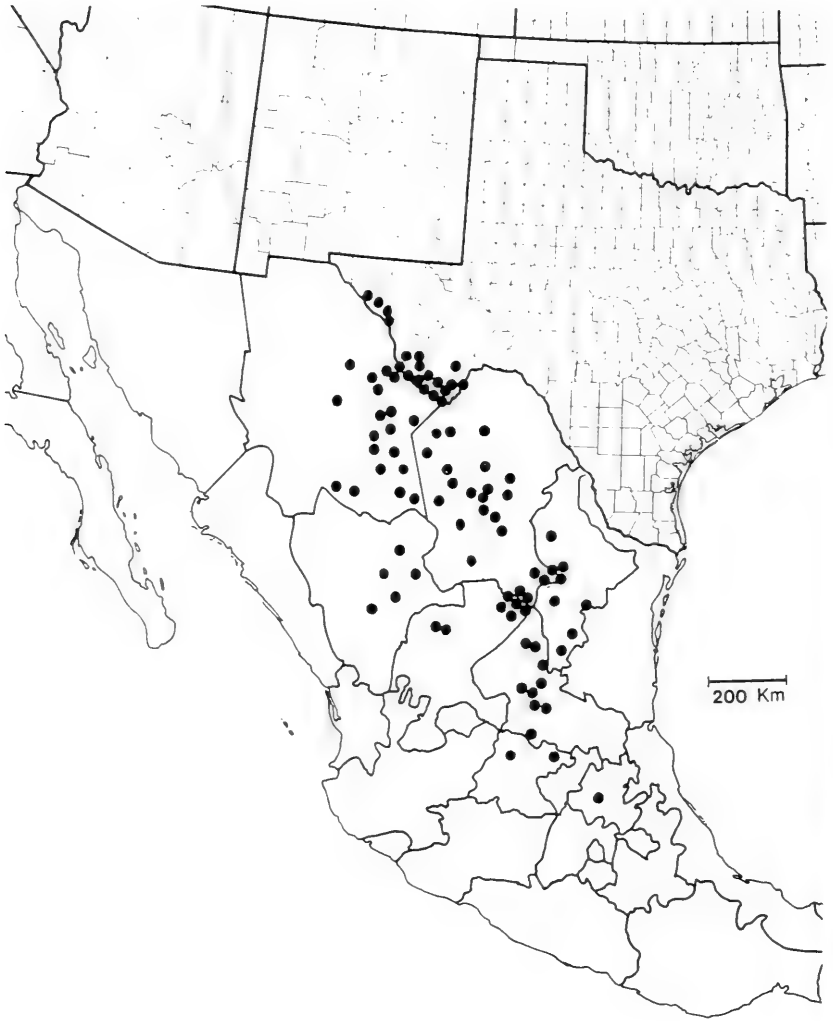


Figure 7. Distribution of *Gilia stewartii*.

Table 1 (continued).

Species	Source, reference, and/or voucher	2n number
<i>G. rigidula</i>	U.S.A. Texas: Travis	36*
var. <i>rigidula</i>	Co. (Grant 1959)	
<i>G. rigidula</i>	U.S.A. Texas: Val Verde	36*
var. <i>rigidula</i>	Co. (Grant 1959)	
<i>G. rigidula</i>	U.S.A. Texas: Brewster	10 prs
var. <i>acerosa</i>	Co. (Weedin & Powell 1978)	
<i>G. rigidula</i>	U.S.A. New Mexico: Dona	9 prs
var. <i>acerosa</i>	Ana Co. (Ward & Spellenberg 1986)	
<i>G. purpusii</i>	MEXICO. Nuevo León: Mpio. Galeana, Turner 93-154 (TEX)	9 prs

Mitotic counts.

* As modified by Grant (1959).

Gilia platyloba I.M. Johnst., J. Arnold Arb. 24:95. 1943. TYPE: MEXICO. Coahuila: Saltillo, 1898, *E. Palmer* 799 (HOLOTYPE: GH!).

This is a widespread highly variable taxon largely distinguished from *Gilia stewartii* by its larger corollas and leaves which tend to have broader ultimate divisions. Type material of *G. purpusii* has pinnately divided leaves with very broad ultimate divisions, while type material of what has been called *G. platyloba* has leaves with relatively narrow ultimate divisions. Between these extremes occur a large number of intermediates scattered over much of the range of the species. Selected examples of such intermediates follow:

Coahuila: 1 mi SW of Las Delicias, *Henrickson* 6056 (TEX); 39 mi (air) NE of Tlahualilo, *Henrickson* 12192 (TEX); ca. 67 mi (air) SW of Cuatro Ciénegas, *Henrickson* 12475 (TEX); 27 mi SE of Torreon, *Henrickson* 13226 (TEX); near Cuatro Ciénegas, *Bacon et al.* 1089 (TEX); ca. 15 mi S of Cuatro Ciénegas, *Johnston et al.* 10335 (LL); a few mi W of Las Delicias, *Stewart* 2817 (GH). Durango: Cerro de San Ignacio, *Purpus* 4595 (GH).

Most of the specimens of this species which I examined tend to have leaves with relatively narrow segments; otherwise these differ little, if at all, from specimens with broader leaf segments.

I have included under the fabric of *Gilia purpusii*, ten specimens from pine forests of Nuevo León, mostly in the vicinity of Galeana, which were collected

on gypseous soils and which I think belong to a distinct taxon (Figure 5). Such plants have generally more pinnately divided lower leaves with smaller ultimate divisions and their corollas, at least in the field, are decidedly blue, vs. pale blue or lavender as in the more typical elements of *G. purpusii*, the latter occurring at usually lower, more xeric habitats (most often with *Agave lechugilla* and associates). I have counted chromosomes of individuals of the Galeana populations and these are diploid with $n=9$ pairs (Turner 93-154, TEX). Additional study of this complex in the field is needed before formal recognition is tendered.

Gilia rigidula Benth. in DC., *Prodr.* 9:312. 1845.

Two well-marked regional varieties (Figure 6) are recognized under this taxon, as follows:

1. Leaves with their divisions mostly stiffly linear, acerose; widespread in western Texas, closely adjacent states and México. var. *acerosa*
2. Leaves with most or many of their divisions broader, scarcely acerose; central and southern Texas. var. *rigidula*

Gilia rigidula Benth. in DC. var. *rigidula*. *Giliastrum rigidulum* (Benth.) Rydb., *Fl. Rocky Mts.* 1066. 1917.

Gilia glandulosa Scheele, *Linnaea* 21:753. 1848. TYPE: U.S.A. Texas: Comal Co.: vicinity of New Braunfels, 1846, *F. Roemer s.n.* (HOLOTYPE: B, probably destroyed).

This taxon is readily distinguished from the following and is largely allopatric with it. Occasional intermediates occur in the regions of overlap.

Gilia rigidula Benth. in DC. var. *acerosa* A. Gray, *Proc. Amer. Acad. Arts* 8:280. 1870. *Gilia acerosa* (A. Gray) Britt., *Man. Bot. N.E. St.* 761. 1901. *Giliastrum acerosum* (A. Gray) Rydb., *Fl. Rocky Mts.* 699. 1917. TYPE: U.S.A. Texas: Pecos Co., Escondido Creek, 30 Jun 1852, *C. Wright* 551, exsic. no. 1645 (LECTOTYPE [selected here]: GH!; Isolectotypes: [2] GH!).

As noted in the above, a distinctive taxon well worthy of recognition. Brand (1907) recognized both *acerosa* and *rigidula* as varieties, but several workers have treated these as distinct species.

**TWO NEW GYPSOPHILIC SPECIES OF *PINGUICULA*
(LENTIBULARIACEAE) FROM NUEVO LEON, MEXICO**

Billie L. Turner

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ABSTRACT

Two new species of *Pinguicula* are described from southern Nuevo León, México: *P. jorgehintonii* B.L. Turner and *P. hintoniorum* B.L. Turner. Both are believed to be gypsophilous endemics and relate to the recently described *P. esseriana* B. Kirchner, a calciphile from Tamaulipas, México.

KEY WORDS: Lentibulariaceae, *Pinguicula*, México, Nuevo León

Identification of gypsophilous species from Nuevo León, México has revealed the following two novelties, both known only by collections of the Hinton family.

Pinguicula jorgehintonii B.L. Turner, *sp. nov.* TYPE: MEXICO. Nuevo León: Mpio. Aramberri, N of Aramberri, 1145 m, 23 Nov 1993, *G.B. Hinton et al.* 24000 (HOLOTYPE: TEX!).

Pinguiculae esserianae B. Kirchner similis sed plantis minoribus (4-6 cm altis vs. 8-11 cm), pedicellis glabris (vs. conspicue pubescentibus), et corollis plus minusve regularibus lobis plerumque brevioribus (5-15 mm longis vs. 15-20 mm) etiam calcaribus brevioribus (5-12 mm longis vs. 15-20 mm).

Annual (?) herbs 4-6 cm high. Leaves of the early rosettes oblanceolate to spatulate, 5-10 mm long, 1.0-1.5 mm wide; leaves of flowering rosettes thin, broadly obovate, 1.2-1.8 cm long, 6-8 mm wide, sparsely pubescent with multiseptate hairs. Pedicels mostly 3-6 cm long, glabrous. Calyces zygomorphic, the lobes acute, 1.0-1.5 mm long, minutely sparsely glandular-pubescent.

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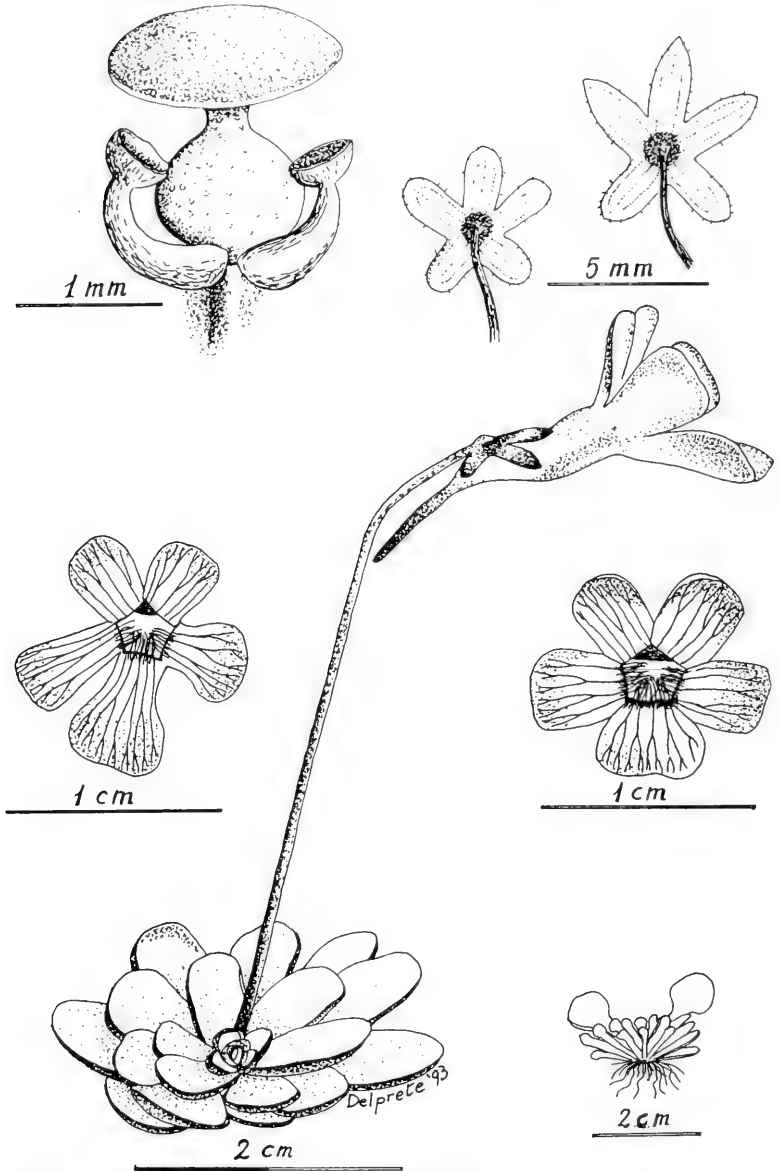


Figure 1. *Pinguicula jorgehintonii*, from holotype.

Corollas pink to purplish-white, \pm zygomorphic to nearly regular, the lobes 5-8 mm long, 5-8 mm wide, the throat (fully developed) ca. 8 mm long, ca. 6 mm across, the spurs mostly 5-8 mm long, glabrous or nearly so, the orifice of the throat with numerous slender glandular trichomes. Fruiting material not available.

ADDITIONAL COLLECTION EXAMINED: MEXICO. Nuevo León: Mpio. Galeana, road from Agua Blanca to La Purisima, pine-oak woodland, 3 Mar 1992, *G.B. Hinton et al.* 21812 (TEX).

This taxon is similar to *Pinguicula esseriana*, both species having relatively reduced thin leaves and relatively short pedicels. *Pinguicula jorgehintonii* can be distinguished from the latter by its nearly regular corollas, glabrous, shorter pedicels (3-6 cm long vs. 7-10 cm) and shorter glabrous spurs (5-8 mm long vs. 15-20 mm).

The type is accompanied by numerous excellent close up photographs of the plant. Living specimens were collected in the field and taken to the home of Jaime and George Hinton and maintained in their garden until flowering at which time the photos were taken. It is a pleasure to name this delicate species for George Hinton, grandson of the well known Mexican collector, G.B. Hinton. The collection from Mpio. Galeana (cited above) has larger flowers with longer spurs and may represent a different taxon. The above formal description is taken from type material. The Galeana plants have spurs up to 15 mm long and corolla lobes up to 15 mm long.

Pinguicula hintoniorum B.L. Turner, *sp. nov.* TYPE: MEXICO. Nuevo León: Mpio. Zaragoza, Dr. Arroyo, below Puerto Pino, gypsum hillsides, 1975 m, 16 Mar 1993, *G.B. Hinton et al.* 22661 (HOLOTYPE: TEX).

Pinguiculae esserianae Kirchner similis sed corollis malvinis vel purpuratis calcaribus glabris longioribusque (2-3 cm long vs. 1.5-2.0 cm) et pedicellis glabris differt.

Annual herbs 5-12 cm high. Leaves of the early rosettes oblanceolate, mostly ca. 1 cm long, 2-5 mm wide; leaves of flowering rosettes thin, broadly obovate, mostly ca. 2 cm long, 0.4-0.6 cm wide, sparsely pubescent with multiseptate hairs. Pedicels mostly 4-10 cm long, glabrous or nearly so. Calyxes zygomorphic, 6-8 mm across, the lobes acute, 3-4 mm long, minutely glandular-pubescent, especially along the margins. Corollas reportedly "purple" or "mauve", strongly zygomorphic, the lobes oblanceolate, 8-16 mm long, 4-9 mm wide, the throat (fully developed) 3-6 mm long, 2-4 mm across; spurs 2-3 cm long, glabrous or nearly so, the orifice of the throat sparsely pubescent with relatively few multiseptate hairs.

ADDITIONAL COLLECTION EXAMINED: MEXICO. Nuevo León: Mpio. Zaragoza, below Puerto Pino, gypsum hillside, 1840 m, 8 Feb 1989, G.B. Hinton et al. 19312 (TEX).

This taxon superficially resembles *Pinguicula esseriana* but the pedicels are glabrous (vs. densely pubescent) and the corollas are a deeper purple with longer glabrous spurs. It differs from *P. jorgehintonii* in having strongly zygomorphic purple corollas with shorter tubes and much longer spurs.

I take pleasure in naming this taxon for the remarkable Hinton family, which includes George, eponymized above, who has taken a special interest in the gypsophilous *pinguiculas* of southern Nuevo León.

ACKNOWLEDGMENTS

I am grateful to Guy Nesom for the Latin diagnoses, and him and Mark Mayfield for reviewing the manuscript. Especial thanks to D. Kearns of MO for providing literature of recently described species of *Pinguicula* from México. Piero Delprete provided the illustration.

A REVISED SYNOPSIS OF THE PINES 5: THE SUBGENERA OF *PINUS*, AND THEIR MORPHOLOGY AND BEHAVIOR

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ABSTRACT

Seven subgenera of *Pinus* are proposed on the basis of morphological and behavioral characters. The taxonomic separations are made by detaching special species or groups of species from the two older subgenera *Pinus* and *Strobus*. From subgenus *Pinus*, three "new" subgenera are detached: *Pinea*, *Sabinia*, and *Tamaulipasa*. From subgenus *Strobus*, two "new" subgenera are detached: *Gerardia* and *Balfouria*. Clear keys are given: one morphological, the other proposing behavioral differences.

KEY WORDS: *Pinus*, Pinaceae, systematics

INTRODUCTION

Starting with a brief history of the nomenclature, we recall that Koehne (1893, pp. 28, 30) keyed the pines according to only two basic groups: The *Diploxyton* or "Hard Pines" with needles having two vascular bundles, and the *Haploxyton* or "Soft Pines" having only one vascular bundle in their needles. Then Shaw (1914, pp. 1, 24, 25) accepted totally Koehne's taxonomy, but he preferred to set his key otherwise: instead of mentioning the vascular bundles, he mentioned that the said two subgenera "are even more accurately characterized" by the fact that in *Diploxyton* the bases of the "fascicle-bracts" that subtend the sheaths wrapping the lower parts of the needles are decurrent on the shoots, while in *Haploxyton*, the said bases are not decurrent on the shoots.

But recently Carvajal & McVaugh (1992, pp. 38, 50, 95) reported that that system does not hold very well. In some of the *Haploxyton* species (with only one vascular bundle), namely the Piñon Pines and *Pinus rzedowskii* Madrigal & Caballero, the situation differs. By the end of the current growing season

and during the following autumn and winter, "it is usually evident that the said bases are indeed decurrent".

Nevertheless, in accordance with well established custom, our key presented here below retains the same basic division, while specifying that 1) the distinction between the the number of vascular bundles is discarded, 2) the easy to observe distinction of the decurrence is retained, 3) but we must also look at the recently elongated section of the twig as it appears at the end of the growth season and during the next autumn (dead season).

More precisely we recall that the said "recently elongated section of the twig" is also termed "young shoot" or "current season's twig" in modern botanical literature. It must also be understood that the end of the growth season varies according to latitude and altitude. However, it can be witnessed by the state of development of the winter buds situated at the very tip of the twig. Fully grown buds, no longer increasing in size, indicate that the growth season is over.

Many manuals, including that of Krussmann (1985, p. 207), show a drawing of both striped ("furrowed") shoots due to the decurrent bases, and smooth shoots due to the non decurrent bases. Photos are also helpful, and here we present Photo 1 of the striped shoot of *Pinus sylvestris* L., and Photo 2 of the smooth shoot of *Pinus strobus* L.

Then, within each basic division, we key further subgenera, which we distinguish according to the easy-to-see characters of the cones and seeds. Yes, the mature cones are generally easy to observe and the fundamental seed types (wing present or absent, long or short, retained or not) can be found readily when one looks at the interior side of the cone scale, where the seed marks and the wing marks (if they exist) are evident.

A behavioral key is furnished to justify the morphological one. It consists of an attempt to show the interaction of both time and efficiency with morphology.

Logic-wise it is systematically more practical to divide a genus of about 98 species into more subgenera than the two previously recognized ones. We are thus proposing seven. Each "new" subgenus includes extraordinary species or groups of species, well and clearly defined.

MORPHOLOGICAL KEY

- A. Twigs (aged one year older than current season's) striped (photo 1). ..B
 - B. Cones with double concentric umbos.subgenus *Pinea*
 - BB. Cones with simple umbos.C
 - C. Umbos all around the middle of the cones are terminal, long (at least 5 mm) and stout.subgenus *Sabinia*



Figure 1. *Pinus sylvestris*, one-year old twig showing the striped rough surface constituted by the decurrent needle sheaths.



Figure 2. *Pinus strobus*, showing the smoother surface resulting from the non-decurrent needle sheaths. Even the twig's two-year old section is smooth except that the small bumps are bigger. Shaw (1914, p. 1) cautions the reader that the difference between those two characters is better seen on long, vigorous twigs because the intervals between the needle sheaths (or fascicles) are wider.

- CC. Umbos at least on the interior face of the cones are dorsal, short (at most 5 mm) and small.D
 D. Cones sessile or with short peduncle, or with long, thin peduncle turning less than 60°.subgenus *Pinus*
 DD. Cones with long, thick peduncle turning at least 60°. ..
subgenus *Tamaulipasa*
- AA. Twigs (aged one year older than current season's) smooth (photo 2). E
 E. Seeds three times longer than broad.subgenus *Gerardia*
 EE. Seed at most twice longer than broad. F
 F. Umbos terminal.subgenus *Strobos*
 FF. Umbos dorsal.subgenus *Balfouria*

ESSENTIAL BIBLIOGRAPHY

Below are listed the first valid publications of the above subgeneric names:

Pinus subgenus *Pinea* (Endlicher) Landry, *Nat. Canad.* 101(5):774. 1974.

Pinus subgenus *Sabinia* E. Murray, *Kalmia* 13:18. 1983.

Pinus subgenus *Pinus* from genus *Pinus* Linné, *Sp. Pl.* 1000. 1753.

Pinus* subgenus *Tamaulipasa P. Landry, *subgenus novum*

Curvus pedunculorum strobilorum 60° vel pluribus. Strobilorum juniorum crescentia trimestris. Folia connata. Monotypicum: *Pinus nelsonii* Shaw.

The curve of the cone peduncles turns at least 60°. Conelets mature over three months. Needles connate, *i.e.*, fused. Named after the State of Tamaulipas, berth of the species.

Pinus subgenus *Gerardia* E. Murray, *Kalmia* 13:13. 1983.

Pinus subgenus *Strobos* Lemmon, *Handb. West-Amer. Cone-Bearers*, ed. 3. 20. 1893.

Pinus subgenus *Balfouria* E. Murray, *Kalmia* 13:11. 1983.

EXCLUDED NAME

Subgenus *Ducampopinus* (A. Chevalier) de Ferré ex Critchfield & Little, U.S. Dept. Agric. Misc. Pub. No. 991. 5. 1966.

The plant represented by this name does not belong in the genus *Pinus*. It belongs to *Ducampopinus* A. Chevalier, Rev. Bot. Appl. D'Agr. Trop. 24:30. 1944. Distinguishing features are the "frog's head" apophysis, the flat, lanceolate leaves smooth on one side, scabrous on the other, the different wood anatomy (absence of ray tracheids), etc. The main reference is Gaussen (1960, pp. 40, 93, 94, and 99), who relates *Ducampopinus* to *Pinus*, but also to *Pseudolarix* and *Keteleeria*.

BEHAVIORAL KEY

- A. Branchlets with thicker, more protective bark. B.
- B. Cones take more than 2 years to mature. subgenus *Pinea*
- BB. Cones mature in about $1\frac{1}{4}$ years. C.
- C. Apophyses grow longitudinally from large conelets, about 4 cm long. subgenus *Sabinia*
- CC. Apophyses grow radially from small conelets, about 2 cm long.
- D.
- D. Non vertical cones, less effective at dispersal.
 subgenus *Pinus*
- DD. Vertical cones, better seed dissemination.
 subgenus *Tamaulipasa*
- AA. Branchlets with thin, less protective bark. F.
- F. Seed fusiform, thinner, penetrates the soil more deeply.
 subgenus *Gerardia*
- FF. Seed more ovoid, broader, penetrates the soil less easily. G
- G. Apophyses grow longitudinally. subgenus *Strobis*
- GG. Apophyses grow radially and take less time to do so.
 subgenus *Balfouria*

RECOGNITION

Due to their classicism, we have well relied on the two complete monographs of *Pinus* published during this century, those of George Russell Shaw (1914) and Henri Gaussen (1960). The monograph of Little & Critchfield (1969) contains no species descriptions, but it is also very informative.

LITERATURE CITED

- Carvajal, S. & R. McVaugh. 1992. *Pinus* L. in *Flora Novo-Galiciana* by R. McVaugh, University of Michigan Press, Ann Arbor, Michigan 17:32-100.
- Gaussen, H. 1960. Les Gymnospermes actuelles et fossiles, fasc. 6, chap. 11, généralités genre *Pinus*. Toulouse, France. 272 pp.
- Koehne, E. 1893. *Deutsche Dendrologie*. Stuttgart, Germany. 601 pp.
- Krussmann, G. 1985. *Manual of Cultivated Conifers*. Timber Press, Portland Oregon. 361 pp., 160 pl.
- Little, E. & W.B. Critchfield. 1969. Subdivisions of the genus *Pinus* (Pines). Misc. Pub. U.S. Dept. Agric. No. 1144. IV + 51 pp.
- Shaw, G.R. 1914. The genus *Pinus*. Publ. Arnold Arb., No. 5. 96 pp.

BOOKS RECEIVED

Grass Evolution and Domestication. G.P. Chapman (ed.). Cambridge University Press, 40 West 20th Street, New York, New York 10011-4211. xviii. 390 pp. Price unknown. (hardcover). ISBN 0-521-41654-X.

Fourteen authors have contributed eleven chapters to this volume. Organized into two major sections (natural diversity and domestication), the book contains discussions of taxonomic systems for grasses, photosynthetic diversification, reproduction, evolutionary trends, domestication processes, treatments of three grains (wheat, corn, and rice) as models of domestication, and trends in domestication. The book is illustrated by a color plate, and black and white photographs and drawings. The appendix consists of a grass classification system including brief descriptions to the level of subtribe, and lists of genera included in each subtribe.

INDEX TO REVIEWERS, VOLUME 75

The editor express his most sincere appreciation to the following individuals. These are persons who have reviewed papers that were submitted for publication in volume 75 of *Phytologia*. Without the willingness and diligence of these reviewers, the task of the editor would be much more difficult, and the quality of the papers published would be lessened. To each of you, I offer my most sincere thanks.

Michael J. Warnock, Editor.

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|-------------------|-------------------|
| Anderberg, A. | MacRoberts, D.T. |
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DISPOSITION OF MANUSCRIPTS RECEIVED FOR VOLUMES 74 AND 75

Manuscripts listed below include those received after examination by two or more reviewers. A note of appreciation to reviewers is found on page 81 with the list of reviewers. Manuscripts received without review are not considered for publication until review has been completed.

Manuscripts received: 132

Manuscripts accepted without revision: 9

Manuscripts accepted after revision: 110

Manuscripts returned to authors without publication: 4

Manuscripts currently under revision: 9

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Papers published: 116

Days elapsed from receipt of manuscript to publication (includes only those manuscripts selected for publication): mean = 58; range = 18-302

Days elapsed from acceptance for publication to publication of manuscript: mean = 34; range = 18-93

PUBLICATION DATES FOR VOLUME 75

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Volume 75(3): Date on title page—September 1993; Date of mailing—26 January 1994.

Volume 75(4): Date on title page—October 1993; Date of mailing—28 February 1994.

Volume 75(5): Date on title page—November 1993; Date of mailing—9 March 1994.

Volume 75(6): Date on title page—December 1993; Date of mailing—13 April 1994.

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Authors should arrange for two workers in the appropriate field to review the manuscript before submission. Copies of reviews should be forwarded to the editor with the manuscript. Manuscripts will not be published without review.

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