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For contents, see the unnumbered pages forming front cover of the separate issues.

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**FORESTIERA GODFREYI (OLEACEAE),
A NEW SPECIES FROM
FLORIDA AND SOUTH CAROLINA**

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Tallahassee, FL 32306, U.S.A.*

ABSTRACT

Forestiera godfreyi (Oleaceae) is formally described and illustrated. The new species has previously been confused with *F. acuminata* and *F. pubescens*; comparisons amongst the three are given.

Several populations of pubescent *Forestiera* in northern Florida and one in South Carolina have been difficult to place taxonomically. Johnston (1957) included them in *F. acuminata* (Michx.) Poir. in Lam. forma *vestita* (Palmer) M. C. Johnst. Typical glabrous forms of *F. acuminata* occur in our area mostly on river banks, in swampy woodlands, and on pond or lake shores, whereas the pubescent plants occur on bluffs and high hammocks underlain by limestone as well as differing morphologically. In her dissertation, Brooks (1977) included these plants in *F. pubescens* Nutt., a species from limestone hills in Oklahoma, Texas, and New Mexico. She suggested floral characters of our plants were more like those of *F. pubescens* than like those of *F. acuminata*.

R. K. Godfrey provided me additional collections and field observations incidental to his work on the trees and shrubs of north Florida. He and I believe these pubescent plants are more closely related to *F. acuminata* than to *F. pubescens* but that they are distinct from both those species. Therefore, I am describing a new species to accommodate them.

FORESTIERA godfreyi L. C. Anderson, sp. nov.

Frutices vel arbusculae deciduae dioeciae; rami novelli petioli et folia pubescentia; folia opposita ovata vel elliptica apice obtusa 5–8 cm longa 2.5–4 cm lata; flores in fasciculi umbellati redactissimi pedunculis et pedicellis pubescentibus dispositae; staminatae apetae staminibus 2–5, 2.1–4 mm longis; pistillatae apetae staminibus abortivis 3 et pistillis 2.4–3.5 mm longis; drupa matura 8–12 mm longa 8–9 mm lata glauca caerulea.

Deciduous, dioecious shrubs or small trees 2.5–5 m tall, main stem arching or leaning, branches rigid or divaricate, occasionally a few branchlets (5–7 cm long) developing enlarged bases to become spine-like, young twigs pubescent; leaves opposite, simple, ovate to lance-ovate or

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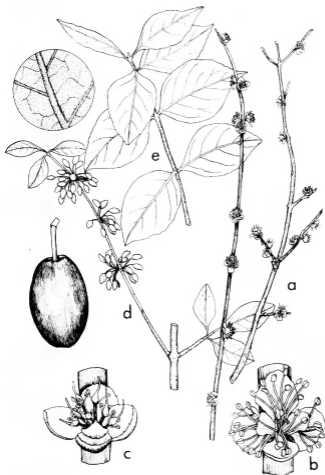


Fig. 1. *Forestiera goffreyi*: a., flowering branches, staminate on left, functionally pistillate on right; b., cluster of staminate flowers; c., cluster of functionally pistillate flowers; d., fruiting branch with immature fruits, mature fruit enlarged to left; e., branch of mature leaves (short petiolate), with enlarged portion of abaxial surface to left.

West & L. E. Arnold in 1937, fl (FLAS); JACKSON CO.: Florida Caverns State Park, L. E. Arnold & E. West in 1948, veg (FLAS), R. K. Godfrey 78536, veg (FLAS, FSU, US, USCH), R. K. Godfrey 78480a, veg (FSU), R. K. Godfrey 79326, fl (staminate: A, FSU, GA, MO, NY); JEFFERSON CO.: E side Lake Miccosukee, R. K. Godfrey 73268, fr (FLAS, FSU-2 sheets, MO), 78375, fl (staminate and pistillate: A, FSU, MO, NY, TEX, US; pistillate only: GA, NCU), 78572, fr (FSU); LEON CO.: Lake Miccosukee, E. J. Palmer 38464, veg (MO); LEVY CO.: 5 mi NE Inglis, L. E. Arnold s.n., veg (FLAS); LIBERTY CO.: Apalachicola River, S of Long Creek, R. K. Godfrey & A. Gholson 79840, veg (FLAS, FSU), S. W. Leonard et al. 7827, fr (FSU), Torreya State Park, P. Ellist 267, veg (FSU), R. K. Godfrey & A. Gholson 79648, fr (FLAS, FSU); Marion Co.: Silver River, R. W. Simon in 1984, fr (FSU). SOUTH CAROLINA. BEAUFORT CO.: Bluffton, J. H. Millichamp s.n., fr. (A).

Brooks (1977) lists the following collections that I have not seen that apparently belong to *F. godfreyi*: FLORIDA. HERNANDO CO.: 13 m NE of Brooksville, J. D. Smith 368 (GH, NY, US); COUNTY UNKNOWN: Tampa Bay, Leavenworth s.n. (GH, NY). SOUTH CAROLINA. BEAUFORT CO.: several Millichamp collections from near Bluffton.

Plants of *F. godfreyi* are less pubescent than those of *F. pubescens* but more so than those of *F. acuminata* forma *vestita*. They are also intermediate, yet distinctive, in several other features listed in Table 1, in which data from Brooks (1977) were used to supplement personal observations.

Structure of the inflorescences in *F. godfreyi* can perhaps best be described as a reduced umbel; it is a very highly reduced umbel or cyme in *F. pubescens* and a thyrses in *F. acuminata*. The new species is separated from the other two fairly well phenologically; it blooms from mid-January to mid-February, and the other two bloom in February and March. *Forestiera godfreyi* fruit matures in late April or early May, whereas fruits of the other two mature in May and June (occasionally in late April for *F. acuminata*).

Mature fruits of *F. godfreyi* are dark blue with smooth surfaces, whereas those of *F. acuminata* are reddish-purple with wrinkled surfaces (Godfrey, pers. comm.). Nuttall (1837) recorded *F. pubescens* fruit as black. Fruits of these three taxa also have distinctive sizes and shapes; measurements of dried fruits are given in Table 1 because those are represented on herbarium

TABLE 1. Comparison of vegetative and female floral features in selected *Forestiera* taxa.

FEATURE	<i>F. ACUMINATA</i>	<i>F. GODFREYI</i>	<i>F. PUBESCENS</i>
Maximum height, m	9	5	3
Leaf length, cm	(6)7-8(9)	(5)5.4-7(8)	(2.8)3.6-4.3(5)
Leaf width, cm	2-2.8(3.6)	(2.3)2.7-4	(1.3)1.5-1.6
Floral bract length, mm	5.5-6	3.8-4.1	2-3
Mature peduncle length, mm	8-11(14)	2.5-5	0-1(2)
Mature pedicel length, mm	1-2	5-7	4.5-6(10)
Flower number	9-23(27)	(5)7-10	5-15
Fruit length, dry, mm	11-12	8-9	6-7
Fruit width, dry, mm	3-4(5)	4-5	3.5-4

specimens. Fresh fruit sizes are given by Brooks (1977) for *F. acuminata* and *F. pubescens* and here in the species description for *F. godfreyi*.

Calyx development in *F. godfreyi* flowers appears to be more extensive than in the other taxa. Certainly, additional populations should be examined for enlarged, petaloid sepals as found in *Godfrey* 79326; staminate flowers of *Godfrey* 78375, *Hall* 1270, and *Murrill* in 1940 lack them.

ACKNOWLEDGMENTS

R. K. Godfrey kindly made available illustrations prepared by M. Darst; photography was done by K. Womble, and Latin diagnosis by M. Garland. The Arnold Arboretum loaned the type specimen of *F. acuminata* forma *vestita*, and the British Museum and Royal Botanical Gardens, Kew, supplied photographs of type specimens of *F. pubescens*.

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- NUTTALL, T. 1837. Collections towards a flora of the Territory of Arkansas. *Trans. Amer. Philos. Soc. n.s.* 5:139–203.

PETRORBAGIA (CARYOPHYLLACEAE) OF NORTH AMERICA

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ABSTRACT

As an outgrowth of the discovery of *Petrorbagia prolifera* (L.) P. Ball & Heyw. in Michigan, a review is presented of North American material of *Petrorbagia* (Ser. in DC.) Link, a genus revised by Ball and Heywood (1964). Four species, all introduced from Europe, are ascribed to North America based on field study and an extensive herbarium survey that included European material. The history of introduction (where known), distribution, and current status of each species is presented. Petal vein color is described as an additional character that can be used in distinguishing the three species of the *P. prolifera* complex. A partial synonymy emphasizing names used in major floristic manuals and additional synonyms not listed by Ball and Heywood (1964) is presented to establish a transition to previous treatments.

INTRODUCTION

Introduced plants often receive a very casual treatment in floristic literature, being dismissed by such phrases as "sparingly established in waste places in our range," or "found as a weed here and there in the n. part of our range" (Gleason & Cronquist, 1963). The current distribution of an introduced plant may be quite different than what is recorded in the literature, as shown by Shinnars (1965) in his study of *Holosteum umbellatum* L. Identification of aliens can be problematic since recent introductions may not be represented in regional manuals; see Shinnars (1969), Pringle (1976), and Rabeler (1980) for examples. An evaluation of the documentation, in the literature and in herbarium collections, of the genus *Petrorbagia* (Ser. in DC.) Link in North America shows a similar pattern: frequent misidentifications, species with poorly documented distributions, and a complex nomenclature. The account presented here is aimed at dispelling the confusion surrounding *Petrorbagia* as it exists in North America.

An additional problem encountered in dealing with introduced plants is the ambiguous use of terminology employed to describe their status in a given flora. Robbins (1940) defined two of the most frequently used terms, naturalized and adventive, as follows:

NATURALIZED: "introductions that have been within our borders for a long period, are rather widely distributed, multiply readily, may compete more or less favorably with native species, and behave much as in their own geographical range."

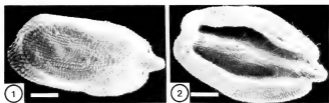
ADVENTIVE: "relatively recent introductions, less widely distributed than naturalized species and not so firmly established."

Depending on the size of the geographic unit considered, both terms could be applied correctly to three of the four species of *Petrorhagia*. For example, *Petrorhagia prolifera* (L.) P. Ball & Heyw. was first collected in North America shortly after 1800 and its current distribution suggests a naturalized species. Yet, collections from Georgia, Tennessee, and Michigan suggest that "adventive" is a better term for these populations. Because the probability of reintroduction from cultivation or other means is relatively high at a given site, a local definition of status of introduction is desirable and will be used whenever possible.

METHODS AND MATERIALS

Many of the data for this study were gathered from herbarium specimens. Five hundred and thirty-one specimens representing North American collections were examined from 82 herbaria (see acknowledgments) [all symbols for herbaria cited follow Holmgren et al. (1981) with the exception of EGV (personal herbarium of Dr. Edward G. Voss)]. Morphological and distributional data presented are based on these specimens. Measurements cited are based on dried materials, using a millimeter rule and an ocular micrometer at 10-30X magnification. For comparative study of *Petrorhagia* from its native environs, 718 Old World specimens from 26 herbaria, including BH, F, MICH, MO, NA, ND, NY, and US were consulted. Field observations and collection of *Petrorhagia* was concentrated in Michigan (1976 - 1982), with brief visits to California (1980), Texas (1980), and Maryland (1981) added for gathering data on *Petrorhagia* species occurring there. Forty-seven voucher specimens documenting this work are deposited at MSC.

The distinctive external morphology of the seeds of these species was examined using two methods. Scanning electron micrographs were taken of the seeds of *Petrorhagia prolifera* (Figs. 1 and 2) and *P. saxifraga* (L.) Link. The seeds were attached to stubs with Tube-Koat adhesive, coated with about 200Å of gold under a vacuum in a sputter coater, and photographed at 30X in an ISI Super Mini SEM. Scanning photomicrographs of the seeds of all four species (Figs. 3-6) were taken at 20X by Darwin Dale using the apparatus described in Dale (1982).



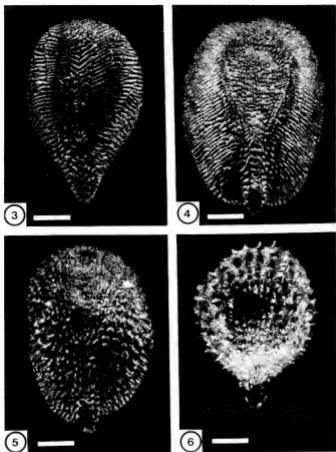
FIGS. 1-2. Scanning electron micrographs of seed surface of *Petrorhagia prolifera*, Michigan, Rabelel 154 (MSC). Scale = 250 μ m. 1. Dorsal surface. 2. Ventral surface.

HISTORICAL ACCOUNT

The most recent revision of *Petrorhagia* is that of Ball and Heywood (1964), in which 25 species, 4 subspecies, and 4 varieties are recognized. Since the appearance of this work, additional taxa totaling three species¹ (Phitos, 1966; Greuter & Mouterde, 1970; Brullo & Furnari, 1979), two varieties (Damboldt & Phitos, 1972; Huber-Morath, 1977), and one from (Gamisans, 1974) have been recognized. In addition, Greuter and Burdet have published combinations altering the rank of two Ball and Heywood combinations, raising one variety to the species level (in Greuter & Raus, 1982) and one variety to the subspecific level (in Greuter & Raus, 1984). Most *Petrorhagia* species are native to the eastern Mediterranean region, with 16 of the 29 species restricted to local areas of Greece, Crete, and/or Turkey. Only three species, each of which has been introduced in North America, have natural distributions that extend northward into Europe and, thus, out of the Mediterranean climatic regime.

One problem complicating the status of *Petrorhagia* is the name itself. Most of the species have at some time been placed in the genus *Tunica*. Ludwig published *Tunica* in 1757, but his usage of it as a substitute for *Dianthus* L. (1753) is illegitimate. In American references, authorship of *Tunica* is usually attributed to Scopoli (1772) who also used the name as a substitute for *Dianthus* (Ball & Heywood, 1964). Mertens and Koch (1831) redefined *Tunica*, distinguishing the genus from both *Gypsophila* L. and *Dianthus* on the basis of seed and petal characters. Even in this form, *Tunica* Mertens & Koch remains a later homonym of *Tunica* Ludwig, which is a

¹Two unnecessary combinations have been made: *P. kennedyae* (A. K. Jackson & Turrill) Meikle in 1977 (see Rabelel, 1984) and *P. obscurata* (Margoe & Reuter) S. M. Thomas in 1983 (see Rabelel, in press).



FIGS. 3-6. Scanning photomicrographs of dorsal seed surface of *Petrorragia* spp. Scale = 250 μm . 3. *P. saxifraga*, Michigan, Rabeler 262 (MSC). 4. *P. prolifera*, Michigan, Rabeler 154 (MSC). 5. *P. nanteuili*, California, Batigalupi, Robbins, & Hoffman 5676 (JEPS). 6. *P. ulatina*, California, Serpa s.n. (MSC).

synonym of *Dianthus* (Ball & Heywood, 1964). Therefore, *Tunica* must be rejected as illegitimate under Article 64 of the International Code (Voss et al., 1983). Maire (1963) used *Tunica* and cited "*Tunica* Boehm. in Ludw. (1760), *nom. abort.*, *emend.* Mert. et Koch (1831); *nom. conserv.*" This citation reflects the "*nomen abortivum*" approach Sprague (1927) used to define the early misapplications, which, before the Cambridge Congress of 1930, were not considered as sufficient grounds for rejecting a name as a later homonym (Lawrence, 1951), thus allowing an "*emendatum*", or redefinition, as noted by Maire. Maire (1963) went one step further in noting *Tunica* as a *nomen conservandum*. Janchen (1965) argued for conservation of *Tunica* as defined by Mertens and Koch, suggesting that *Petrorbagia* is a superfluous name. I have seen no evidence to indicate that any proposal to conserve *Tunica* has ever been formally presented.

Another name suggested for plants placed in *Tunica* is *Imperatia*, published by Moench (1794) to include one species, *Imperatia filiformis* (= *Gypsophila saxifraga*). Degen (1937) noted *Imperatia* was the correct name for all *Tunica* species except those in section *Kobltrauschia*. However, as Dandy (1957) noted, this name cannot be used since it is a later homonym of *Imperata* Cirillo, a genus in the Gramineae published in 1792 (Farr et al., 1979).

Petrorbagia was established as a genus of four species by Link (1831), based implicitly on *Gypsophila* section *Petrorbagia* as recognized by Seringe in 1824 (Ball & Heywood, 1964). Dandy (1957) considered this derivation to be a good reason to consider *Petrorbagia* as a synonym of *Gypsophila*, and suggests that the proper name for the genus is *Kobltrauschia*, a name published by Kunth (1838) for separating two species from *Dianthus*. Dandy's argument and choice of *Gypsophila glomerata* Pallas ex M. Bieb. as lectotype of the genus were rejected by Ball and Heywood (1964). They supported Britton's (1913) choice of *P. saxifraga* as lectotype of *Petrorbagia*, citing the bract condition present in *P. saxifraga* more closely fits Seringe's description than *G. glomerata* and noting that *Petrorbagia* is the Greek word for "saxifraga." I agree with the argument of Ball and Heywood and propose the lectotype as *P. saxifraga* (*vide* Ball & Heywood, Bull. Brit. Mus. (Nat. Hist.), Bot. 3:130. 1964). Dandy (1957) did not specifically mention Britton's lectotypification, giving no indication he was intentionally superseding Britton. Ball and Heywood's action also means that the Britton lectotypification cannot be superseded on the grounds that it is based solely on a largely mechanical method (see Article 8, International Code; Voss et al., 1983).

Some authors, including Holub et al. (1972), still consider *Kobltrauschia* as a distinct genus of five species. Ball and Heywood (1964) indicated the

three character states usually used to separate *Koblauschia* from *Petrorragia*, namely the annual habit, a capitulate inflorescence, and petals possessing a distinct claw and limb, are found in some *Petrorragia* species outside of their section *Koblauschia*. Evidence presented by Schaper (1936) illustrates a great degree of ultrastructural similarity in the seeds of *P. prolifera* and *P. saxifraga*, species that would be in different genera if *Koblauschia* is recognized.

TAXONOMIC CRITERIA

Petrorragia is a difficult genus to characterize morphologically since variability which can include the predominant states found in both *Dianthus* and *Gypsophila* is present in some characters (e.g., presence/absence of "epicalyx" bracts, petal structure). *Petrorragia* can be defined as having a combination of seed characters found in *Dianthus* (a straight embryo in the center of a dorsiventrally compressed seed as in Figs. 1 and 2) and calyx characters found in *Gypsophila* (few veins per sepal and scarious commissures separating adjacent sepals). The separation of *Petrorragia* from *Gypsophila* is a bit more distinct than the boundary between *Dianthus* and *Petrorragia*. As Ball and Heywood (1964) noted, the seed offers a constant feature that clearly aligns *Petrorragia* with *Dianthus* and *Velesia*. Pollen data presented by Candau (1980) suggest a similar alignment; pollen shape differences existed between species of *Dianthus* and *Petrorragia*, while pollen of *Petrorragia* and *Gypsophila* species differed in both grain size and aperture number. On the other hand, calyx characteristics offer a clear separation between most species of *Petrorragia* and *Dianthus*, except for two species of section *Diantbella* which possess calyces that approach a *Dianthus* condition, having more veins per sepal and almost lacking scarious commissures between adjacent sepals.

A similar situation exists at the species level, with some very evident characters having little if any diagnostic value. The best example of this situation involves *Petrorragia velutina* (Guss.) P. Ball & Heyw., a species introduced into California, Oklahoma, and Texas. Most plants of this species, such as those in California, show obvious glandular pubescence on the middle internodes of the stem, illustrating the "velvety" nature implied by the epithet *velutina* (Smith, 1972). The stems of plants collected in Oklahoma and Texas are almost always glabrous, a condition Ball (in Turin et al., 1964) indicated as occurring in some native populations, especially in Italy. Other morphological characters, such as sheath length, petal venation, and seed surface morphology, are very similar on plants from both areas, showing the fallability of pubescence as a diagnostic character.

The size and surface morphology of the seeds are often very useful features in distinguishing species of *Petrorhagia*, including those found in North America (Figs. 3–6). Three of our taxa, *P. prolifera*, *P. nanteuilii*, and *P. velutina* are very closely related, with *P. nanteuilii* probably derived from hybridization of *P. prolifera* and *P. velutina* sometime in the past. Inspection of the dorsal seed surfaces of these taxa offers a constant character for distinguishing them, with seeds of *P. nanteuilii* (Fig. 5) possessing the basic size and shape of *P. prolifera* (Fig. 4) and a tuberculate surface approaching that of *P. velutina* (Fig. 6).

Other morphological features are correlated with the seed characters to allow positive identification of collections in the absence of seed; these features are noted in the key and descriptions wherever possible. One apparently overlooked character useful in analyzing North American collections is the presence and pattern of darkened petal veins in three of our four species (Figs. 7–10). This character offers another feature that can be used to distinguish members of the *P. prolifera* "complex." Petals of *P. prolifera* (Fig. 8) are uniformly colored; darkened stripes are absent. Petals of *P. nanteuilii* (Fig. 9) that were examined possessed one prominent dark pink stripe on the central vein, while a very faint dark area may be present on the two veins adjacent to the central vein. At least three dark stripes were evident on *P. velutina* petals (Fig. 10) with five or more stripes occasionally present. A similar pattern of petal vein coloration on European specimens of these taxa was noted.

TAXONOMIC TREATMENT

The material presented below deals with the delimitation of the genus as it appears in North America. Synonymy present in Ball and Heywood (1964) will not be repeated here except in cases where usage in this paper or North American references warrant it. Several additional binominals noted during the study will be presented to supplement Ball and Heywood's listings. Abbreviations for major works are taken from Stafleu and Cowan (1976, 1979, 1981, 1983) where possible, with additional abbreviations taken from Tutin et al. (1976, 1980)

PETRORHAGIA (Ser. in DC.) Link, Handbuch 2:235. 1831.

Imperatia Moench, Methodus. 60. 1794.

non *Imperata* Cirillo, Pl. Rar. Neapol. 2: xxvi, t. 11. 1792.

Gypophila sect. *Petrorhagia* Ser. in DC., Prodr. 1:354. 1824.

Tunica sensu Meert. & Koch in Rühling, Deutschl. Fl. ed. 3. 3:182. 1831.

non *Tunica* Ludw., Inst. Regn. Veg. ed. 2. 129. 1757.

non *Tunica* Boehmer in Ludw., Def. Gen. Pl. ed. 3. 298. 1760.

non *Tanica* Adans., *Fam. Pl.* 2:255. 1763,

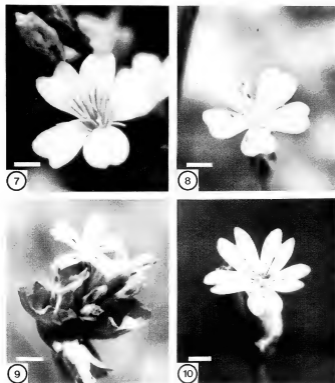
non *Tanica* Scop., *Fl. Carn.* ed. 2. 1:298. 1772.

Koblerauschia Kunth, *Fl. Berol.* 1:108. 1838.

Kaltrauschia Kunth ex Fourr., *Ann. Soc. Linn. Lyon sér. 2.* 16:345. 1868. *orb. var.*

Petroragia Link ex Kuntze, *Lex. Gen. Phan.* 427. 1903. *orb. var.*

Annual or perennial herbs. Stem internodes pubescent or glabrous, pubescence glandular or not. Leaves simple, opposite, linear to narrowly



FIGS. 7-10. Flowers of *Petroragia* spp. Scale = 2 mm. 7. *P. saxifraga*, Canfield Lake, Michigan. 8. *P. prolifera*, Grand Haven, Michigan. 9. *P. nanteuillii*, N of Cazadero, California. 10. *P. velutina*, S of Athens, Texas.

lanceolate, usually 1- or 3-veined, margin often basally scabrous or ciliate; sheath of variable length, often 1-3 times as long as broad. Inflorescence basically a dichasial cyme, bracteate or not, with flowers solitary, fasciculate, paniculate, or capitate (ours solitary or capitate). An "epicalyx" of bracts directly subtending the calyx present (ours) or absent; when present, 1-3 pairs evident. Sepals 5, fused, each 1-3 (rarely 5-7) veined, a veinless commissure separating adjacent sepals. Petals 5, clawed (ours) or not; often pink or white; apex entire to bifid; primary veins 1-3 per petal, with or without contrasting color stripes on veins of the limb. Stamens 10, anthers of ours often pink, blue, or white. Styles 2, can be stigmatic along entire length. Capsule oblong, 4-lobed, dehiscent by 4 apical teeth. Seeds dorsiventrally compressed with facial hilum and straight, central embryo; reddish-brown (immature) to blackish-brown (mature); size variable. Pollen oblate-spheroidal, porate; tectum bearing small spines (Candau, 1980). $X = 13$ and 15 (Favarger, 1966).

TYPE: *Petrorhagia saxifraga* (L.) Link, *vide* Ball and Heywood (Bull. Brit. Mus. (Nat. Hist.), Bot. 3:130. 1964.).

KEY TO *PETRORHAGIA* AND THREE RELATED
GENERA IN NORTH AMERICA

- 1 Bracts subtending the calyx present
 - 2 Commissures (veinless scarious areas) present between adjacent sepals, 1-3 veins per sepal *Petrorhagia*
 - 2 Commissures absent, 5 or more veins per sepal *Dianthus*
- 1 Bracts subtending the calyx absent
 - 3 Commissures present between adjacent sepals, seed laterally compressed with curved embryo *Gypsophila*
 - 3 Commissures absent, seed dorsiventrally compressed with straight embryo *Valezia*

The "epicalyx", although more evident than calyx commissures, is not completely diagnostic for *Petrorhagia* since 14 of 29 species do not possess subtending bracts. A key, such as that in *Flora Europaea* (Walters in Tutin et al., 1964), using calyx commissures as the first character is appropriate for separating all *Petrorhagia* species from related genera.

KEY TO SPECIES OF *PETRORHAGIA* IN NORTH AMERICA

- 1 Flowers solitary, or rarely in fascicles of 2-3 (a few cultivars); subtending bracts narrow and short, enclosing to \pm one-half the calyx 1. *P. saxifraga*
- 1 Flowers borne in capitate inflorescence (solitary in some very young plants); bracts of the inflorescence very broad and long, enclosing entire calyx of most flowers
 - 2 Leaf sheath about as long as broad, 1-2 (rarely 3) mm long; petals truncate or emarginate, no dark colored areas on vein of petal limb 2. *P. prolifera*

- 2 Leaf sheath 1.5 – 3 times as long as broad, usually 3 mm or longer; petals obcordate to bifid, 1 – 3 (or more) dark areas present on veins of limb
- 3 Leaf sheath (2)3 – 4 mm long; inner inflorescence bracts obtuse or mucronate; 2 of 3 dark veins of petal limb often faint; seeds (1.3) 1.5 – 1.8 mm long, tuberculate 3. *P. nantenilii*
- 3 Leaf sheath variable in length, (3)4 – 6(9) mm long; all inflorescence bracts mucronate; 3 (or more) dark areas on veins of petal limb; seeds 1.0 – 1.3(1.4) mm long, covered with conical papillae 4. *P. retatina*

1. PETRORHAGIA SAXIFRAGA (L.) Link, Handbuch 2:235. 1831.

- Dianthus saxifragus* L., Sp. Pl. 1:413. 1753. *Gyrophila saxifraga* (L.) L., Syst. Nat. ed. 10. 2:1028. 1759. *Tunica saxifraga* (L.) Scop., Fl. Carn. ed. 2. 1:300. 1772. *Silene tunica* E. H. Krause in Sturm, Deutschl. Fl. ed. 2. 5:107. 1901. *Imperatia saxifraga* (L.) Degen, Fl. Veleb. 2:94. 1937. *Kobrawiachia saxifraga* (L.) Dandy, Watsonia 4:42. 1957. TYPE: not seen. LINN 579.25 (photo at FI; microfiche at US!) is authentic material. See Savage (1945) for explanation of panned names of 579.24 and 579.25. Described from Switzerland, France, and Germany.
- Gyrophila scabra* Schultes ex Steudel, Nomencl. Bot. ed. 1. 386. 1821. *Tunica saxifraga* var. *scabra* (Steudel) Schur, Oesterr. Bot. Z. 19:16. 1869. Original material not seen.
- Gyrophila permixta* Guss., Suppl. Fl. Sic. Prodr. 120. 1832. *Tunica permixta* (Guss.) E. & A. Huet in Hohen., Bot. Zeitung (Leipzig) 16:295. 1856. *Tunica saxifraga* var. *permixta* (Guss.) Nicotra, Prodr. Fl. Messan. 122. 1883. TYPE LOCALITY: SICILY, original material not seen (NAP?).
- Gyrophila arenicola* Dufour, Bull. Soc. Bot. France 7:240. 1860. *Tunica arenicola* (Dufour) Nyman, Consp. Fl. Eur. 100. 1878. TYPE LOCALITY: SPAIN; "frequens in arena maritima valentina (Debesa)", original material not seen.
- Gyrophila rigida* Sibth. & Smith, Fl. Graeca IV. p. 75, t. 382. 1823, non L., *fula* Gürke in Richter (1903) and Degen (1937). *Imperatia bithynica* Degen, Fl. Veleb. 2: 95. 1937. TYPE LOCALITY: TURKEY, Olympus Bithynus, original material not seen.

Perennial, sometimes woody at base. Stems much branched near the base, 5 to 40 cm [to 45 cm in Ball and Heywood (1964)] tall; internodes glabrous above, scabrous below. Leaves linear, 5 – 20(30) mm long, 1(2) mm or less wide, 1-veined, margin basally ciliate; leaf sheath 1 mm or less long, about as long as broad. Flowers solitary (fasciculate in some cultivars and var. *glomerata*), terminal, 10 mm or less long, on long peduncles. Subtending bracts 2(4), ovate, membranous, mucronate, 1-veined, enveloping up to one-half of the calyx. Sepals 1-veined, margin often ciliate. Petals clawed, limb white to pink, claw often white; primary veins 3 per petal, often dark pink near base of limb; apex obcordate. Anthers pink or white. Seeds with tuberculate surface, (0.8)1.0 – 1.2(1.3) mm long, 0.5 – 0.8(1.0) mm broad. $2n = 30, 60$ (Favarger, 1966). Figs. 3, 7, and 11.

All North American collections I have seen are referable to *P. saxifraga* var. *saxifraga*. Variation within var. *saxifraga* is formally recognized in a

few works [Soó (1970) listed six forms and a "variant"], although it is dismissed by Ball and Heywood (1964) as being of questionable significance. Cultivars, for the most part, are not significantly different from naturalized collections, although some "modifications", such as doubled petals, do occur.

Schlisling and Iltis (1962) cited two common names for this plant; Tunic Flower and Coat Flower, both names referring to the bracts surrounding the flower. Britton (1913) listed Saxifrage Pink and Tunica as common names. A translation of the binomial reveals that both parts are derived from words meaning "rockbreaking", *Petrorhagia* from Greek, *saxifraga* from Latin, alluding to its prevalence in rock crevices (Smith, 1972).

FLORAL BIOLOGY: Meusel and Muhlberg (1979) reported that *P. saxifraga* is strongly protandrous and suggested that self-pollination is hardly possible. Knuth (1908) noted that the style usually matures late enough to prevent selfing. The flowers produce abundant nectar and are visited mainly by small bees, flies, and butterflies (Meusel and Muhlberg, 1979).

ECOLOGY AND DISTRIBUTION: Ball and Heywood (1964) summarized the native range as "Central and southern Europe and south-western Asia", with naturalized introductions noted for Sweden and Great Britain.

Within North America, most records represent either obvious cultivations or adventive populations (see Fig. 13). From label data, it is clear that many collections were made along roadsides, often from dry sandy areas, while others represent plants in lawns, waste areas, field edges, sandy forest slopes, a lake edge, and gravelly banks. Flowering reported from June to October, the last flowering possibly limited by first autumn frost.

HISTORY OF INTRODUCTION: *Petrorhagia saxifraga* appeared in North America just over 100 years ago, with initial collections being made along roadsides at College Point and Flushing (Queens Co.), New York (Schrenk in 1876, AC, CU). According to a note on the AC specimen, the populations remained "well established" there through 1879. The next collections seen were made at London, Ontario in 1886 and 1887, cited by the collectors (Burgess in 1886, CAN, GH; Dearness in 1886 and 1887, MTMG) as introduced and spreading in gardens, waste places, and roadsides.

A look at popular manuals will reveal that these sites are often the only ones listed for *P. saxifraga*, a practice started by Robinson (1897) and Britton (1897) and continued by Maguire (1950, 1952). Robinson and Fernald (1908) listed these sites in the 7th edition of Gray's Manual, but Fernald (1950) omitted them from the 8th edition along with any mention of the genus or the species! After studying extant collections, it is readily

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 UNIVERSITY AND Jepson Herbaria



Number of plants: 1
 Date: 1952
 Locality: ...
 Collector: ...
 Number of specimens: 1
 Date: 1952

11



Number of plants: 1
 Date: 1952
 Locality: ...
 Collector: ...
 Number of specimens: 1
 Date: 1952

12

FIGS. 11–12. Representative herbarium specimens of *Petrorragia* spp. Scale = 5 cm.
 11. *P. saxifraga*, Rabeler 313 (MSC). 12. *P. prolifera*, Rabeler 314 (MSC).

apparent that, by 1950, this expression of range was grossly inadequate; *P. saxifraga* had been collected in at least 16 additional states (19 including literature references) and 2 provinces (records of six states and one province are obvious cultivations) by that date!

CURRENT STATUS: The list of specimens cited below includes the earliest and most recent records seen from a given state or province that are not thought to be cultivated.

It appears that the non-cultivated range of the species is much smaller today, with post-1960 collections seen only from only Michigan, Virginia, Wisconsin, and Ontario. In Michigan, *P. saxifraga* has been collected in 10 counties since 1960, almost all specimens representing naturalized populations. It is extremely abundant as a lawn and roadside weed in the Manistee area, where the first collection dates from 1924.

Post-1960 collections of cultivated plants were seen from Massachusetts (*Wiegel and Hodgeon 12043*, NHA), Michigan (*Bourdo 4056 & 5865*, MCTF; *Rabaler 308*, MOR, MSC, NA), Minnesota (*McWilliams* in 1966, NA), and New York (*Stites* in 1978, BH), indicating the potential for growth and possible escape in other areas. Since *P. saxifraga* is available commercially as a landscape plant, it is difficult to predict when or where the next escape may take place, and whether or not an adventive population will result.

Representative specimens: UNITED STATES. IDAHO. KOOTENAI CO.: Sandy lake shore, Coeur d'Alene, Oct 1914, *Rat 446* (WTU). ILLINOIS. CHAMPAIGN CO.: Roadside, Champaign, 28 Jun 1950, *Elkin 147* (ILL). COOK CO.: South Park, Jun 1887, *Oblendorf s.n.* (F). MAINE. KNOX CO.: Rockport, 23 Aug 1930, *Steyermark 4163* (F). MASSACHUSETTS. BRISTOL CO.: Rockery, North Easton, 1 Jul 1916, *Schweinfurth s.n.* (LL). WORCESTER CO.: Dooryard, Leominster, 9 Aug 1943, *Clark s.n.* (NEBC). MICHIGAN. DELTA CO.: Gravel bank fill, Fishdam River, 3 mi E of Isabella, T41N, R18W, S33, SW ¼, 11 Sep 1981, *Rabaler 670* (FLAS, MIN, MSC, RM, VT); 12 Jul 1982, *Rabaler 723* (MSC, UTC, VDB); 17 Aug 1982, *Hewson 1436* (MICH). KENT CO.: Grand Rapids, 22 Jun 1899, *Stevenson s.n.* (MICH). MINNESOTA. ST. LOUIS CO.: Wooded slope at Vermillion Dam, 7 Aug 1940, *Lakela 3992* (DUL, MIN, MO, SMU, UC). NEW JERSEY. CAPE MAY CO.: Roadside, Cold Spring, 12 Aug 1915, *Brown s.n.* (PH); roadside fence-row, Cold Spring, 25 Sep 1920, *Brown s.n.* (PH). NEW YORK. QUEENS CO.: College Point, 1876, *Schrenk s.n.* (AC); Flushing, L. I., 1876, *Schrenk s.n.* (CU). TOMPKINS CO.: Lawn weed, Cornell Heights, Ithaca, 17 Jul 1940, *Eames, Flora of New York 20162* (CU). PENNSYLVANIA. MONTGOMERY CO.: Pennsburg, 28 Jun 1919, *Brendle s.n.* (PH). SOUTH DAKOTA. LAWRENCE CO.: Glade on talus slope, alt. 3900 ft, 11 Aug 1942, *Bennett 1521* (MO). VIRGINIA. PAGE CO.: Old homesite, Skyland, 4 Jul 1965, *Mazzo 1084* (NA); 25 Sep 1966, *Mazzo 1781* (NA). WISCONSIN. COLUMBIA CO.: Outskirts of a cornfield and roadside, Okee, T10N, R8E, S7, 29 Sep 1967, *Dawes s.n.* (WIS). SHEBOYGAN CO.: Roadside, Sheboygan, Aug 1912, *Gaust s.n.* (WIS).

CANADA. BRITISH COLUMBIA. Prince George, Sep 1937, *Travis s.n.* (DAO). ONTARIO. MIDDLESEX CO.: Gardens and waste places, London, Sep 1886, *Burgess s.n.* (CAN).

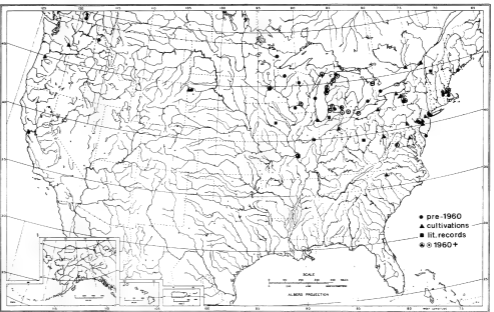


FIG. 13. North American distribution of *Peromyscus saxifraga*.

SIMCOE CO.: Waste soil near grain elevator, Collingwood, 9 Sep 1978, A. A. and S. A. Reznick 4866 (MICH, [TRT]).

Records mapped from literature (specimens not seen): IOWA. Grinnell(?) (Conard, 1943). MASSACHUSETTS. Worcester (Potter & Woodward, 1935). MICHIGAN. Niles (Beal, 1908). OHIO. Hocking County in 1930 (Cusick & Silberhorn, 1977). VERMONT. Morrisville (Dole, 1937).

Literature records rejected: DISTRICT OF COLUMBIA. Brookland (McAtee, 1940; Hermann, 1946). This record is based on a misidentified collection of *Gypsophila muralis* (Ulke s.n., without date, US).

2. *PETRORHAGIA PROLIFERA* (L.) P. Ball & Heyw., Bull. Brit. Mus (Nat. Hist.), Bot. 3:161. 1964.

Dianthus prolifer L., Sp. Pl. 1:410. 1753, nec Foesskål, Fl. Aegypt. - Arab. xv. 1775, nec Sibth. & Smith, Fl. Graec. Prodr. 1:285. 1809, *fula* Graebner and Graebner (1921). *Tunica prolifer* (L.) Scop., Fl. Carn. ed. 2. 1:299. 1772. *Kobtrauschia prolifer* (L.) Kunth, Fl. Berol. 1:109. 1838. *Cylichnanthus prolifer* (L.) Dulac, Fl. Hautes-Pyrénées, 261. 1867, *nom. illeg.* *Gypsophila prolifer* (L.) Arcang., Comp. Fl. Ital. ed. 2. 303. 1894. *Silene prolifer* (L.) E. H. Krause in Sturm, Deutschl. Fl. ed. 2. 5:107. 1901. LECTOTYPE (Thomas, 1983): ex Horti Uppsal. (S, microfiche at US). See Thomas for argument rejecting earlier lectotypification of Ball and Heywood (1962) with LINN 581.7 (photographs at BH!, Fl, GH!, NY!). Described from Germany and southern Europe.

Dianthus diminutus L., Sp. Pl. ed. 2. 1:587. 1762. *Caryophyllus diminutus* (L.) Christm., Vollst. Pflanzensyst. 6:563. 1780, *fula* Merrill (1938), *nom. illeg.* *Kobtrauschia diminutus* (L.) Reichb., Icon. Fl. Germ. Helv. 6:43, t. 247, f. 5008. 1844. TYPE: not seen. Described from Germany.

Dianthus carolinianus *sensu* Torrey & A. Gray, Fl. N. Amer. 1(2):195. 1838, non Walter. TYPE: from South Carolina, Walter (?) (BM, photo at A!).

Annual. Stems simple or branched near the base, (6) 11–60 (commonly 30) cm tall; internodes mostly glabrous, middle internodes may be slightly scabrous. Leaves linear to linear-oblong, 10 mm long, 2(3) mm or less wide, 3-veined, margin scabrous; leaf sheath 1–2 (rarely 3) mm long, as long as broad, or at lower nodes, often broader than long. Inflorescence capitate (occasionally reduced to one flower), 10 mm or more long, usually 5–20 mm broad. Subtending bracts broadly ovate, brown-scarious, many veined, enclosing the flowers; tips of bracts obtuse, or outermost may be mucronate. Sepals 3-veined, outer surface not scabrous, margin glabrous. Petals clawed, pink or slightly purplish (rarely white); primary veins 1 per petal, dark coloration near base of limb absent; apex truncate or emarginate. Anthers pink or blue; pollen 40 μ m in diameter, apertures of 4 μ m (Candau, 1980). Seeds with fine to coarse reticulate surface, (1.1) 1.3–1.6(1.8) mm long, (0.7)0.8–1.0(1.1) mm broad. $2n = 30$ (Ball & Heywood, 1962; Thomas & Murray, 1983). Figs. 1, 2, 4, 8, and 12.

Variance shown in the above characters is, for the most part, distributed throughout the range, although slightly scabrous internodes and finely reticulate seeds are more prevalent in plants from New Jersey, Pennsylvania, and Virginia. I agree with Ball and Heywood (1964) in not applying subspecific categories, such as those used by Briquet (1910) and Maire (1963) to describe leaf margin texture variation, or the seven forms and two "variants" listed by Soó (1970), to segregate minor variants within *P. prolifera*.

Britton (1913) gave three common names for *P. prolifera*: Proliferous Pink, Childing Pink, and Childing Sweet William. Smith (1972) defined the epithet "prolifera" as: "Proliferous, i.e. free flowering or producing side shoots or buds in order to increase." This is an appropriate description of the plant and "proliferous" can be extended to include the relatively large quantity of seed produced by each plant.

FLORAL BIOLOGY: Thomas and Murray (1981) described two "races" of *P. prolifera* after finding selfing and outcrossing populations that were reproductively isolated from each other. Subsequently, Thomas (1983) treated the large-flowered outcrossing plants as a separate "sister" species (*P. obcordata*), leaving *P. prolifera* as having small, autogamous flowers that produce little nectar and are homogamous, or as in one of their study populations, protandrous. I have observed distinctly protandrous flowers with protruding stamens and (later) style branches at Grand Haven, Michigan, suggesting that some outcrossing may take place from chance insect visits.

ECOLOGY AND DISTRIBUTION: Ball and Heywood (1964) stated the native distribution as "Central Europe, mountains of southern Europe, Caucasus, Turkey (northern Anatolia), mountains of western North Africa", with introductions noted in Great Britain.

Nearly all collections of *P. prolifera* within North America are from the southeastern portion of the continent (see Fig. 14), most being gathered from roadside localities, either in sand, gravel, or shale fill. Dry fields and pastures are mentioned as collection sites from Pennsylvania to North Carolina, while seven Virginia collections are of plants found growing in cinder railroad ballast. The calcareous soils of the Ozark region may be a factor in the spread of *P. prolifera* away from the roadside and into the glades and pastures in northern Arkansas and southern Missouri. Flowering reported from late May through late September.

HISTORY OF INTRODUCTION: *Petrorhagia prolifera* apparently first appeared in North America near Philadelphia, Pennsylvania shortly after 1800. The earliest specimens seen bear the name *Dianthus carolinianus*, a

name published by Walter (1788) in his *Flora Caroliniana*. A problem develops when one attempts to determine what plant Walter had in mind for *D. carolinianus*. *Index Kewensis* (Hooker & Jackson, 1895) lists *D. carolinianus* as a synonym of *Dianthus armeria* L. Asa Gray inspected Walter's herbarium in 1839 (at the time in possession of John Fraser in England) and wrote "his '*Dianthus carolinianus*' is *Frasera!* in fruit." (Britten, 1921). In his monograph of *Dianthus*, Williams (1893) considered *D. carolinianus* a synonym of *Dodecatheon Meadia* L. Britten (1921) reached the same conclusion when he investigated Walter's herbarium, stating "but the *Dianthus* is not *Frasera*, but *Dodecatheon Meadia*." A translation of Walter's description of *D. caroliniana* is not of much help: "with flowers clustered on long peduncles, tube scales smaller by one-half." (Walter, 1788), characteristics which could apply to fruiting material of all of the above-mentioned taxa! An inspection of the set of photographs of Walter's herbarium at A (Schubert, 1946-47) revealed a small specimen in the upper left corner of page 40 inserted in a small piece of paper labeled "334 *Dianthus carolin.*" It is indeed *Dodecatheon meadia*, consisting of several erect capsules and attached calyces and a 7.5 cm section of the scape.

Torrey and Gray (1838) listed *D. carolinianus*, citing South Carolina for its range and add the following note: "*D. prolifer* was sometime since cultivated at Bartram's garden under this name", connecting the name to early collections from the Philadelphia area. The actual dates of cultivation of *P. prolifer* at Bartram's garden remain a mystery. John Bartram started a seed exchange with a number of European botanists in the late 1730's, trading native American plants for those of Europe for cultivation in his garden. This activity continued into the 1830's under the guidance of Bartram's children after his death in 1777 (Berkeley & Berkeley, 1982) and would provide a logical explanation of the appearance of *P. prolifer*. The earliest evidence of its cultivation is the specimen at PH collected by S. W. Conrad labeled "*Dianthus carolinianus* Walter. At, and in the vicinity of Bartram's Garden." This collection would have been made prior to 1815 based on details of Conrad's life and his use of Linnaean classification (Decandria Digynia) on the label (Harshberger, 1899).

The earliest dated collection seen was that of E. M. Durand (*Durand* in 1837, GH) on which he noted: "It seems to be perfectly naturalized on that spot [a rock near the garden] and is not found in the garden itself." On both this specimen and an undated collection from South Carolina (*Durand*, NY), Durand questioned his determination of *D. carolinianus*, with the South Carolina specimen labeled: "*D. prolifer* of Europe and believe it to be the same, introduced." The site of the first naturalized population referred to by Durand is most likely the same one that at least 10 collectors visited in



FIG. 14. North American distribution of *Paroschizus prolixus*.

the next 60 years; a hill, described as "dry, micaceous-sand" (C. E. Smith, NY), along the Schuylkill River, near Bartram's garden and Gray's Ferry. It is not known how long this population existed, but the most recent collection seen was dated 21 October 1891 (Crawford, PH).

Other pre-1900 collections exist for Delaware (1896-97), Maryland (1887), New Jersey (1871), New York (Britton, 1879, specimens at SIM?), and Ohio (1891-96).

CURRENT STATUS: The specimens cited below include the earliest and most recent records seen from a given state excluding collections of cultivated material. The distribution of post-1960 collections (Fig. 14) is far different from that listed by major manuals. Fernald (1950) stated "sandy fields and roadsides, local, s. N.Y. to Del., Va., Ky. and O.", which, except for the Ohio reference, corresponds to the distribution of pre-1949 specimens present in the loan received from GH for this study. Maguire (1952) considered *T. prolifera* "sparingly introduced in waste places, N.Y. to S.C. and Cal." This description nearly matches the pre-1952 specimens seen from NY, the institution Maguire was associated with at that time (the California specimens at NY are *P. velutina*, although labeled *T. prolifera*; one Idaho collection (cultivated?) labeled *D. armeria*, one Ohio collection not mentioned). Both treatments generalize the distribution by inserting "to" and thus connecting widely separated local populations, making the species seem more widespread than it may actually be. The reader is referred to three similar situations recorded elsewhere (Shinners, 1965; Shinners, 1969; Rabeler, 1981) which treat discontinuities between current ranges and those given in the literature.

In light of the discrepancies noted, a few general conclusions are in order. Several states should be dropped from previously published ranges; California (the origin of the Congdon collection (1902) remains a mystery), Ohio (last collected there in 1896), South Carolina (record relies on Durand collection of early 1800's), and Texas, as listed by Shinners (1969) and Correll and Johnston (1970), since all Texas collections are in fact *P. velutina*. Several areas might be retained, since populations could exist there in spite of available records; Delaware (last collected there in 1897, but present in all neighboring states; see Phillips (1978) for opposing view), Kentucky (single record in Braun (1943) based on a 1941 collection), New York (several collections on Long Island, 1920-48), North Carolina (1949 collection mapped in Radford et al. (1965), but not discussed by the collectors in their report on additions to the flora of North Carolina found in 1949 and early 1950 (Fox, Godfrey, & Blomquist, 1950), or in Radford et al. (1968)), and West Virginia (single report by Core (1941), but Monroe

Co. is close to "active" Virginia populations).

Post-1960 records define a pattern of scattered, local populations from New Jersey southwestward into Virginia and then generally westward into Arkansas and Oklahoma, along with disjunct populations in western Michigan [discussed in more detail in Rabeler (1980)]. The southwestward expansion has taken place for the most part since 1930, with an invasion into the westernmost states occurring since 1950. The irregular timing of appearance in adjacent states makes a theory of multiple introduction into the southeast far more plausible than trying to derive all these populations from the initial introduction in Philadelphia.

Several collections seen indicated that *P. prolifera* has been present at some sites for over 30 years, suggesting naturalization has taken place in areas of Maryland, Pennsylvania, and Virginia. The absence of *P. prolifera* from a recent survey of roadside vegetation at selected sites in southwestern Virginia (Schmaltz, 1981) reinforces the local distribution of *P. prolifera*, even in the vicinity of naturalized populations, since it has been reported at least once in five of the seven counties included in the study. Other post-1960 collections represent adventive occurrences, especially records in three states (Georgia, Michigan, and Tennessee) where the earliest specimen seen was collected after 1975.

How then does *P. prolifera* get around? Soó (1970) listed anemochory, endozoochory, and autochory as dispersal mechanisms of *P. prolifera* in Hungary. *Petrorhagia prolifera*, as well as *P. nanteuillii* and *P. velutina*, would be defined by Van der Pijl (1982) as wind-ballistics, with seeds falling from the capsules as the long, wiry stems sway in the wind; a combination of anemochory and autochory would be ideal in open areas such as road shoulders. Ridley (1930) reported Dymes has found that one of the common seeds in an ant grainery in Italy was *P. saxifraga*; similarities between the seeds of *P. saxifraga* and the above-mentioned species suggest that harvester ants may be responsible for occasional short distance dispersal events.

The presence of "roadside" on a large number of labels suggests that occurrences of *P. prolifera* may be partially "transportation-related". Frenkel (1970), in a study of roadside vegetation in California, listed several attributes present in many roadside plants, some of which apply to *P. prolifera*: annual habit; small, light, non-appendaged seeds produced in abundance; and tolerance of high light intensity. Wofford et al. (1977) suggested that *P. prolifera* has appeared in Tennessee as a contaminant of grass seed planted along Interstate 40; contaminated seed is likely responsible for the appearance of *P. velutina* in Texas (Shinners, 1969; Correll & Johnston, 1970) and possibly some of the plants in Michigan (Rabeler, 1980). This situation may easily have occurred in other areas along the

recently constructed interstate highways of the region, a system primarily built since 1960.

Some roadside populations of *P. prolifera* may be unintentionally enlarged if the shoulder area is mowed in mid-summer, since plants would have open capsules of seed awaiting dispersal. This notion became evident after observing a tremendous increase in both number of plants and the area they occupied along an infrequently mowed Michigan roadside 5 years after discovering the population, an increase that I find hard to explain if only "natural" dispersal is invoked.

Representative specimens: UNITED STATES. ALABAMA. FRANKLIN CO.: Roadside, Co. 79, 1 mi N of AL 24 jct., Russellville, 28 May 1967, *Baskin, Caudle, and Turner* 582 (VDB); Roadside, Co. 83, 0.8 mi N of AL 24 jct., E of Russellville, 5 Jun 1981, *Godfrey, Gholson, and Webb* 78789 (FSU). MARION CO.: Sandy clearing by AL 17, N of Hamilton, 20 Jul 1970, *Kral* 40202 (AUA, GH, MICH, MO, OS, SMU, TENN, UNA, US, VDB). ARKANSAS. FULTON CO.: Old pasture near creek, Mammoth Spring, 17 Jun 1951, *Moore* 510472 (UARK); beside US 63 at Trace Creek, T21N, R5W, S4, 4 Jul 1968, *Thomas* *Bio. (Bot.)* 451 class 10046 (A, CHSC, CM, NCU, NLU(2), NY, SMU, TENN, USF, WTU). WASHINGTON CO.: Along Hwy 71, 6 mi S of Westfork, 8 Jul 1975, *Merbs* 127 (UARK). CALIFORNIA. MARIPOSA CO.: Mariposa Creek, 15 Jun 1902, *Congdon s.n.* (MIN, US). DELAWARE. SUSSEX CO.: Sandy fields and roadsides, S. Milford, 16 Jul 1896, *Comms s.n.* (GH, NYS); road to Slaughter Beach, 12 Aug 1897, *Comms s.n.* (PH). GEORGIA. GREENE CO.: Pasture with granite outcrops, W of Siloam, 5 Jul 1983, *Allison* 1836 (GA). ROCKDALE CO.: Roadside granitic flatrock, Conyers, 28 Jul 1983, *Allison* 1845 (GA). IDAHO. BONNER CO.: Gravel slope, Sandpoint Substation, 11 Sep 1932, *Christ* 2093 (NY). KENTUCKY. ROBERTSON CO.: Roadside, Kentonville [Kenton town?], 8 Jul 1941, *Braun* 4041 (GH, US). MARYLAND. CALVERT CO.: Sandy roadside fill, 1.2 mi S of Bowens, 13 Jun 1981, *Rabaler* 378 (FLAS, MARY, MSC). KENT CO.: Sandy fields near Millington, 18 Jun 1887, *Brinton s.n.* (PENN, PH). MICHIGAN. MUSKEGON CO.: Beside paved area, main entrance, P. J. Hoffmaster State Park, 18 Jul 1983, *Wells and Thompson* 83221 ([BLH], MSC). OTTAWA CO.: Kitchel Dune, Grand Haven, 8 Aug 1976, *Atwood, Bauman, and Rabaler* 409 (MSC); sandy roadside, S edge of Kitchel Dune, [Nature Conservancy Preserve] T8N, R16W, S20, SW 1/4, 9 Aug 1979, *Rabaler* 314 (CAN, DAO, GA, HSC, MICH, MSC, NY, SMU, WAT). MISSOURI. GREENE CO.: Open limestone barrens, Kissick, T28N, R21W, S19, 6 Jun 1982, *Summers* 1025 (MO). STONE CO.: Rocky places near pasture, 5.5 mi SE of Shell Knob, T22N, R24W, NE sect. 18, NW sect. 17, 13 Jul 1956, *Steyermark* 81924 (F, GH, ILL, MO, UMO). NEW JERSEY. CAMDEN CO.: Roadside, Haddonfield, 3 Jun 1871, *Parker s.n.* (F, GH, MO, PENN, PH). CUMBERLAND CO.: Fallow fields, NJ 548, near Mauricetown, 31 Jul 1975, *Reel* 98005 (NCU). NEW YORK. SUFFOLK CO.: Dry sand-pit, Southampton, 18 Aug 1920, *St. John* 2878 (CU, GH, NYS, PH, US); Noyack, 16 Sep 1948, *Latham* 28248 (NYS). NORTH CAROLINA. ASHE CO.: Dry hillside pasture, near US 221, N of Laurel Knob Gap, 7 Sep 1949, *Fox and Godfrey* 3368 (GH, NCSC, NY, TENN, US). FORSYTH CO.: Edge of field near Mt. Carmel Church, 19 Jul 1935, *Correll* 2702 (NA). OHIO. CUYAHOGA CO.: Cleveland, May 1891, *Beardslee s.n.* (MICH, NY(2)); Cleveland, 8 Aug 1896, *Starr s.n.* (OS). OKLAHOMA. CHEROKEE CO.: Open roadside, OK 51, 7.2 mi E of Hulbert, 2 Jun 1951, *Wallis* 533 (OKLA); Roadside, OK 10, 4.5 mi NE of Talequah, 30 Jun 1976, *Taylor* 22206 (DUR, NLU). PENNSYLVANIA. BERKS CO.: Roadside, NE of Virginsville, 16 Jul 1965, *Wilens* 11659 (PENN).

PHILADELPHIA Co.: At, and in vicinity of Bartram's Garden, without date, *Conrad s.n.* (PH); below Bartram's garden, 18 Jul 1837, *Durand s.n.* (GH). SOUTH CAROLINA. CHARLESTON Co.: Vicinity of Charleston, without date, *Durand s.n.* (NY). TENNESSEE. CUMBERLAND Co.: Roadside, E lane of I-40, near mile 313.8, 28 Jun 1976, *Phillippe, Wofford, Webb, Rader, and Smith 51790* (TENN); 13 Jun 1977, *D. H. and B. Webb 971* (TENN). VIRGINIA. BATH Co.: Weedy railroad margin at Copeland, 23 June 1982, *Wiesboldt 4359* (VPI). FAUQUIER Co.: In quarry lane S of US 55, 8 Jun 1941, *Allard 8889* (CM, F, GH, MO, NY, US, VPI). MONTGOMERY Co.: Pasture, near Blacksburg, 8 Jun 1930, *Morton 1838* (US).

Records mapped from literature (specimens not seen): MARYLAND. Annapolis (Shreve, 1910). NEW YORK. Staten Island (Britton, 1879). VIRGINIA. Augusta, Bedford, Nelson, Pittsylvania, and Roanoke Counties (Harvill et al., 1981). WEST VIRGINIA. Monroe Co. (Core, 1941).

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Literature record rejected: MICHIGAN. KENT Co.: Grand Rapids (Cole, 1901). This record is based on a misidentified collection of *Petrorhagia saxifraga* (Stevenson in 1899, MICH).

3. *PETRORHAGIA NANTEUILII* (Burnat) P. Ball & Heyw., Bull. Brit. Mus. (Nat. Hist.), Bot. 3:164. 1964.

Dianthus nanteuilii Burnat, Fl. Alpes Marit. 1:221. 1892. *Dianthus prolifer* var. *nanteuilii* (Burnat) Coincy, J. Bot. (Morot) 12:55. 1898. *Tunica nanteuilii* (Burnat) Gürke in K. Richter, Pl. Eur. 2(3):338. 1903. *Tunica prolifer* var. *nanteuilii* (Burnat) Briq., Prodr. Fl. Corse. 1:569. 1910. *Tunica prolifer* subsp. *nanteuilii* (Burnat) Graebner & P. Graebner in Asch. & Graebner, Syn. Mitteleur. Fl. 5(2): 264. 1921. *Kobbrauschia nanteuilii* (Burnat) P. Ball & Heyw., Watsonia 5:115. 1962. *Kobbrauschia prolifer* subsp. *nanteuilii* (Burnat) M. Lainz, Bol. Inst. Estud. Asturianos (Suppl. Ci.) 10:177. 1964. *Petrorhagia prolifer* subsp. *nanteuilii* (Burnat) O. Bolòs & Vigo, Bul. Inst. Catalana Hist. Nat., 38 Bot 1:87. 1974. TYPE: "Description sur 38 éch [antillons], de diverses localités de Cannes et d'Agay, dus à l'obligeance de M. R. de Nanteuil." Original material not seen (G?).

Kobbrauschia volutina var. *intermedia* Pérez Lara in Willk. Suppl. Prod. Fl. Hisp. 282. 1893. *Tunica pinetorum* Pérez Lara, Anales Soc. Esp. Hist. Nat. 25:197. 1896. TYPE LOCALITY: SPAIN, Cadiz province. Original material not seen (MAF).

Dianthus prolifer var. *atapuercae* Coincy, J. Bot. (Morot) 12:54. 1898. *Tunica prolifer* var. *atapuercae* (Coincy) Gürke in K. Richter, Pl. Eur. 2(3):338. 1903. TYPE LOCALITY: SPAIN, "Les bords de la grotte jurassique d'Atapuerca près Burgos." (P?). Original material not seen.

Annual. Stems simple or branched near the base, 21–52 (often 30) cm tall; internodes glabrous or lower and center internodes somewhat scabrous with eglandular pubescence. Leaves mostly linear, 3-veined, margin scabrous; leaf sheath mostly (2)3–4 mm long, 1.5 to 2 times as long as broad. Inflorescence capitata as in *P. prolifer*, 10–12 mm long, 9–17 mm broad, but with tips of inner inflorescence bracts either obtuse or mucronate. Sepals 3-veined, outer surface may be very slightly scabrous, margin glabrous. Petals clawed, pink or slightly purplish (limb rarely white);

primary veins 3 per petal, at least the center vein darkly colored at the base of the limb, 2 side veins may show faint darkening; apex obcordate or somewhat bifid. Pollen $46\ \mu\text{m}$ in diameter, apertures of $4.9\ \mu\text{m}$ (Candau, 1980). Seeds tuberculate, (1.3)1.5–1.8 mm long, (0.7)0.9–1.0 mm broad. $2n = 12$, 36 (Borgen, 1974), 60 (Fernandes & Leitão, 1971; Thomas & Murray, 1983). Figs. 5, 9, 15.

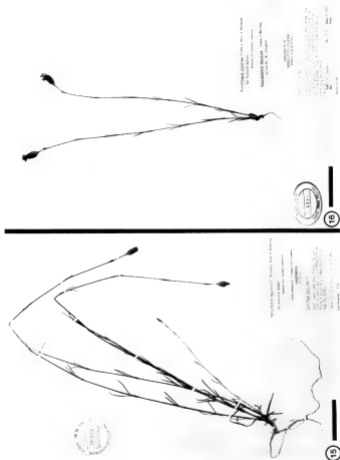
A note on the inclusion of *Tunica pinetorum* Pérez Lara as a synonym of *P. nanteuilii* (Burnat) P. Ball & Heyw. is in order. In his description, Pérez Lara (1896) clearly considered the plant intermediate between *T. prolifera* and *T. velutina* and cited leaf sheath, bract, petal, and seed characteristics that are clearly referable to *P. nanteuilii*. In their catalog of the flora of Cadiz province, Galiano and Silvestre (1977) listed the four collections cited by Pérez Lara after the description of *T. pinetorum* under *P. velutina* without any explanation. The specificity of the description of *T. pinetorum* makes an examination of the specimens crucial before resolution of this discrepancy can be obtained.

Much debate has taken place concerning the status of this plant, as shown by the above list of synonyms. Most chromosome counts of this species indicate a tetraploid condition, with $2n = 60$. The question then arises as to the origin of the tetraploidy; is it an auto- or allopolyploid? Of hybrid or non-hybrid origin?

Böcher et al. (1953) conducted the first investigation of these tetraploids, concluding they represent an autopolyploid race of *Kobluerschia prolifera*. In their study, the only clear cut morphological difference cited was seed size, with other characters showing a great deal of overlap between diploid and tetraploid plants. Böcher et al. (1953) used the term "polyplotype" to describe the situation and summarized the problem by stating: "There is greater reason to distinguish the diploid *Kobluerschia velutina* from the diploid *K. prolifera* than to distinguish the polyplotypes within the latter." This idea roughly parallels the taxonomy most recently expressed by Bolòs and Vigo (1974). In considering *P. nanteuilii* as a subspecies of *P. prolifera*, they believed *P. nanteuilii* to be a race of *P. prolifera* that has not attained a degree of difference great enough to warrant treatment as a distinct species.

Ball and Heywood (1962) first suggested the alternative view; an allotetraploid with *K. prolifera* and *K. velutina* as parents. Their position was based on the presence of characteristics, including flowering time and seed surface texture, that are intermediate between the two species. They noted this heritage would be shown in the karyotype by the presence of a pair of very short chromosomes present only in *K. velutina*.

As part of their study on the breeding systems in *Petrorhagia* sect. *Kobluerschia*, Thomas and Murray (1983) conducted a cytological investiga-



FIGS. 15 – 16. Representative herbarium specimens of *Petrorhagia* spp. Scale = 5 cm. 15. *P. nantuilii*, Bacigalupi, Robbins, & Hoffman 5676 (DAV). 16. *P. selatina*, Carter 368 (CHSC).

tion of *P. nanteuillii*. They noted the presence of 29 pairs of metacentric chromosomes and one pair of small telocentric chromosomes, reinforcing the contention of Ball and Heywood (1962), and found that *P. nanteuillii* behaved as an allotetraploid during meiosis, with strictly bivalent pairing. They suggested one genome was supplied by *P. prolifera* [based in part on homeologous pairing in artificial sterile hybrids noted earlier by Thomas (1980)], the other most likely coming from *P. velutina*, although breeding barriers within *P. velutina* prevented formation of any *P. velutina-nanteuillii* hybrids. In addition, Thomas (1980) found that all attempts to cross *P. velutina* with *P. prolifera* were unsuccessful, suggesting that any hybridization that may have led to *P. nanteuillii* would have taken place prior to the development of the breeding barrier now present in *P. velutina*. This is confirmed by the lack of transitional forms between *P. nanteuillii* and the reputed parents, a situation first noted by Nanteuil (Burnat, 1892) and emphasized by Ball and Heywood (1962).

On the basis of the above cytological evidence and observed morphological continuity, I have decided to follow both Ball and Heywood (1964) and Thomas and Murray (1983) in recognizing *P. nanteuillii* as a separate species. Maire (1963) used stem pubescence to recognize two varieties, a useless distinction considering the instability of this character in section *Koblerauschia*.

The common name Childing Pink is not used only for *P. prolifera*, Perring and Farrell (1977) applying it to *P. nanteuillii*. The epithet "nanteuillii" was chosen by Burnat (1892) in commemoration of Edmond Nanteuil, who discovered this species near Cannes, France in 1885.

FLORAL BIOLOGY: Thomas and Murray (1981) reported *P. nanteuillii* to be primarily autogamous, noting that the timing of anthesis and stigma emergence tended to coincide and seed set was high under insect-free conditions. Limited cross-pollination may occur since the stigmas do protrude above the corollas.

ECOLOGY AND DISTRIBUTION: Ball and Heywood (1964) reported the species from "western Europe and western North Africa" with collections cited from the Channel Islands, Madeira, and the Canary Islands, areas where neither *P. prolifera* nor *P. velutina* have been collected. Two specimens have been seen from Australia (Clemens in 1944 and 1949, MICH), indicating an introduction to Queensland. Perring and Farrell (1977) listed it as endangered in England, citing the small number of localities and their accessibility to the public as reasons to be concerned about its status.

The single California population (Fig. 17) is located among grasses in dry roadside soil, a habitat similar to several of the sites supporting *P. prolifera*

and *P. velutina* in other states. Flowering is reported in late May, with a few plants continuing into early August.

HISTORY OF INTRODUCTION AND CURRENT STATUS: Unfortunately, the early history of *P. nanteuilii* in North America is unknown. Although both species that appear to have contributed to the genome of *P. nanteuilii* have been collected in California (*P. prolifera* only once, about 200 miles southeast of Cazadero), evidence presented by Thomas (1980) and Thomas and Murray (1983) suggests that no such hybridization is currently possible. No evidence of previous cultivation either at or near the roadside site was present, suggesting that *P. nanteuilii* may have arrived as a seed contaminant.

The specimens cited below illustrate the restricted occurrence of *P. nanteuilii* in North America; a single wild population in California known since 1956 and an intentional cultivation at the Bailey Hortorium in 1969. An investigation of seeds and vegetative material from eastern Sonoma County provided by Dr. Charles Quibell revealed no trace of *P. nanteuilii* among the *P. velutina* plants there, suggesting the population may be spreading slowly if at all.

Representative specimens: UNITED STATES. CALIFORNIA. SONOMA CO.: Along secondary road following Big Austin Creek, at base of "The Butcher Knife", elev. c. 600 ft, 31 May 1956, *Bacigalupi, Robbins, and Hoffman* 5676 (DAV, JEPS); along trail to Big Austin Creek, N side of King Ridge Rd., 4.4 mi N of Cazadero, T9N, R11W, "S31", 8 Aug 1980, *Rabaler* 507 (CHSC, GH, HSC, MSC, ROPA, UC, US). NEW YORK. Tompkins Co.: Hortorium Garden, Ithaca, 2 Aug 1969, *Druss* 10606 (BH69-192) (BH).

4. PETRORHAGIA VELUTINA (Guss.) P. Ball & Heyw., Bull. Brit. Mus. (Nat. Hist.), Bot. 3:166. 1964.

- Dianthus velutinus* Guss., Ind. Sem. Boccad. 1825:2. 1825; Pl. Rar. 166, t. 32. 1826.
Tunica velutina (Guss.) Fischer & C. Meyer, Index Sem. Hort. Petrop. 6:66. 1840.
Kobranuschia velutina (Guss.) Reichb., Icon. Fl. Germ. Helv. 6:43, t. 247, f. 5010. 1844. *Dianthus prolifer* subsp. *velutinus* (Guss.) Battand. in Battand. & Trabut, Fl. Algérie 1:143. 1888. *Dianthus prolifer* var. *velutinus* (Guss.) Coincy, J. Bot. (Moroc) 12:55. 1898. *Tunica prolifera* subsp. *velutina* (Guss.) Briq., Prodr. Fl. Corse 1:570. 1910. *Petrorhagia prolifera* subsp. *velutina* (Guss.) O. Bolòs & Vigo, Burl. Inst. Catalana Hist. Nat., 38 Bot. 1:87. 1974. TYPE: SICILY; "Val di Mazzara, e Val di Noro, Madonie" (Fl. NAP?), *fvé* Meikle (1977). Original material not seen.
Dianthus ambiguus Nicotra, Prodr. Fl. Messan. 123. 1883., *nov. illeg.*, non Salisb., Prodr. 305. 1796., non Pančić, Fl. Serbiae 178. 1874, nec Pančić, Nova Elem. Fl. Bulg. 185. 1886. TYPE LOCALITY: SICILY. Original material not seen.
Dianthus sartorii Fruehl ex Nyman, Consp. Fl. Eur. 107. 1878. *Dianthus velutinus* var. *sartorii* (Fruehl) F. Williams, J. Bot. 23:347. 1885. Original material not seen.
Dianthus diminutus sensu Desf., Fl. Atlant. 1:345. 1799, non L.
Dianthus prolifer sensu Friedr., Reise. 270. 1838, non L.
Petrorhagia prolifera sensu Shinn., Sida 3:345. 1969, sensu Correll & M. Johnston, Contr.

Texas Res. Found., Bot. Stud. 6:613. 1970, *et sensu pro parte* Kartesz & Kartesz, Syn. Check. Vasc. Flora. 153. 1980, non (L.) P. Ball & Heyw.

Tunica prolifera sensu Munz & Keck, Calif. Fl. 293. 1959, *et sensu* H. St. John, Pac. Trop. Bot. Gard. Mem. 1:160. 1973, non (L.) Scop.

Annual. Stems often simple or sometimes branched near the base, 9.5–60(CA)-91(TX) [commonly 25–40] cm tall; all internodes glabrous or nearly so (most Oklahoma and Texas collections), or middle internodes densely glandular-tomentose (most California collections). Leaves linear to linear-oblong, 10–60 mm long, 1.5(2) mm or less wide, lowermost oblanceolate, often broader (to 5 mm wide), 3-veined, margin scabrous; leaf sheath variable in length, (3)4–6(9) mm long, 2–3 times as long as broad. Inflorescence capitate as in *P. prolifera*, (10) 14–20 mm long, 6–10(23) mm wide, but with tips of all inflorescence bracts mucronate, reddened when young. Sepals 3-veined, outer surface often scabrous, especially along veins; margin glabrous. Petals clawed, pink or purplish (rarely white); primary veins 3 per petal, "pencilled crimson at base of limb" (Meikle, 1977), central vein may fork in bifid petals and at least 2 minor veins may also be colored, producing 5–6 dark veins; apex obcordate or (more commonly) bifid. Anthers blue or pink; pollen 32 μm (Candau, 1980). Seeds semipyriform, more angled (concave-convex) than above species, surface covered with conical papillae, 1.0–1.3(1.4) mm long, 0.7–0.8(1.0) mm broad. $2n = 30$ (Böcher et al., 1955; Thomas & Murray, 1983). Figs. 6, 10, and 16.

One of the most obvious morphological characters, stem pubescence, proves problematic in *P. velutina*. The absence of pubescence on many collections from Oklahoma and Texas has led to repeated misidentifications, as mentioned earlier. Maire (1963) considered glabrous-stemmed plants to represent a distinct variety, a concept not recognized by Ball and Heywood (1964). I agree it is best not to add a formal infraspecific name to the glabrous plants since this character does not correlate with differences in seed testa and, as Briquet (1910) observed in Corsica and I observed in Texas, glabrous- and glandular-stemmed plants may grow together.

The consideration of *P. velutina* as a subspecies of *P. prolifera* by Bolòs and Vigo (1974) is based on the treatment of Briquet (1910) and reflects the ideas of Malinvaud (1893), who suggested placing all members of the "*prolifera*" group within a single species, limiting "secondary units" to subspecies and varieties. Acceptance of such a classification would minimize the importance of distinct karyotypic differences between *P. prolifera* and *P. velutina* shown by Böcher et al. (1955) and Thomas and Murray (1983) and

the breeding barriers isolating *P. velutina* from all other taxa in section *Kohlranschia* noted by Thomas and Murray (1981).

Four common names have been used for *P. velutina* in North America, although in each case, the epithet *prolifera* is used in the accompanying scientific name. Howell (1962) used Childing Pink when describing plants from Butte County, California. St. John (1973) cited Tunic Flower in reference to plants in Hawaii, which would be introduced *P. velutina* according to Ball and Heywood (1964). Niehaus (1974) used Proliferous Pink, while Niehaus and Ripper (1976) preferred Wild Carnation as the common name for plants in the Sierra Nevada foothills. The epithet "*velutina*" is an obvious reference to the "dense, glandular-tomentose indumentum" on most middle internodes of the typical *P. velutina* (Ball & Heywood, 1962).

FLORAL BIOLOGY: Thomas and Murray (1981) reported that *P. velutina* is normally autogamous, finding that the timing of anthesis and stigma receptivity coincide and that the average lengths of filaments and styles are very similar. Some cross-pollination may occur if vectors are present since the stigmas do protrude above the corolla.

ECOLOGY AND DISTRIBUTION: *P. velutina* is native to the Mediterranean region, with introduced populations found in Australia, Hawaii, and South Africa (Ball & Heywood, 1964). Two specimens have been seen from Chile (Junge 2636, US: Looser 4349, GH), indicating an introduction to South America. Except for two cultivated records, the North American distribution of *P. velutina* is restricted to northern California (Fig. 17), southeastern Oklahoma, and eastern Texas (Fig. 18.).

Nearly all *P. velutina* collections from Texas and Oklahoma came from roadside localities, with little evidence of invasion of adjacent communities. *P. velutina* is also a roadside plant in northern California, although Frenkel (1970) did not list it as a "high presence species" in his study of roadside vegetation. An inspection of collection labels revealed that *P. velutina* has left the roadside and has invaded at least two of the Woodland-Savanna communities described by Munz and Keck (1949, 1950); the Northern Oak Woodland and the Foothill Woodland as they occur in the North Coast ranges and the Sierra Nevada foothills. The presence of a Mediterranean climate (hot, dry summer; mild rainy winter) in California (Gleason and Cronquist, 1964) may be a positive factor in the expansion of *P. velutina* into oak and oak-pine woodlands, valley meadows, and stream banks. Flowering is noted from early April to early June.

HISTORY OF INTRODUCTION: It is evident from both time and morphological considerations that *P. velutina* has been introduced to North

America at least twice (excluding known cultivations); once in northern California and once in eastern Texas. For this reason, a separate account will be presented for each region.

CALIFORNIA: It appears that *P. velutina* was introduced in northern California in the late 1920's, with six collections noted in a 30 mile \times 20 mile \times 20 mile triangular area, including parts of NE Butte, SW Nevada, and NE Yuba counties between 1927 and 1940 (Fig. 17). None of the collection labels indicated cultivated origin; two were gathered along roadsides, three from streamside areas, while the sixth was found on rocky hillocks west of a town. The literature is of little help on this point. Robbins (1940) listed only one location for *P. velutina* (*T. prolifera*), indirectly citing Yates' collection (Yates 3616 in 1933, UC) in Yuba County. Wolf (1938) summarized the situation when he wrote "we have recently found it in California [Wolf 8632 in 1937] where it apparently has been established for many years, but has been overlooked by collectors."

TEXAS: Most evidence points to a 1967-1968 introduction of *P. velutina* to eastern Texas. The only contradictory report is the listing of *Dianthus prolifer* for region 2, the Coastal Prairies, by Cory and Parks (1937). I have seen no specimen to document this statement, no recent collections of *P. velutina* from this area, and furthermore, Gould (1962) did not list the species as present in Texas.

Shinners (1969) noted the "sudden appearance" of *P. velutina* (his *P. prolifera*) in May, 1968 along highways in east Texas which "I have traveled almost yearly for two decades without finding it." He postulated it could have been introduced as a result of state highway department planting of rye grass, *Lolium perenne* L. var. *italicum* (A. Braun) Parnell. Correll and Johnston (1970) concurred, noting "its very recent introduction into Texas, probably in contaminated rye grass seed."

On the labels of the earliest Texas collection seen (*D. S. and H. B. Correll* 35641; CM, LL), the Corrells suggested another vector when they wrote: "probably introduced with Italian clover seed by Texas Highway Dept." Italian clover, *Trifolium incarnatum* L. (per Bailey et al., 1976), is listed by Turner (1959) as being "cultivated in the eastern part of the state, but occasionally escaping", his map showing its presence in eight counties. The Corrells' suggestion may be the "correct" source for several reasons. The Texas State Department of Highways and Public Transportation did spread *T. incarnatum* seed in the 1960's, the species "generally seeded throughout the eastern one-third of Texas, from Dallas eastward", although the seeding plans have been revised "to the extent that *Trifolium incarnatum* is no longer specified for our current seeding practices." (B. C. Blaschke, pers. comm.).

Trifolium fragments were present at the base of plants in four collections seen spanning four neighboring counties and three growing seasons. Finally, personal observations suggest *T. incarnatum* as the vector, the species being a dominant associate at each collection site, while *Lolium perenne* was absent from four of the sites visited (Rabeler 351, 352, 353, and 356).

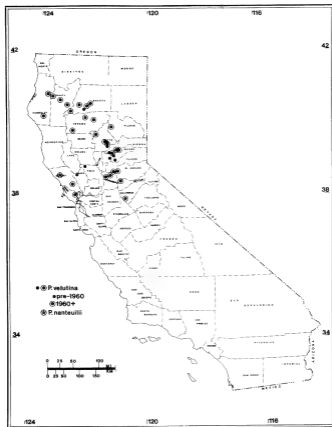


FIG. 17. Distribution of *Petrorhagia nanteuilii* and *Petrorhagia velutina* in California.

CURRENT STATUS: Since the California and Texas-Oklahoma populations still appear as distinct entities with no range overlap yet documented, the status of *P. velutina* in these areas will be treated separately.

CALIFORNIA: The list of specimens cited below includes the earliest and most recent collections seen from a given county. Once again, the floristic manuals present a vastly different picture from that of the specimens examined (also see Fig. 17). As noted previously, Robbins (1940) listed *P. velutina* for Yuba County. Munz and Keck (1959) described *Tunica prolifera* as "occasional as a weed reported from Butte, Nevada, Yuba cos." Raven (1965) cited the same distribution in a note giving the correct name as *P. velutina* based on Ball and Heywood (1964) and a confirming identification of the California material by Heywood. Munz (1968) added Sacramento and Shasta Counties and changed the name to *Kobltrauschia velutina* [Howell (1972) adopted *Petrorhagia velutina* in his commentary on Munz (1968)].

Niehaus (1974) stated that *T. prolifera* (*P. velutina*) was "common as a pink mass under foothill oaks, Nevada Co. and north below 3000 ft."; a very accurate generalized description of the current status of *P. velutina* in California. He went on to note that this species is "rapidly spreading throughout the foothills", a statement that is easily verified by arranging the specimens examined in chronological order by date of collection. The following pattern appears: pre-1939, 3 counties; 1940-1949, 1 added; 1950-59, 2 added; 1960-69, 6 added; 1970-on, 5 more counties added. This totals 17 counties, 15 of which are represented by collections dating from after 1960, 10 from 1970 or later. It is evident that this species is fully naturalized and probably still expanding into other areas of northern California.

TEXAS: The earliest collection seen from a given county is included in the list of specimens cited below. Most specimens of *P. velutina* examined were collected between 1968 and 1971. During those years, it apparently spread rapidly, with eight additional counties added to the four counties represented by the 1968 collections (Fig. 18). Correll and Johnston (1970) described it as "an extremely aggressive plant," noting that it has spread to much of east Texas. My observations in 1980 confirmed that statement, with a large number of plants seen along the roadsides in eight counties during my brief visit. The stature and density of *P. velutina* at some sites clearly suggested a naturalized species. Collections made in three counties (Cherokee, Henderson, and Rains) represented new records, indicating that *P. velutina* was still invading additional sites. Two 1983 collections from southeastern Texas roadsides (Colorado and San Jacinto counties) and a

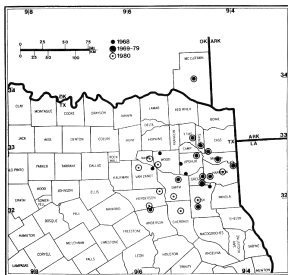


FIG. 18. Distribution of *Petrorhagia velutina* in Oklahoma and Texas, 1968-1980. 1983 collections from Colorado and San Jacinto counties, Texas excluded.

1978 collection from a roadside in southeastern Oklahoma suggest that this species may be more widely distributed than either literature or collections currently indicate.

Representative specimens: UNITED STATES, CALIFORNIA. AMADOR CO.: Bank of Consummes River, S of Lacrobe, 5.6 mi N of Ca 16 jct., 2 May 1974, *McNeal 1456* (NY). BUTTE CO.: Bidwell Bar bridge, 10 mi E of Oroville, 10 May 1940, *Cantelow 3078* (RSA); sandy grassland along CA 99, 11 mi N of Chico, 18 Apr 1978, *Joslin 11* (GM); Bidwell Bar, 21 Apr 1929, *Wilkins s.n.* (UC). CALAVERAS CO.: Wooded slope, 4 mi SE of Milton, 5 May 1963, *Broadlove 4768* (SMU). EL DORADO CO.: Open grassland, Folsom Lake State Park, 18 Apr 1964, *Hueber 34* (DAV); E shore of Folsom Lake, 5 mi NE of Folsom, 1 May 1960, *Simonds s.n.* (CDA). HUMBOLDT CO.: Gravel bank along Eel River floodplain, 20 Apr 1973, *Anderson s.n.* (HSC). MARIN CO.: Along road to Black Point, 1.5 mi NE of Ignacio, 20 Apr 1971, *True 6477* (CAS, JEPS, NY). NAPA CO.: Valley clay, 6 mi N of Aetna Springs, Pope

Valley, 8 May 1948, *Smith s. n.* (DAV). NEVADA CO.: Roadside bank, Hwy 20, 7 May 1938, *Heller 15077* (ILL, MO, NY, POM, UC); rocky roadside bank along CA 49, 2 mi N of North San Juan, 4 May 1963, *Rice 176* (NCU). PLACER CO.: Edge of beach, Folsom Reservoir, 2 mi N of Folsom, 4 May 1964, *Clegg 27* (DAV); near old homestead, Orangevale, 26 Apr 1976, *Van Ess 3485* (SACT). PLUMAS CO.: Rocky slope near Murphy Creek along CA 70, 2.2 mi W of Belden, T25N, R6E, S26, SW1/4, 9 Aug 1980, *Rabaler 514* (CHSC, GH, HHH, MSC, ROPA, UC). SACRAMENTO CO.: 0.25 mi S of fish hatchery, American River, 20 Apr 1963, *Gustafson s. n.* (SACT). SHASTA CO.: Dry grassland, 1.5 mi N of Anderson, 12 Apr 1952, *Cutright 32* (JEPS); oak-pine woodland, Co. Rd. A16, 9.7 mi NE of CA 36, T30N, R8W, S33, 9 Apr 1978, *Smith, Sawyer, and Nelson 9719* (HSC). SONOMA CO.: Grassy area, W slope of Sonoma Mtn, Osborn Nature Conservancy Preserve, E of Rohnert Park, May 1979, *Serpa s. n.* (MSC, OSH, ROPA). TRHAMA CO.: Along creek bank at rest area, 1-5, 9 mi S of Shasta Co. line, T28N, R4W, S25, 26 May 1977, *Halte 1585* (WTU); bank of Reeds Creek at Paskenta Road, 30 Apr 1967, *Wheeler 20* (CHSC). TRINITY CO.: Along CA 299 at Hayden Flat Campground, T5N, R7E, S24, 17 May 1975, *Smith 8118* (HSC); grassy canyon slope, 3 mi SW of Douglas City, 22 Apr 1965, *Weber 12284* (DAO, ILL). YOLO CO.: Cache Creek cañon, along CA 16, 2.5 mi NW of Rumsey, 22 Apr 1958, *Bacigalupi, Mason, and Mason 6277* (JEPS). YUBA CO.: Oak woodland, Foothill Range Exper. Station, 19 Apr 1966, *Carr 160* (MIN); flat W of North San Juan, 11 May 1927, *Mason 3735* (JEPS, UC); edge of creek bed, 2 mi N of Brown's Valley, 13 May 1937, *Wolf 8632* (CAS, [DS], GH, [LA], NY, POM, RSA, UC, US); Spencerville Rd. at Indian Springs, T15N, R7E, S19, 23 May 1933, *Yates 3616* (UC). OKLAHOMA. McCURTAIN CO.: Along roadside near Yanubbee Creek, US 259, 2.5 mi N of Broken Bow, 30 Apr 1978, *Taylor 25906* (DUR, LSU, MO). TEXAS. ANDERSON CO.: Roadside, TX 19, 12 mi S of Athens, 22 May 1969, *Barclay 3054* (NA). CASS CO.: Roadside, 3.2 mi SW of Avinger, 28 Apr 1970, *Shinners 33022* (*Southern Appalachian Botanical Club 2618*) (FLAS, KNK, MASS, MICH, MSC, NLU, SMU, WVA). CHEROKEE CO.: Red sandy clay along US 79, 3.2 mi W of New Summerfield, 2 May 1980, *Rabaler 346* (MIN, MSC, NY, SMU). COLORADO CO.: Along I-10, 1 mi W of FM 949, 15 May 1983, *Brown 6033* (SMU). GREGG CO.: Roadside, US 259, Kilgore, 12 May 1969, *Shinners 32631* (SMU). HARRISON CO.: Roadside, W side of Hallsville, 13 May 1969, *Shinners 32635* (MSC, SMU). HENDERSON CO.: In red sandy clay along E side of TX 19, 10 mi S of Athens, 1 May 1980, *Rabaler 330* (GH, MSC, SMU, UC). MARION CO.: Sandy clay road shoulder, TX 49, 2.2 mi W of Jefferson, 13 May 1969, *Shinners 32643* (MSC, SMU). MORRIS CO.: Re-graded road cut, TX 11, Daingerfield, 21 Apr 1969, *Shinners 32597* (SMU, TENN). RAINS CO.: Roadside, E side of US 69; 6.4 mi NW of Alba, 3 May 1980, *Rabaler 353* (MSC, SMU). RUSK CO.: Roadside, 4.2 mi NW of Tatum, 5 May 1968, *Shinners 32222* (FLAS, MASS, MSC, SMU, TENN, VDB). SAN JACINTO CO.: along TX 2025, 2 mi S of TX 150, 27 May 1983, *Brown 6136* (SMU). SMITH CO.: Harris Creek Cemetery, W of Winona, 22 May 1971, *Thomas 23207* (AUA, DUL, ILL, NLU, TENN). TITUS CO.: Roadside, TX 49, 7 mi E of Mt. Pleasant, 28 Apr 1971, *Amerison 389* (SMU). UPSHUR CO.: Road shoulder, 5.8 mi ESE of Big Sandy, 7 May 1968, *Shinners 32233* (MASS, SMU); grassy roadside, TX 155, 5 mi W of Ore City, 1 May 1969, *Correll 37154* (FSU, GH, LL, MICH, NA, NCU, NY, OKLA, TEX). VAN ZANDT CO.: Roadside, 2.8 mi E of Grand Saline, 7 May 1968, *Shinners 32238* (MASS, SMU). WOOD CO.: Near pond along Farm Rte 514, 4 mi E of Yantis, 25 Apr 1968, *D. S. and H. B. Correll 35641* (CM, LL).

Cultivations: MARYLAND, PRINCE GEORGES CO.: In Glenn Dale Introduction Garden (seed from Turkey), 23 June 1938, *Couggill 808* (BH, GH, MICH, NA). PENNSYLVANIA. PHILADELPHIA CO.: cultivated, Mehans Garden, without date, *Bark s. n.* (PENN).

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PORTULACA PILOSA L., P. MUNDULA
I. M. JOHNST. AND P. PARVULA
GRAY IN THE SOUTHWEST

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ABSTRACT

Historically the taxonomic interpretation of three species of *Portulaca*—*P. pilosa* L., *P. mundula* I.M. Johnst., *P. parvula* Gray has been unsettled. The basis for each interpretation has been reevaluated using material representing collections from both the Southeast and the Southwest United States. Morphological characters traditionally used in descriptions and keys, along with an examination of the seed surfaces by scanning electron microscopy, have provided evidence that *P. mundula* is conspecific with *P. pilosa*. The interpretation of *P. parvula* is still uncertain due to lack of study material. Theoretical patterns of the migration of *Portulaca* are presented.

TAXONOMIC HISTORY

In 1753 Linnaeus described *Portulaca pilosa* as having alternate, subulate leaves, with axillary hairs and sessile flowers. He did not mention flower color, but cited publications by Herman and Commelin as treating the same red-purple flowered species.

In 1887 Asa Gray published the name *Portulaca parvula*, describing the species as having yellow to copper-colored petals. He noted that *P. parvula* in Texas, New Mexico and Mexico was part of several specimens labeled *P. pilosa* which were collected by Wright, Fendler, Schaffer (772) and Pringle (543). From Gray's comments it is apparent that he was treating mixed collections and segregating the yellow-flowered taxon from the red-flowered *P. pilosa*. He gave the distribution of *P. pilosa* as Florida to Arizona.

Gray's Manual of Botany, ed. 7 (Robinson and Fernald, 1908) recognized *P. pilosa* as the red-flowered taxon in the Southwest, with no mention of a yellow-flowered taxon. Ivan M. Johnston (1948) examined the mixed specimens that Gray had cited. In his judgment, the red-flowered specimens constituted a new species, *P. mundula* I.M. Johnst. Johnston commented that an examination of illustrations and comments from Commelin (1697) and Herman (1705) left little doubt as to the Linnean concept of *P. pilosa*. Hence, in his opinion the red-flowered specimens were not *P. pilosa*.

Gray's manual, ed. 8 (Fernald, 1950) recognized *P. parvula* as the only southwestern species, including in the description both red and yellow flowers, and noting that the treatment in ed. 7 was not *P. pilosa* of Linnaeus.

Shinners (1958) treated *P. mundula* as a synonym of *P. pilosa* and commented that the yellow-flowered species, *P. parvula*, occurred to the west and south of the Dallas-Fort Worth area. Legrand (1962) in his monograph of the American species of *Portulaca* treated *P. mundula* as a variety of *P. pilosa*. He noted that var. *mundula* differed from the typical variety by a reduction in size of all its organs. The distribution of var. *mundula* is given by Legrand as from the tropics to northern Mexico (Chihuahua and Coahuila), the southwest United States into Colorado, Texas, Oklahoma, Kansas and Missouri. Legrand commented that there was clearly a transition of morphological traits from var. *pilosa* to var. *mundula* from the tropics to the northern arid habitats. Legrand treated the yellow-flowered *P. parvula* as part of *P. halimoides* L. He stated that *P. parvula* Gray sensu Johnston represented the depauperate form of *P. halimoides* resulting from the adaptation to desert regions. Correll and Johnston (1970) modified their treatment of *Portulaca* from Legrand but recognized *P. mundula* and *P. parvula* as species, without recognizing *P. pilosa*.

A NEW EXAMINATION

In the course of preparing the treatment of *Portulaca* for the Vascular Flora of the Southeastern United States it was necessary to decide whose treatment was the most accurate. Additionally, since the Southeast extends into Arkansas and Louisiana, it became necessary to examine specimens from herbaria in the Southwest. *Portulaca mundula* is reported from Arkansas and some specimens from Louisiana have been identified as *P. mundula*. Several problems emerged: 1. Does *P. pilosa* occur in the southwest? 2. Can *P. mundula* be differentiated from *P. pilosa*? 3. What does the name *P. parvula* represent?

To address these problems over 1,800 specimens were borrowed from the following herbaria: ALU, ASTC, DUR, FLAS, FSU, G, GA, JSU, KNK, KY, LAF, LL, MO, NCU, NLU, NO, NY, SMS, SMU, TENN, TEX, UARK, UNA, UNCC, US, USAM, USCH, USF, VDB, VPI, VSC, WILLI.

Examination of the specimens both for distribution and morphological variability indicated problems in separating *P. mundula* from *P. pilosa*. Since no taxonomic treatments have compared all three taxa, including *P. parvula*, with analyses of the distinguishing character states separating them, an attempt was made to do so, using the characters provided by I.M.

Johnston, Legrand, and Correll and Johnston. Comparison of all of the morphological traits used to define the species showed that the characters of capsule diameter, capsule pedicel length, seed diameter, color and surface texture, and flower color seemed to provide the clearest traits for identification. These literature data are shown in Table 1.

Additionally the Southeastern treatments have been limited to state boundaries without consideration of variation throughout the range. Specimens were examined by state, beginning in Florida because *P. pilosa* is the original taxon to which to compare any later segregates. *Portulaca pilosa* has been unchallenged as the Florida taxon in treatments by Small (1933), Legrand (1962), Long and Lakela (1971) and Wunderlin (1982). Legrand,

TABLE 1. Key morphological features for the three taxa, taken from the literature. Multiple entries are character states given by I.M. Johnston, Legrand, and Correll and Johnston respectively. Lack of a statement is shown by ----.

	P. PILOSA	P. MUNDULA	P. PARVULA
Capsule diameter in mm	---- 2.5-4.3 ----	2.5-3.5 2.0-3.0 2.5-3.5	1.5-2.0 ---- 1.5-2.0
Pedicel length in mm	---- Up to 1.0 ----	Short stipitate Up to 1.0 Lightly stipitate	1.0-1.5 ---- 1.0-1.5
Seed diameter in mm	---- 0.5-0.65 ----	0.3-0.5 0.5-0.6 0.3-0.5	0.3-0.5 ---- 0.5
Seed color	---- Black ----	Black Black Black	Black ---- Black
Seed surface	---- Small tubercles dorsally, stellate on sides ----	Stellate-tuberculate Stellate-tuberculate Stellate-tuberculate	Stellate flattened roughenings ---- Stellate flattened roughenings
Flower color	---- Purple ----	Purple Purple Red-purple	Yel-orange, bronze ---- Yel-orange, bronze

being very familiar with the Central and South American taxa, cited specimens which he considered as *P. pilosa* from Florida. We have accepted Legrand's conclusion that *P. pilosa* is the correct name for the Florida taxon.

Specimens were selected from counties throughout Florida to provide a basis of variability for *P. pilosa*. Observations of the same character states, as shown in Table 1, were made. If two specimens from the same county appeared morphologically dissimilar, both were included. Thirty eight specimens were measured or scored, with three observations on each specimen, for the traits of capsule diameter, capsule pedicel length and seed surface features. Following this, the same observations were made on all specimens from Alabama (n = 6), Mississippi (n = 16), Louisiana (n = 57). Specimens that could not be positively identified as having red flowers were excluded. Since Texas represents a large diversity of regions and habitats, capsule and pedicel measurements were grouped according to distributions in the coastal plain (CP), in the high prairie (HP) and in the Trans-Pecos (TP). Additionally, 23 specimens from Missouri, Oklahoma and Texas, cited by Johnston in his original description of *P. mundula* were measured and compared. These paratypes, as well as the populations and subpopulations defined above are compared in Table 2.

The ANOVA (Table 2) for pedicel length for the seven states, with Texas segregated into three subpopulations, including Johnston's paratypes show no significant differences between any two populations (unplanned comparisons using the Tukey-Kramer procedure, Sokal and Rohlf, 1981). Some interesting relationships are evident. The specimens from the high prairie (HP) of Texas are separate from the other Texas subpopulations. The other Texas subpopulations (CP & TP) are grouped with the Florida population while Johnston's paratypes are intermediate.

For the capsule comparisons, using the same geographical grouping, an ANOVA (Table 2) with unplanned comparisons using the Tukey-Kramer procedure shows the following: Capsule diameters of plants from Arkansas, Oklahoma and Johnston's paratypes are significantly smaller ($p < .05$) than the capsule diameters of plants from Texas, Mississippi, Florida and Alabama. Plants from Louisiana are intermediate between the two groups. However none of the Texas subpopulations are significantly different from those of Florida.

Since there is no significant difference among the nine geographical populations and the paratypes in the pedicel comparisons, and since the two groups in the capsule comparisons are of mixed geographical arrangement, the variability of the taxonomic characters traditionally used cannot be predictably segregated to represent two taxa. A comparison of capsules vs pedicels shows a strong positive correlation ($r = 0.310$, $df = 174$, $p < .01$);

TABLE 2. Comparison of pedicel lengths and capsule diameters for Alabama (AL), Arkansas (AR), Florida (FL), Louisiana (LA), Mississippi (MS), Oklahoma (OK), Texas coastal plain (TX-CP), Texas high prairie (TX-HP), Texas Trans-Pecos (TX-TP) and Johnston's Paratypes (JP). Means connected by lines are not significantly different at the .05 level.

PEDICELS										
Pop.:	AR	TX-HP	LA	MS	OK	JP	FL	TX-TP	TX-CP	AL
Mean	<u>0.363</u>	<u>0.429</u>	0.441	0.453	0.500	0.539	0.595	0.605	0.613	0.617
SE	0.077	0.053	0.053	0.056	0.053	0.046	0.035	0.050	0.055	0.089
N	8	17	17	15	17	23	38	19	16	6
CAPSULES										
Pop.:	AR	OK	JP	LA	TX-HP	TX-TP	MS	FL	AL	TX-CP
Mean	<u>1.875</u>	<u>1.924</u>	<u>1.965</u>	<u>2.212</u>	2.335	2.426	2.447	2.518	2.600	2.619
SE	0.112	0.077	0.066	0.077	0.077	0.073	0.082	0.052	0.130	0.080
N	8	17	23	17	17	19	15	38	6	16

but these characters do not vary together.

Comparison of the averages shown in Table 2 with the ranges listed in Table 1 show that the southeastern United States specimens (Florida, Alabama, Mississippi, Louisiana) fall at the lower range for capsule diameter and pedicel length as given by Legrand for *P. pilosa* throughout its range. This is not surprising since most of Legrand's measurements were made on more tropical, hence more robust specimens. His studies centered on Central and South American specimens and *Portulaca* is primarily a genus of these areas. He did however examine specimens from Florida, Georgia and Mississippi to develop his concept of *P. pilosa* for the United States.

Seed surface texture, Table 1, has been used as a character for species separation. In fact, many specimens lacking petals have been identified using the seed surface texture character. Representatives of the seed surface patterns for known red-flowered specimens from seven states are grouped to illustrate the variability over the entire geographic range, Figs. 1-22. Original labels were either *P. pilosa*, *P. mundula*, or *P. parvula*. The bar on each figure represents 100 μ m. Seeds were sputter coated with gold-palladium on a Hummer V and viewed on a Jeol JSM-35CF SEM. Specimen citations from which seeds were taken are shown elsewhere.

FLORIDA—Thirty eight specimens had stellate-tuberculate surfaces; the tubercles varied from very short to medium, none were flattened (Figs. 1-3).

ALABAMA—Six specimens had stellate-tuberculate surfaces; the tubercles varied from very short to short (Fig. 4).

MISSISSIPPI—Nine specimens had stellate-tuberculate surfaces; five had stellate flattened roughenings and two had seeds in which some were tuberculate and some were flattened (Fig. 5).

LOUISIANA—Twelve specimens had stellate-tuberculate surfaces (Fig. 6), five had stellate flattened roughenings (Fig. 7). At this location in the geography, the variability of stellate flattened roughenings in northern Louisiana is evident.

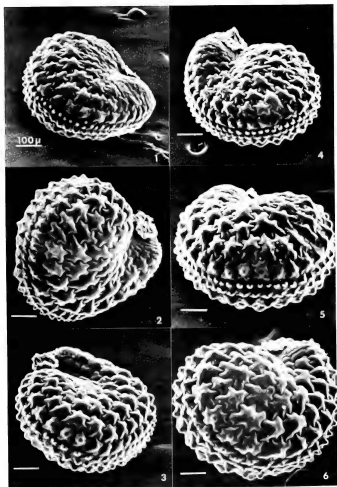
ARKANSAS—All 20 specimens had stellate flattened roughenings (Fig. 8). This pattern complements that of northern Louisiana.

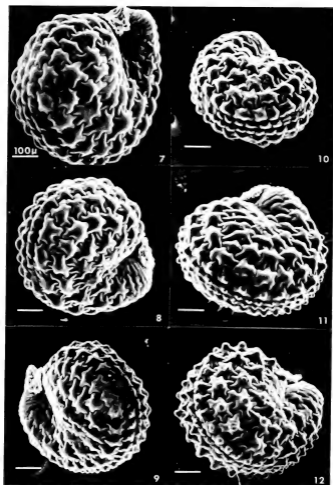
TEXAS—Twenty eight specimens scattered over the state had stellate-tuberculate surfaces, 23 had stellate flattened roughenings. Texas specimens exhibited the greatest range of diversity. Figures 9–12 present the coastal plain variability. Figure 17 shows the same stellate-tuberculate pattern farther inland. Figures 18–21 present the range of variability in the Trans-Pecos region, from stellate flattened to highly stellate-tuberculate.

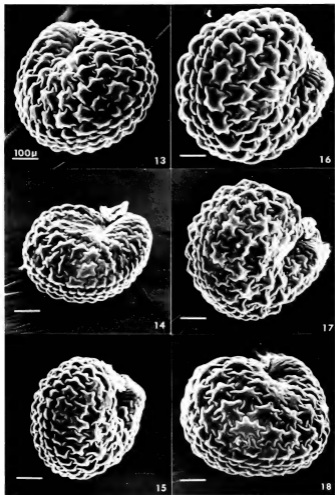
OKLAHOMA—Figures 13–16 & 22 show the same pattern found in the high prairie of Texas with none to only slight impressions of the stellate-tuberculate pattern. Figure 22 illustrates the extreme flattening in the western populations.

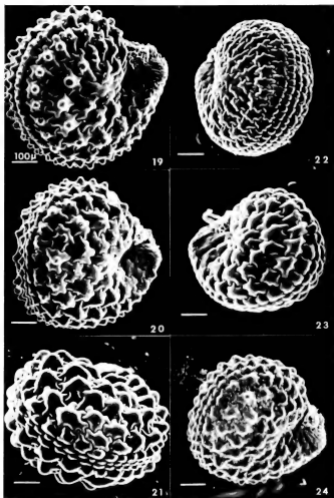
To obtain an overall perspective of variability in seed surface texture over the western geographical area, a three × five inch scale map of Louisiana,

Figures 1–24. Scanning electron micrographs of seeds of red-flowered portulacas, originally labeled *Portulaca pilosa*, *P. mundula* or *P. parvula*. 1. Florida. Dade Co.: 1 Aug 1940, *Arnold s.n.* (FLAS). 2. Florida. Citrus Co.: 13 Aug 1958, *Kral 7825* (NY). 3. Florida. Escambia Co.: 8 Aug 1981, *Barkhalter 7859* (FSU). 4. Alabama. Mobile Co.: 20 Aug 1968, *Kral 32710* (GA). 5. Mississippi. Harrison Co.: 6 Jul 1952, *Demaree 32138* (SMU). 6. Louisiana. Allen Co.: 23 Oct 1964, *Thieret 18690* (FSU). 7. Louisiana. Morehouse Co.: 27 Jul 1977, *Thomas & Pias 54274* (NLU). 8. Arkansas. White Co.: 14 Oct 1974, *Demaree 64262* (GA). 9. Texas. Hardin Co.: 27 Aug 1970, *Anmeron & Watson 244* (SMU). 10. Texas. Refugio Co.: 13 Oct 1956, *Shinners 25232* (SMU). 11. Texas. Cameron Co.: 22 May 1959, *Traverse 1046* (G). 12. Texas. Austin Co.: 12 Oct 1971, *Thomas 26208* (NLU). 13. Oklahoma. Bryan Co.: 30 Sep 1974 *Turner 39* (DUR). 14. Oklahoma. Oklahoma Co.: 7 Jul 1976, *Taylor 28950* (NLU). 15. Oklahoma. Harmon Co.: 26 Aug 1948, *Waterfall 8716* (G). 16. Oklahoma. Woods Co.: 5 Oct 1913, *Stevens 2882* (MO). 17. Texas. Frio Co.: 24 Jul 1941, *Thorp s.n.* (SMU). 18. Texas. Brewster Co.: 18 Jul 1936, *Warnock 121* (SMU). 19. Texas. Brewster Co.: 23 Aug 1970, *Semple 408* (MO). 20. Texas. Culberson Co.: 21 Jul 1943, *Waterfall 5242* (G). 21. Texas. Ward Co.: 18 Sep 1966, *Correll 33652* (NCU). 22. Oklahoma. Cimarron Co.: 11 Aug 1977, *Taylor 25255* (NLU). 23. Oklahoma. Indian Terr.: 21 Sep 1894, *Bush 31* (MO). 24. Mexico. Coahuila: 24–26 Aug 1938, *Jobston 7088* (G).









Arkansas, Missouri, Oklahoma and Texas was covered with clear, double-sided tape and individual seeds were placed on the map in the locations of their collections. Examination under a $30\times$ stereoscopic microscope made possible an analysis of local and broad patterns of variability. The maximum diversity of seed surface texture was noted in the Trans-Pecos (Figs. 17–21). There was an overall trend of flattened roughenings and less tubercles toward the north and west. To see this, compare Figs. 6–8 from Louisiana and Arkansas, Figs. 9–12 from south and central Texas with Figs. 12–16 from central Oklahoma and Figs. 17–21 from the Trans-Pecos with Fig. 22 from Western Oklahoma.

From an analysis of these surface patterns (Figs. 1–22) it is apparent that variability of seed surface patterns occurs within geographic regions and within the species. Since all these seeds were taken from known red-flowered plants, seed surface texture is not a trait which alone can be used to separate red-flowered *P. mundula* from *P. pilosa*. Legrand stated that seed surface texture was not a good character for distinguishing varieties of *P. oleracea*, so the implication is that it is not a good character for distinguishing species, which our data support.

THE CONCEPT OF *PORTULACA MUNDULA*

The character states taken from descriptions and keys, listed in Table 1 show very little difference between the taxa called *P. pilosa* and *P. mundula*. When Johnston formulated the idea of *P. mundula* he stated that he had taken his concept of *P. pilosa* from pictures portraying the Linnean taxon, but there is no indication that he examined any specimens of *P. pilosa* outside of the Southwest. It would be difficult, in our opinion, to develop a concept of variability of as widespread a taxon as *P. pilosa* from pictures, particularly those as stylized as Commelin's and Herman's. Examination of their descriptions shows only one inconsistency in the typical morphological expression of *P. pilosa*; this being in the leaf morphology. Herman notes that the tops of the leaves are flat, Commelin makes no such reference. In our observations, the typical terete leaf cross-section may become hemispherical (flat on top) in robust plants growing in richer soils. The overall shape, whether terete or hemispherical, is linear and not spatulate or oblanceolate.

The general lack of consistency in character states for the specimens from Texas made us wonder about the consistency of the material cited by Johnston. The holotype from Coahuila, Mexico, was measured or scored for the same characters; capsule diameter, pedicel length and seed surface, using 15 capsules from the type instead of three. The pedicel length

averaged 0.65 mm, with a range of 0.3–1.1, and the capsule diameter averaged 1.95 mm, with a range of 1.6–2.4. Note the ranges are from a single plant. These results also show a smaller set of averages than the ranges given by Johnston in his original description (Table 1). Of the paratypes which were compared in Table 2, only one specimen, Texas, Mill Creek, Aug 1843, *Lindheimer s.n.*, (G) had capsules 2.5 mm in diameter. For the seeds of the paratypes, 11 had seed surfaces that were stellate flattened roughenings, not stellate-tuberculate. These 11 specimens were from west Texas, Oklahoma and Missouri, while the stellate tuberculate seed surfaces were found on specimens from the remainder of Texas. Johnston cited no specimens from Arkansas. Figure 24 is a seed from the holotype, while Fig. 23 is a paratype from Oklahoma, (Indian Territory): Sapulpa, 21 Sep 1894, *Bush 31* (G). Note the close resemblance of Fig. 24, the type, to that of Fig. 3 from Florida, and that Fig. 23 does not fit the tuberculate pattern of the type. This tuberculate pattern has been used as a distinguishing morphological feature for the species. In fact, these findings on Johnston's paratypes show the same trends noted above, with flattened stellate roughenings toward the northern part of the distribution.

Portulaca pilosa has long been recognized as a taxon in Florida (Small, 1933). Legrand cited specimens from Florida, Georgia and Mississippi. Our measurements and analysis of capsule diameter, pedicel length, seed size and surface texture show no clearcut separation of red-flowered plants between Florida and Texas. Our data also support the comments of Legrand regarding the decreased size of capsules in plants growing in arid regions in contrast to larger capsules found in the tropics. The specimens with the smallest capsule diameters are from specimens recently collected from Arkansas, Oklahoma and Missouri. Some of the recent Texas specimens had small capsules, but the average of all Texas red-flowered specimens fits easily into the range of *P. pilosa*. It is possible to select specimens from dry habitats with small capsules and specimens from wet habitats with larger capsules. Unfortunately the habitat data on most of the labels are insufficient to permit an extensive analysis. Modern records from Arkansas, Missouri and Oklahoma show that the red-flowered species, which we are calling *P. pilosa*, is mostly restricted to dry ridges, bluffs and outcrops with sandy soil.

THE QUESTION OF *PORTULACA PARVULA*

Concerning the *P. pilosa*-*P. parvula* separation, as noted above, Gray treated the yellow-flowered taxon as *P. parvula*. Johnston redefined *P.*

parvula by adding the traits of small capsules, long pedicels and flattened stellate roughenings on the seed surfaces (Table 1). Measurements of the lectotype designated by Johnston: Mexico, Chihuahua: Sierra Santa Eulalia, fl. yellow 18 Aug 1885, Pringle 543 (G), provided six capsules measuring 1.02 mm in diameter and pedicel lengths averaging 0.6 mm, both less than stated by Johnston, but the seed surfaces had stellate flattened roughenings. We have seen red-flowered specimens from Oklahoma with capsules 1.5 mm in diameter, pedicels 1.0 mm long and seeds with stellate flattened roughenings (Fig. 23). In examining over 700 specimens labeled *P. pilosa*, *P. mundula*, or *P. parvula*, only two were found with yellow flowers. This low number shows that either yellow-flowered, pilose *Portulacas* are rarely collected or they are less common than one would think. Taylor (R.J. Taylor, DUR 1984, pers. comm.) reported that yellow-flowered plants occasionally occur with red-flowered plants in Oklahoma. Smith (E.B. Smith, UARK 1984, pers. comm.) and Tucker (G. Tucker, APCR 1984, pers. comm.) have not seen yellow-flowered, pilose *Portulacas* in Arkansas. Steyermark (1963) does not report a yellow-flowered, pilose taxon in Missouri.

Legrand treated the yellow-flowered *P. parvula* under *P. halimoides* L. citing the depauperate growth in the deserts and reaching its northern limit in the United States. *Portulaca halimoides* is a Mexican species, occurring chiefly in the western half of that country which could be invading the Trans-Pecos through or around the Chihuahuan Desert. *Portulaca halimoides* may not have been known by Gray, hence his describing the yellow-flowered taxon as a new species. Johnston also may have been unfamiliar with it, and accepted Gray's interpretation. Before any final conclusions can be reached, further studies should be made of yellow-flowered species from a greater southwestern geographical range. Field studies to determine intermixing with red-flowered plants should also be undertaken.

There is another possibility for the occurrence of few yellow-flowered plants. More than one species of *Portulaca* has both red and yellow flowers. *Portulaca grandiflora* exhibits a wide range of petal colors and Legrand reports that *P. amilis* Speg. has a yellow-flowered form in South America, although in the United States so far only the red-flowered form has been seen (Judd and Wunderlin, 1981). There have not been any reports of *P. pilosa* having anything other than red flowers but it is possible that a genetic analysis of western populations may show an occasional yellow-flowered plant. This would account for the low incidence of yellow flowers overall or for the infrequent mention on herbarium labels of both red and yellow flowers in the same population as did Waterfall: Texas: Jeff Davis Co.: 20 mi SSE of Kent, 31 Jul 1943, Waterfall 5415 (G).

THE PRESENT STATUS OF *P. PILOSA*,
P. MUNDULA AND *P. PARVULA*

This study points up the problems of limiting the consideration of species concepts to unnatural boundaries and the importance of examining species complexes over a broad geographic range. Even in this case, the final answer will only come with a more extensive look at the Mexican flora.

In this study, comparison measurements of the character states of the morphological traits taken from descriptions and used in keys to distinguish *P. mundula* from *P. pilosa* show that there are no consistent characters which can be used, singly or together to separate the taxa. We conclude that *P. mundula* is conspecific with the more widespread and variable species *P. pilosa* and the name *P. mundula* should be treated as a synonym of *P. pilosa*.

For *P. parvula*, the only consistent identification trait is yellow petals. Specimens without petals cannot be identified by the seed surface texture as proposed by Johnston. However, without a more extensive examination of known yellow-flowered *P. parvula* along with a concept of *P. halimoides* we cannot reach any conclusion on the validity of *P. parvula* as a species.

CYTOLOGY

Very little information is known about the cytology of the genus *Portulaca* and there are some chromosome counts that are unusual. The cytoplasm stains darkly with aceto-carmin but fortunately the number of chromosomes is not large. The base numbers have been accepted as $\times = 4$ and 9, with polyploid multiples and possible aneuploid sequences.

The lowest number, $n = 4$ (Steiner, 1944), has a direct bearing on the *P. pilosa*-*P. mundula* problem. Steiner's report, unfortunately unvouchered, was taken from a plant collected at Springdale, Arkansas, in the NW corner near Oklahoma and Missouri. Steiner could not identify the plant to species and speculated that it may be a new species. The senior author has verified this count on plants grown from seed collected from a sandstone outcrop in Benton Co., Arkansas near Springdale. This species would now be interpreted as *P. pilosa*, and the specimen appears to be such. This count would represent a new number for this species, giving a sequence of $n = 4, 8, 9, 18$. The $n = 4$ is interesting in that it is the lowest number for the genus. The highest number for *P. pilosa*, $n = 18$, was reported by Hsu (1968).

Since *P. pilosa* is geographically widespread, the variation in chromosome number is not unexpected. However, it appears that *P. pilosa* exhibits polyploidy from both base numbers of the genus. How widespread the $n = 4$ number is for the high prairie of the United States and what relationship this number has to the actual numbers and to the potential for gene

exchange with the southwestern populations is unknown. Chromosome data need to be determined for the western populations. All counts for *P. pilosa* from the Southeast have been $n=8$. A study of the cytology of this taxon in Oklahoma, Texas, Arkansas and Missouri would help to clarify the species concept in that area. If study shows that designation of a new species is warranted, then a new name would be needed, since the description associated with the name *P. mundula* probably would not encompass this new taxon. Also, the perpetuation of the name *P. mundula*, redefined to new limits, would only add to the confusion of the species concept.

THEORETICAL PATTERNS OF MIGRATION OF *PORTULACA*
IN CENTRAL AMERICA AND THE UNITED STATES

Portulaca, with a large concentration of species in South America, has spread north into Central and North America, including the Caribbean (Legrand). *Portulaca pilosa* probably entered Florida from the Caribbean and spread northeast along the Atlantic coastal plain into North Carolina. A greater movement has taken place westward along the Gulf Coast, but there is no indication of an inland movement up the Mississippi embayment into Arkansas and Missouri. Only one isolated population, with measurements similar to those of the coastal plain has been reported from Tennessee, that along Interstate-40 (Wilson Co.). A scattered distribution is noted in northern Louisiana with most of these collections associated with recent human activity, e.g. railroads, road fills and dumps.

Northeast Texas shows the same scattered distribution as northern Louisiana, while the greatest concentration of *P. pilosa* is in south Texas along the Gulf Coast and in the Trans-Pecos region. There is a similarity of the plants in the Trans-Pecos area with those of the panhandles of Texas and Oklahoma, having a general reduction in size northeastward. Our label data show the distribution of *P. pilosa* in Arkansas in the mountains; the measurements show affinities with the gene pool of Oklahoma and not the coastal plain. The dates of collection also show a more recent movement eastward into Arkansas. The habitats in Arkansas are in the highlands and represent affinities with Oklahoma physiographically (G. Tucker, APCR 1984, pers. comm.).

Legrand commented on the existence of *P. pilosa* in the Caribbean Islands, Florida and Mexico, stating there was a morphological change toward smaller plants as one moves toward drier habitats, particularly in Mexico. These statements support the patterns of distribution indicated by the herbarium specimens we have seen. A two-directional pattern of movement of *P. pilosa* into the United States can be postulated: 1. From the Caribbean into Florida, northeast along the Atlantic coastal plain and also

westward along the Gulf Coast to the Mississippi embayment and, 2. From South America into Central America (Mexico) and northeastward into Texas, Oklahoma, Arkansas and Missouri.

A similar pattern can be postulated for the movement of *P. parvula*, if indeed it is really *P. halimoides*. *Portulaca halimoides*, according to Legrand, is found in central and western Mexico and "appears to be spreading along major highways." Its invasion into northern Mexico and southwest Texas (Trans-Pecos) is probably controlled to some extent by human activity and the availability of habitats as has been shown in other cases, particularly that of *P. amilis* (Judd and Wunderlin, 1981).

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SIDUS SIDARUM — V. THE NORTH AND CENTRAL AMERICAN SPECIES OF *SIDA*.

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The genus *Sida* L. is one of the larger and more difficult genera of the Malvaceae. Over 1000 names have been published in the genus, although recent estimates admit only 150–250 species. Even this range may be too high. There is much synonymy. Many species that were originally (or at one time) placed in *Sida* have been relegated to other genera because the early concept of *Sida* was as a very inclusive genus, more or less encompassing all mallows that were uniovulate and lacked an involucrel.

A contemporary revision of *Sida* is needed. The nearest approach to such a comprehensive treatment for the New World are the two "tentative keys" published by Kearney (1954, 1958) and the detailed study of Clement (1957). In the subsequent quarter century understandings of *Sida* have deepened, additional species have been described, others have been segregated out of the genus, and a clearer understanding of sections within the genus has emerged. Hence, it is felt that the time is opportune to begin a new treatment of *Sida*. The present treatment of the North and Central American species is a beginning.

I follow Kearney (1954) and others in taking "North America" to include the West Indies and Central America as far as (and including) Panama, but use the more expanded designation in the title for the sake of clarity. Those Caribbean islands that are primarily South American in location and phytogeography (Aruba and Curaçao to Trinidad and Tobago) are excluded.

Numerous species have been segregated to other genera, e.g. to *Allosidastrum* (Hochr.) Krapov. Fryx. & Bates (ined.), *Bastardiopsis* (Schum.) Hassl., *Billieturnera* Fryx., *Dendrosida* Fryx., *Krapovickasia* Fryx., *Malvella* Jaub. & Spach, *Meximalva* Fryx., *Rhynchosida* Fryx., and *Sidastrum* E. G. Baker. The removal of such species has made the residual genus less heterogeneous and more natural—and thus more readily characterized.

I earlier (Fryxell, 1978) emphasized the morphology of the mericarps and

of the calyx in delimiting *Sida*. The mericarps are differentiated into a lower, one-seeded, indehiscent cell and an upper, empty, dehiscent portion that is often ornamented with a pair of spines. The upper and lower portions of the mericarp are set apart dorsally by a distinctive "shoulder" that is an extension and joining of two lateral ribs. The presence of this shoulder is distinctive. The lower cell is trigonal in cross section and is often laterally reticulate.

The calyces in *Sida* are typically 10-costate at the base, the ten ribs leading alternately to the sinuses and the apices of the 5-lobed calyx. The former (the commissural nerves) are relatively more prominent (especially in sect. *Sida*); the latter become the midribs of the calyx lobes. These ribs are often yellowish where they come together at the base of the calyx.

Growth habit also distinguishes *Sida* to a degree. The genus includes annual and perennial herbs and relatively small shrubs, seldom exceeding 1–1.5 m in height.

Characters of the calyx and of the mericarps are useful not only in delimiting the genus but also in subdividing it into sections. Previous subdivisions of the genus (e.g. Gray, 1849; Schumann, 1891, who were followed by Baker, 1892; Rodrigo, 1944; Kearney, 1951, 1954; and Hutchinson, 1967) have not been entirely satisfactory, in part because it was difficult for them to establish natural sections when they accepted the genus as a heterogeneous group. Clement's (1957) subdivisions were more natural (except his sect. *Physalodes* A. Gray, which included elements of three or more genera), but Clement dealt with only selected sections and omitted a major portion of *Sida*. Monteiro's (1942, 1949) subdivisions were too complex to be coherent. In the following treatment I recognize 11 sections of *Sida* that I believe represent natural groups. I will comment on species not represented in North America that are included in these sections and will allude to those two sections not represented in North America and include them in the key to the sections.

Leaf morphology is a strong supporting character in delimiting the sections of *Sida* and to a lesser degree in distinguishing species. The accompanying figures (Figs. 1–6) are presented to facilitate understanding of the sectional descriptions and to demonstrate the characters of leaf form that support the sectional divisions. The figures are not intended (except in certain instances) to be critical in making identifications at the specific level.

KEY TO THE SECTIONS OF *SIDA*

- a. Leaves entire, narrowly linear to elliptic or broadly lanceolate (Fig. 1, I–J);
inflorescence corymbiform, terminal, essentially leafless sect. *Stenoidae* (p. 65)

- a. Leaves crenate, dentate, or serrate (rarely subentire), variously shaped; flowers solitary in the axils or variously aggregated into inflorescences, seldom corymbiform.
- b. Leaves deeply palmately lobed.
- c. Mericarps (and styles and stigmas) commonly 5 (sometimes 7-9), strongly differentiated, with two apical spines or arista; anthers 5-20 (Bolivia, Peru, Ecuador) sect. *Oligandrae* (p. 65)
- c. Mericarps (and styles and stigmas) 8-10, relatively undifferentiated, mucicous; anthers 10 or more.
- d. Flowers in ample terminal inflorescences; anther numerous (United States) sect. *Pseudo-Napaeae* (p. 66)
- d. Flowers axillary, solitary or paired; anthers 10-20 (Australia, Africa) sect. *Hoskerianae* (p. 66)
- b. Leaves unlobed (or if lobed, shallowly so), linear, elliptic, lanceolate, or broadly ovate.
- e. Leaves lanceolate or ovate, basally more or less cordate, dentate to the base (Fig. 1, G-H; Figs. 2-4).
- f. Mericarps (and style and stigmas) uniformly 5, the spines, if pubescent, antrorsely so; calyx ribs obscure.
- g. Calyx lobes dark-green-margined, trullate; plants often scandent or prostrate sect. *Nelavagae* (p. 68)
- g. Calyx lobes not bi-colored; plants usually erect (sometimes prostrate) sect. *Spinosae* (p. 72)
- f. Mericarps (and styles and stigmas) 7 or more (sometimes as few as 5); calyx ribs pronounced
- h. Flowers and fruits commonly subsessile in axillary glomerules and densely aggregated into racemiform or paniculate inflorescences; mericarps mucicous, weakly (if at all) reticulate; plants sometimes prominently setiferous sect. *Muticae* (p. 76)
- h. Flowers and fruits variously disposed but not densely aggregated as above (except sometimes in *S. cordifolia*); mericarps usually spinose and reticulate, the spines often retrorsely barbed; plants usually not setiferous. sect. *Cordifoliae* (p. 77)
- e. Leaves linear, elliptic, or rhomboid, basally truncate or cuneate, dentate to the base (Fig. 5) or basally entire and distally dentate (Fig. 1, A-E; Fig. 6).
- i. Leaves more or less rhomboid (Fig. 6); mericarps 7-11, usually glabrous sect. *Sidalae* (p. 85)
- i. Leaves linear, oblong, or elliptic.
- j. Mericarps (and styles and stigmas) 5-7, often mucicous; flowers and fruits apically congested with leaves and stipules so as to appear involuclate; leaves often dentate only at apex, even subentire (Fig. 1, A-E); plants often prostrate sect. *Malachroidae* (p. 80)
- j. Mericarps (and styles and stigmas) usually more than 7, smooth; flowers and fruits solitary in the axils or crowded apically but not appearing involuclate; leaves usually dentate throughout (Fig. 5); plants usually erect sect. *Ellipticifoliae* (p. 82)

SIDA section STENINDAE Grisebach, Fl. Brit. W. 1. 76. 1859. TYPE: *Sida linifolia* Cavanilles.

Herbs or subshrubs, hirsute or hispidulous to glabrescent. Leaves entire, narrowly linear to elliptic or broadly lanceolate (Fig. 1, I–J); petioles 3–6 mm long; stipules equaling or exceeding the petioles. Flowers borne in a leafless terminal corymbiform inflorescence of 8–10 flowers; calyx rounded, 5–7 mm long; corolla 8–15 mm long, white or yellowish with dark center. Mericarps 5–9, thin-walled, indehiscent, apically blunt.

Sida sect. *Stenindae* includes two species, one of which, *S. linifolia*, occurs in North America. The other, *S. bassleri* Hochr., is endemic to Paraguay. The two taxa have been distinguished in varietal rank (cf. Clement, 1957).

1. SIDA LINIFOLIA Cavanilles, Diss. 1:14. t. 2. f. 1. 1785. TYPE: in insula Caienae and in Peru.

Sida graminifolia L. Richard, Actes Soc. Hist. Nat. Paris 1:111. 1792. TYPE: none stated.

Sida vimina Fischer ex Link, Enum. Pl. 2:202. 1822. TYPE: BRAZIL.

Sida linearifolia Thonning in Schumacher, Beskr. Guin. Pl. 303. 1827; Dansk. Vid. Selsk. Afh. 4:77. 1829 (non St.-Hilaire, 23 Apr 1827). TYPE: GUINEA. Thonning 120 (C-4; cf. Junghans, 1961, p. 343; Hepper, 1976, p. 72).

Sida angustissima Miquel, Strip. Surin, Sel. 102. 1850 (non St. Hilaire, 1827).

Sida longifolia Brandegee, Zoe 5:212. 1905 TYPE: MEXICO. Sinaloa, Culiacán, Cerro Colorado, 3 Nov 1904, Brandegee s.n. (HOLOTYPE: UC).

Sida fibrigii Ulbrich, Bot. Jahrb. Syst. 54 (Beibl. 117):72. 1916. TYPE: PARAGUAY, Cordillera de Altos, Fibrig 572 (M as photo F-19686).

Sida linifolia is usually a savanna plant at elevations below 1200 m. It occurs from Panama north to Mexico (Chiapas to Sonora on the Pacific slope, and eastward to Tabasco and Veracruz); in the West Indies in Cuba, Hispaniola, Jamaica, and Martinique. It is also found throughout much of South America (Colombia, Venezuela, the Guianas, Brazil, Paraguay, Peru, and Bolivia), in various parts of Africa (Sierra Leone to Tanzania to Angola), and in Fiji.

SIDA section OLIGANDRAE Clement, Contr. Gray Herb. 180:64. 1957.

TYPE: *Sida palmata* Cavanilles.

Erect annual herbs, variously pubescent. Leaves palmately lobed, long-petiolate. Inflorescences more or less paniculate; calyx cupuliform, often ecostate, 6 mm or less at anthesis but often accrescent; petals equaling or somewhat exceeding calyx, often red or purplish; stamens 5–20. Mericarps often 5–9, the lateral walls adnate to the seed, usually long-aristate (4–14 mm long) the aristae retrorsely pubescent.

Sida sect. *Oligandrae* includes eight species, none of which occurs in North America (Fries, 1947, pp. 14–19; Clement, 1957). The section is a distinctive natural group, indigenous to relatively high elevations in Ecuador, Peru, and Bolivia.

SIDA section PSEUDO-NAPAEAE A. Gray, Mem. Amer. Acad. Arts 4 (Pl. Fendl.):23. 1849. TYPE: *Sida hermaphrodita* (L.) Rusby.

Robust perennial herb 1–5 m tall, glabrous or with sparse pubescence. Leaves large (up to 24 cm long), palmately 5–7-lobed, coarsely dentate, petiolate (Fig. 1, F). Inflorescence a terminal panicle composed of umbellate corymbs; calyx cupuliform, ecostulate; corolla white, 8–9 mm long; stamens numerous. Carpels 8–10, indehiscent, with horizontal rostrum, the lateral walls evanescent.

The section is monotypic. Clement (1957) points out that it "has no close affinities with any other [section] in the genus, nor with *Napaea* save in habit." It is also geographically and ecologically distinct from the remainder of *Sida*, being a temperate-zone plant whereas *Sida* is typically tropical and subtropical. One might plausibly argue that the section be elevated to generic rank.

2. SIDA HERMAPHRODITA (L.) Rusby, Mem. Torrey Bot. Club 5:223. 1894. BASIONYM: *Napaea hermaphrodita* L. Sp. Pl. 686. 1753. TYPE: probably from Hort. Cliff. (BM); the species is not represented in the Linnean Herbarium (LINN) in spite of the assertion of Iltis (1963, p. 106). *Sida napaea* Cavanilles, Diss. 5:277. t.132.f.1. 1788.

Napaea laevis L. Mant. 2:435. 1771, pro syn.

Sida hermaphrodita occurs in the United States, in Maryland, the District of Columbia, Pennsylvania, West Virginia, Tennessee, Ohio, and Michigan—possibly escaped from former cultivation at some localities (cf. Iltis, 1963, pp. 106–107; Spooner et al. 1985).

SIDA section HOOKERIANAE Clement, Contr. Gray Herb. 180:77. 1957. TYPE: *Sida hookeriana* Miquel ex Lehmann.

Herbs or subshrubs, sometimes decumbent. Leaves 3–5-lobed, 3–7 cm long, long-petiolate, sparsely pubescent to glabrous. Flowers solitary or paired in the leaf axils on slender peduncles; calyx cupuliform, 5–8 mm long; corolla white or pale yellow, slightly exceeding calyx; anthers 10–20. Mericarps ca. 10, mucicous, indehiscent.

Sida sect. *Hookerianae* was described to include two species, one from southwestern Australia (*S. hookeriana* Miquel ex Lehmann), the other

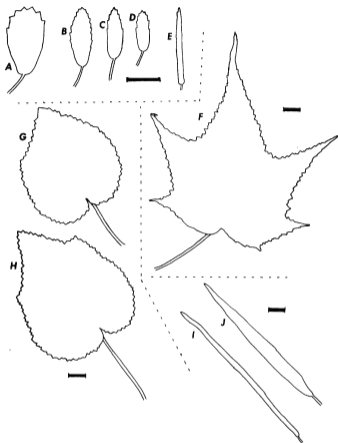


Figure 1. Leaf outlines of *Sida*. A-E, *Sida* sect. *Malachroidae*: A, *S. brittonii*; B-D, *S. ciliaris*; E, *S. brachystemon*; F, *Sida* sect. *Pseudo-najasa*: *S. hermaphrodita*; G-H, *Sida* sect. *Maticae*: *S. aggregata*; I-J, *Sida* sect. *Steninda*: *S. linifolia*. [A, León & Roca 7466; B, Hinton 1469; C, Magallanes 3723; D, Lasalle et al. 810629-1; E, Koch et al. 79424; F, Fryxell s.n.; G, Fryxell & Bates 2107; H, Fryxell & Bates 2123; I, Ventura 5638; J, Koch & Fryxell 82207.] Scale = 1 cm.

African, from Ethiopia to South Africa (*S. ternata* L. fil.). The section is not represented in the Americas.

SIDA section NELAVAGAE Borssum Waalkes, Blumea 14:180. 1966.

TYPE: *Sida cordata* (Burman fil.) Borssum Waalkes [NOMENCL. *Melochia cordata* Burman fil.].

Prostrate or decumbent herbs to erect shrubs, variously pubescent with stellate hairs, glandular hairs, and setose hairs. Leaves ovate-cordate, serrate-crenate throughout (Fig. 2). Flowers solitary in the axils, in axillary glomerules, or in diffuse panicles; calyx pentangular and pyramidal, the lobes trullate, the margins and midribs dark green against a light green background; corolla white, yellow, or orange, sometimes with a red center. Mericarps uniformly 5, mucicous and glabrous or spinescent and antorsely pubescent, the dorsal walls rounded and carinate, the lateral walls thin and sometimes evanescent.

In addition to the North American species treated here, sect. *Nelavagae* includes two additional species from Asia, *S. elongata* Blume and *S. mysorensis* Wight & Arnott (cf. Borssum Waalkes, 1966) and several species from South America, such as *S. dictyocarpa* Grisebach and *S. caudata* St.-Hilaire (cf. Rodrigo, 1944; Kearney, 1958).

Members of sect. *Nelavagae* are characterized by a base chromosome number of $x = 8$ and are distinguished from the remaining species of the genus, which (where known) have a base number of $x = 7$.

KEY TO THE NORTH AMERICAN SPECIES
OF SIDA SECT. NELAVAGAE

- a. Plants prostrate, often repent, never viscid.
 - b. Leaves markedly asymmetrical, ovate (Fig. 2, C-D); calyx lobes cordate, accrescent becoming sagittate in fruit; staminal column glabrous 5. *S. jussiana*
 - b. Leaves symmetrical or slightly asymmetrical, orbicular-ovate; calyx lobes triangular, not accrescent; staminal column pubescent.
 - c. Stems repent; mericarps awned. 7. *S. repens*
 - c. Stems not (or rarely) rooting at the nodes, sometimes ascending; mericarps minutely apiculate. 3. *S. cordata*
- a. Plants ascending to erect, often scandent, viscid or not; leaves symmetrical (Fig. 2, A-B, I-L); calyx not accrescent.
 - d. Flowers subsessile, aggregated into dense axillary glomerules or in axillary pedunculate "heads"; stems often hispid (hairs 2-3 mm long); mericarps mucicous, glabrous 8. *S. urens*
 - d. Flowers pedicellate (the pedicel longer than the calyx), solitary in the leaf axils or in open panicles; stems usually viscid.
 - e. Mericarps usually beaked and pubescent; plants viscid or not. 4. *S. glabra*
 - e. Mericarps mucicous; plants densely viscid.

- f. Mericarps wholly glabrous, blackish at maturity; stems with simple hairs 2–3 mm long in addition to glandular hairs; leaves often with a purplish blotch along the midvein 9. *S. xavieri*
 f. Mericarps pubescent, brownish; stems lacking long hairs; leaves not blotched 6. *S. neogona*

3. *SIDA CORDATA* (Burman fil.) Borssum Waalkes, *Blumea* 14:182. 1966.

BASIONYM: *Melochia cordata* Burman fil. *Fl. Ind.* 143. 1768. TYPE: "*Melochia cordata*" s. coll. s.n. (HOLOTYPE: G). Borssum Waalkes (1966, p. 183) comments on the type.

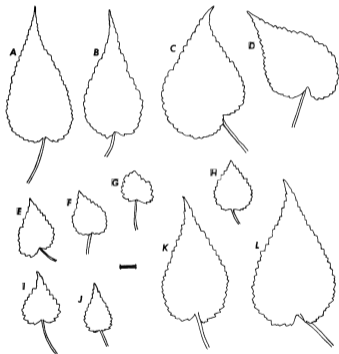


Figure 2. Leaf outline of *Sida* sect. *Nelavaga*. A-B, *S. glabra*; C-D, *S. jussiaea*; E-G, *S. repens*; H, *S. cordata*; I-J, *S. xavieri*; K-L, *S. urens*. [A, Koch et al. 79133; B, Ventura 14012; C, Velasco 8874; D, Fryxell & Lott 3312; E, Molina & Williams 31209; F, Sintenis 2951; G, Sintenis 179; H, Tyson 144; I, Koch et al. 79470; J, Koch et al. 79502; K, Dorantes et al. 5274; L, Fryxell & Lott 3234.] Scale = 1 cm.

- Sida veronicaefolia* Lamarck, *Encycl.* 1:5. 1783. TYPE: "Les Indes," *Sonnerat s.n.* (HOLOTYPE: P-LA, MA as photo F-29795). *Sida humilis* var. *veronicaefolia* (Lamarck) Masters, *Fl. Brit. Ind.* 1:322. 1875.
- Sida radicans* Cavanilles, *Diss.* 1:8. t.9.f.3. 1785. TYPE: Rheede, *Hort. Malabar.* t.69 (HOLOTYPE).
- Sida morifolia* Cavanilles, *Diss.* 1:9. t.20.f.2. 1785. TYPE: MAURITIUS, *Commerçon s.n.* (HOLOTYPE: MA). *Lamarkia morifolia* (Cav.) Medikus, *Phil. Bot.* 1:28. 1789.
- Sida multicaulis* Cavanilles, *Diss.* 1:10. t.1.f.6. 1785. TYPE: MALABAR, ?*Sonnerat s.n.* (HOLOTYPE: MA). *Sida veronicaefolia* var. *multicaulis* (Cav.) E. G. Baker, *J. Bot.* 30:293. 1892.
- Sida humilis* Cavanilles, *Diss.* 5:277. t.134.f.2. 1788. TYPE: Borssum Waalkes (1966) designated as neotype: Luzon, Port Cavite, *Née s.n.* (MA). Marais (1983) took exception to this choice of neotype, but offered no resolution of the problem, stating only the opinion that the plant in question did not conform to *Sida cordata* (Burm. f.) Borss., giving no description of the plant or any opinion as to its identity. Both authors overlooked the fact that *Sida humilis* Cav. can be satisfactorily typified on the basis of Cavanilles' plate, thus obviating the need to designate a neotype. *Sida veronicaefolia* var. *humilis* (Cavanilles) K. Schumann, *Marr. Fl. Bras.* 12(3):320. 1891.
- Sida unilocularis* L'Héritier, *Scirp. Nov.* 1:117 bis. t.56 bis. 1789. TYPE: L'Héritier's plate is cited as holotype by Borssum Waalkes (1966); it should be noted that L'Héritier cites a Commerçon collection from Mauritius, which may in fact be type material of the earlier *S. morifolia* Cav., thus making L'Héritier's name superfluous.

Sida cordata and *S. repens* (and their several synonyms) have been freely confused in the literature. It is therefore difficult to state their distributions from literature citations without consulting specimens or at least detailed descriptions. In the West Indies *S. cordata* apparently occurs in Puerto Rico and Hispaniola, possibly in Cuba and elsewhere. It also occurs in Malesia (Borssum Waalkes, 1966).

4. *SIDA GLABRA* Miller, *Gard. Dict.* ed. viii, no. 14. 1768 (non Nuttall, 1834). TYPE, fide Fawcett & Rendle (1926): (BM).
- Sida albifolia* Cavanilles, *Diss.* 1:15. t.2.f.2. 1785 (non Miller, 1768). TYPE: INS. SANTO DOMINGO, *Thouin s.n.*
- Sida glutinosa* Cavanilles, *Diss.* 1:16. t.2.f.8. 1785. TYPE: MAURITIUS, *Commerçon s.n.* (LECTOTYPE: P-JU). Borssum Waalkes (1966, p. 90) discusses the choice of lectotype.
- Sida arguta* Swartz, *Prodr. Veg. Ind. Occid.* 101. 1788 (non Presl, 1835). TYPE: JAMAICA, *Swartz s.n.* (HOLOTYPE: S; ISOTYPES: G as photo F-7996, B herb. Willd. no. 12692).
- ?*Sida arguta* Fischer ex Link, *Enum. Pl.* 2:206. 1822 (non Swartz, 1788). TYPE: BRAZIL. *Sida verruculata* DC. *Prodr.* 1:473. 1824.
- Sida nervosa* DC. *Prodr.* 1:465. 1824. TYPE: SANTO DOMINGO, "Sida paniculata," *Bertero s.n.* (HOLOTYPE: G-DC; ISOTYPE: MO, W as photo F-33387).
- Sida viscidala* Blume, *Bijdr.* 2:76. 1825. TYPE: *Blume s.n.* (HOLOTYPE: L).
- Sida fasciculata* Willdenow ex Sprengel, *Syst.* 3:113. 1826 (non Torrey & Gray, 1838). TYPE: Cumaná, *Humboldt & Bonpland s.n.* (B herb. Willdenow no. 12691). *Sida*

willdenowii D. Dietrich, Syn. Pl. 4:847. 1847.

Sida endlicheriana Presl, Reliq. Haenk. 2:111. 1835. TYPE: MEXICO, *Haenke s.n.* (ISOTYPES: BM, MO).

Sida alamosana S. Watson ex Rose, Contr. U.S. Natl. Herb. 1:93. 1891; Proc. Amer. Acad. Arts 26:133. 1891. TYPE: MEXICO, SONORA, Alamos, *Palmer 683* (BM, GH, US.).

Sida ruficula Hassler, Feddes Repert. Nov. Sp. Regni Veg. 12:264. 1913. TYPE: PARAGUAY, pr. Bellavista, in regione flum. Apa, *Hassler 10990* (B as photo F-9394, BM).

Sida caerensis Ulbrich, Notizbl. 6:322. 1915. TYPE: BRAZIL, Ceará, Cerro de Baturité, *Ule 9065* (B as photo F-9374, G).

Sida imperata Standley & Williams, Ceiba 3:51. 1952. TYPE: HONDURAS, DEPT. MORAZÓN, vic. of El Zamorano, *Standley 24639* (HOLOTYPE: US).

Sida glabra is widely distributed from Mexico south to Panama, through much of South America, and in the West Indies. It also occurs in parts of the Old World (cf. Borssum Waalkes, 1966).

5. *SIDA JUSSIEANA* DC. Prodr. 1:463. 1824. TYPE: PERU, *J. de Jussieu s.n.* (P-JU no. 12267, p.p.).

Sida decumbens St-Hilaire & Naudin, Ann. Sci. Nat. Bot. 18:52. 1842. TYPE: BRAZIL, MINAS GERAES, prope Congonhas, *Vaubier 21* (P as photo F-35535, and in Rodrigo, 1944, plate 11). *Avoda decumbens* (St.-Hil. & Naud.) Hochreutiner, Annuaire Conserv. Jard. Bot. Genève 20:56. 1916.

Sida stolonifera Salzmann ex Turczaninow, Bull. Soc. Nat. Mosc. 31:199. 1858. TYPE: BRAZIL, BAHIA, *Salzmann s.n.* (HOLOTYPE: KW; ISOTYPES: K, MO, P). *Physalium stoloniferum* (Salz. ex Turcz.) Monteiro, Anais XX Congr. Nac. Soc. Bot. Brasil 402. 1969.

Sida-begonioides Grisebach, Bonplandia 6:3. 1858. TYPE: PANAMA, *Duchassaing s.n.* (HOLOTYPE: GOET).

Sida jussieana occurs from southern Mexico (Guerrero, Oaxaca, and Chiapas) through Central America and throughout much of South America (to Brazil, Paraguay, and Argentina). Most of the above types are discussed by Krapovickas (1969, pp. 20-21).

6. *SIDA NESOGENA* Johnston, Proc. Calif. Acad. Sci. 20:76. 1931. TYPE: MEXICO, Revillagigedo Islands, Socorro Island, Grayson's Cove, *Mason 1613* (HOLOTYPE: CAS; ISOTYPES: GH, K, MO, US).

Sida nesogena is endemic to the Revillagigedo Islands.

7. *SIDA REPENS* Dombey ex Cavanilles, Diss. 1:7. 1785. TYPE: PERU, Lima, *Dombey s.n.* (MA as photo F-29787, P-JU no. 12267, p.p.). *Sida dombeyana* DC. Prodr. 1:463. 1824 (cf. Krapovickas, 1969, p. 20).

Sida chastodonta Turczaninow, Bull. Soc. Nat. Mosc. 31:199. 1858. TYPE: Guayaquil, *Jameson 392* (HOLOTYPE: KW; ISOTYPES: K, OXF).

Sida repens has a scattered distribution in the West Indies and also occurs

in Central America (Nicaragua, Panama) and South America (at least in Peru) and in Malasia. Borssum Waalkes (1966) treated this taxon as *Sida javensis* ssp. *expilosa* Borss., but the basionym for this name (*Sida pilosa* Cav.) represents a different species, viz. *Sida abutilifolia* Miller, q.v. In the West Indies *Sida repens* occurs in Cuba, Hispaniola, Jamaica, the Bahamas, the Virgin Islands, and Grenada.

8. *SIDA URENS* Linnaeus, Syst. Nat. ed. x. 1145. 1759. TYPE: *Browne s.n.* (LINN-866.20, as photo in Rodrigo, 1944, plate 17).

Sida verticillata Cavanilles, Diss. 1:13. t.1.f.12. 1785. TYPE: BRAZIL. Rio de Janeiro, *Jussieu s.n.* (MA as photo F-29796).

Sida rufescens St.-Hilaire, Fl. Bras. Mer. 1:185. 1827. TYPE: BRAZIL. MINAS GERAIS, prope Formigas, *St.-Hilaire s.n.* (HOLOTYPE: P; ISOTYPE: US). *Sida urens* var. *rufescens* (St.-Hil.) E. G. Baker, J. Bot. 30:294. 1892.

Sida debilis G. Don, Gen. Hist. 1:499. 1831. TYPE: GUINEA.

Sida sessiliflora G. Don, Gen. Hist. 1:499. 1831 (non Hooker, 1828, nec Dietrich, 1847). TYPE: GUINEA. *Sida congensis* D. Dietrich, Syn. Pl. 4:859. 1847.

Sida breviflora Steudel ex Triana & Planchon, Ann. Sci. Nat. Bot. 17:177. 1862, nom. nud.

Sida boivinii Hochreutiner, Annuaire Conserv. Jard. Bot. Genève 6:40. 1902. TYPE: MADAGASCAR, Mayotte, *Boivin 3331* (HOLOTYPE: G).

Sida urens var. *aurea* Hassler, Feddes Repert. Sp. Nov. Regni Veg. 12:267. 1913. TYPE: PARAGUAY, flum. Apa, *Hassler 11037* (K, NY).

Sida margaritensis Hassler, Feddes Repert. Sp. Nov. Regni Veg. 12:266. 1913. TYPE: PARAGUAY, prope Cerro Margarita, in regione flum. Apa, *Hassler 11065* (BM).

Sida urens occurs in southern Mexico and throughout Central America and the Greater and Lesser Antilles. It also occurs in many parts of South America and in Africa.

9. *SIDA XAVIERI* Monteiro, Anais XIX Congr. Nac. Soc. Bot. Brasil 47. 1968. TYPE: BRAZIL, PARAIBA, João Pressoa, 9 Oct 1941, *Xavier 342* (Laboratorio de Fibras) (HOLOTYPE: RBR?).

Sida xavieri is known from Brazil and has more recently been found to occur also in Mexico, Panama, and Venezuela.

- SIDA* section *SPINOSAE* Small, Man. Southeast. Fl. 849. 1933. TYPE: (Article 22): *Sida spinosa* Linnaeus.

Procumbent herbs or erect herbs or subshrubs, variously pubescent. Leaves lanceolate, oblong-ovate, or rotund, dentate-crenate throughout, short- to long-petiolate (Fig. 3). Flowers mostly in the leaf axils, the pedicels long or short; calyx angulate, inconspicuous, 10-nerved; corolla yellow or white. Mericarps uniformly 5, usually spinescent, dorsally carinate.

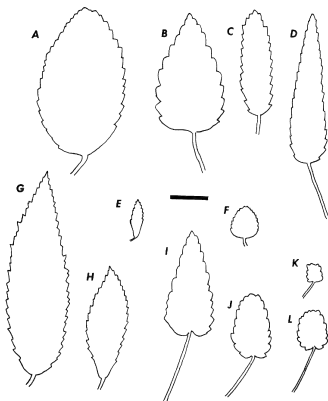


Figure 3. Leaf outline of *Sida* sect. *Spinosa*. A, *S. jamaicensis*; B-D, *S. spinosa*; E, *S. viarum*; F, *S. nummularia*; G-H, *S. glomerata*; I-J, *S. abutilifolia*. [A, Ekman H2760; B, Regel s. n.; C, Steens 9367; D, Vázquez 2165; E, Neil 2972; F, Milne 85; G, Knapp 1905; H, Jiménez 5512; I, Pringle 8440; J, García 250; K, Rzedowski 29547; L, Clarke 17878-1.] Scale = 1 cm.

KEY TO THE NORTH AMERICAN
SPECIES OF *SIDA* SECT. *SPINOSAE*

- a. Plants procumbent (but not repent).
 b. Leaves short-petiolate, the blades rotund (Fig. 3, F), strongly discolorous; pedicel 1–2 times length of calyx. 13. *S. mammularia*
 b. Leaves long-petiolate, the blades oblong (Fig. 3, I–L); pedicel many times length of calyx, often with long (1–2 mm) simple hairs. 10. *S. abutifolia*
- a. Plants erect.
 c. Leaves (and branching pattern) distichous; stipules prominent, lanceolate or falcate.
 d. Plants densely stellate-pubescent throughout; leaves more or less obovate; mericarps with beaks 1–1.5 mm long 12. *S. jamaicensis*
 d. Plants hirsute; leaves acute; mericarps minutely apiculate . . . 11. *S. glomerata*
- c. Leaves spirally disposed; stipules subulate.
 e. Corolla white (or pale yellow) with red center; stipules commonly 3-nerved. 15. *S. siarum*
 e. Corolla yellow without red center; stipules usually 1-nerved . . . 14. *S. spinosa*

10. *SIDA ABUTIFOLIA* Miller, Gard. Dict. ed. viii. no. 12. 1768. TYPE: in cult. Miller *s.n.* (HOLOTYPE: BM). Note: The name is given as "abutifolia" on the type specimen and in Index Kewensis.

Sida procumbens Swartz, Prodr. Veg. Ind. Occid. 101. 1788. TYPE: HISPANIOLA, Swartz *s.n.* (LECTOYPE: S; ISOYPE: BM).

Sida pilosa Cavanilles, Diss. 1:9. t.1.f.8. 1785 (non Miller, 1768, nec Retzius, 1781, nec L'Héritier, 1789, nec Vellozo, 1825). TYPE: INS. SANTO DOMINGO.

Sida ovata Cavanilles, Diss. 6:350. t.196.f.2. 1788 (non Forskål, 1775, nec G. Don, 1831). TYPE: in R. Hort. Paris ex Santo Domingo (P).

Sida supina L'Héritier, Stirp. Nov. 109 bis. t.52 bis. 1789. TYPE: in Hort. Paris ex Hispaniola (G-DC, MA as photo F-29790).

Sida diffusa H.B.K. Nov. Gen. Sp. 5:257. 1822. TYPE: MEXICO, Zelaya, Humboldt & Bonpland *s.n.* (B herb. Willd. no. 12673 as photo F-9799, P). *Sida ramosa* Willdenow ex Sprengel, Syst. 3:120, 1826, pro syn.

Sida filiformis Moricand, Pl. Amer. Rar. 1:10. t.8. ex Bull. Sci. Nat. Géol. 23:79. 1830 (non Jacquin, 1767). TYPE: MEXICO, Tampico, Berlandier 220 (OXF).

Sida filicaulis Torrey & Gray, Fl. N. Amer. 1:232. 1838. TYPE: TEXAS, 1835, Drummond *s.n.* (K).

Sida filicaulis var. *setosa* A. Gray, Smithsonian Contr. Knowl. 5 (Pl. Wright. 2):22. 1853. TYPES: TEXAS, bottoms of the San Pedro, Wright *s.n.* (GH?); between Santa Barbara and the copper mines, Wright 892 (K). *Sida diffusa* var. *setosa* (A. Gray) E. G. Baker, J. Bot. 30:291. 1892.

Sida editorum Gandoger, Bull. Soc. Bot. France 71:630. 1924. TYPE: NEW MEXICO, Wooton 557.

Sida abutifolia occurs from the southern United States, through Mexico, Central America, and the West Indies to northern South America.

11. *SIDA GLOMERATA* Cavanilles, Diss. 1:18. t.2.f.6. 1785. TYPE: Jussieu *s.n.* (P-JU, n.v.).

Sida glomerata occurs widely in South America, and extends northward to the West Indies, Panama, and Costa Rica.

12. *SIDA JAMAICENSIS* Linnaeus, Syst. Nat. ed. x. 1145. 1759 (non Miller, 1768, nec Vellozo, 1825, nec Dietrich, 1847). TYPE: "jamaicensis" (LINN-866.10).

Sida sericea Miller, Gard. Dict. ed. viii. no. 15. 1768 (non Cavanilles, 1802). TYPE: JAMAICA, 1731, *Houstan s.n.* (HOLOTYPE: BM as photo BH, MICH).

Sida mollis L. Richard, Actes Soc. Hist. Paris 1:111. 1792. TYPE: not stated, presumably at P.

Sida bermannioides H. B. K. Nov. Gen. Sp. 5:258 [200]. 1822. TYPE: NOV. GRANAT., prope Honda, *Humboldt & Bonpland s.n.* (P as photo P-35538).

Sida tristis Schlechtendal, Linnæa 3:271. 1828. TYPE: ST. THOMAS, *Ehrenberg s.n.* (HAL?).

Sida carpinifolia var. *antillana* Millspaugh, Publ. Field Mus. Hist., Bot. Ser. 2:71. 1900. Based on: *Sida jamaicensis* Vellozo (non Linnaeus). [Also cited: Acapulco, Palmer 581; near Spot Bay, Grand Cayman, Millspaugh 1303.]

Sida densiuscula Gandoger, Bull. Soc. Bot. France 71:630. 1924. TYPE: ST. THOMAS, Eggers 195.

Sida guadalupensis Gandoger, Bull. Soc. Bot. France 71:630. 1924. TYPE: GUADELOUPE, *Duis 3210* (GH).

Sida cydonifolia Gandoger, Bull. Soc. Bot. France 71:630. 1924. TYPE: STO. DOMINGO, *Bory s.n.*

Sida jamaicensis occurs in Mexico, Central America, the West Indies, and Colombia.

13. *SIDA NUMMULARIA* E. G. Baker, J. Bot. 30:290. 1892. TYPE: CUBA. ISLE OF PINES, *Milne 85* (HOLOTYPE: K).

Sida nummularia is endemic to the Isle of Pines.

14. *SIDA SPINOSA* Linnaeus, Sp. Pl. 683. 1753. TYPE: "spinosa" (LINN-866.1). A photo of the type is reproduced by Rodrigo (1944, plate 13).

Sida alba Linnaeus, Sp. Pl. ed. ii. 960. 1763. TYPE: Hort. Upsal. "alba" (LINN-866.2).

Sida ulmifolia Miller, Gard. Dict. ed. viii. no. 1. 1768 (non Cavanilles, 1785). TYPE: cult., *Miller herb.* (no. 1) (BM)—mounted with a Wright specimens (no. 2) from Jamaica.

Sida angustifolia Miller, Gard. Dict. ed. viii. no. 3. 1768. TYPE: in cult., *Miller s.n.* (HOLOTYPE: BM). *Sida milleri* DC. Prodr. 1:472. 1824 (as *S. miller*).

Sida pempinellifolia Miller, Gard. Dict. ed. viii. no. 4. 1768. TYPE: (fide Fawcett & Rendle, 1926): (BM).

Sida angustifolia Lamarck, Encycl. 1:4. 1783 (non Miller, 1768, nec Medikus, 1783). TYPE: s. loc., *s. coll. s.n.* (HOLOTYPE: P-LA). *Sida spinosa* var. *angustifolia* (Lamarck) Grisebach, Fl. Brit. W. I. 74. 1859.

Sida pusilla Cavanilles, Diss. 1:6. t. 1. f. 4. 1785. TYPES: *Jussiaeu s.n.*; *Thouin s.n.*

Sida truncata L'Héritier, Stirp. Nov. 107. t. 51. 1789 (non Cavanilles, 1785). TYPE: in horto ex Hispaniola, *Saint-Germain s.n.* (presumably at G). *Sida emarginata* Willdenow, Sp. Pl. ed. iii. 3:757. 1800.

Sida linearis Cavanilles, Icon. 4:6. t. 312. f. 1. 1797. TYPE: South America ex Cavanilles (C as photo F-21603) or plate 312, fig. 1. The type is not *Rimat* 1795 (photo F), as stated by Monteiro, because it was not cited by Cavanilles.

Sida hystrofolia Presl, Reliq. Haenk. 2:109. 1835. TYPE: MEXICO, *Haenke s.n.* (PR?).

Sida angustifolia var. *major* Presl, Reliq. Haenk. 2:109. 1835. TYPE: MEXICO, in portum Acapulco, *Haenke s.n.* (PR?).

Sida minor Macfadyen, Fl. Jamaica. 1:79. 1837. TYPE: JAMAICA, Port Royal Mountains.

Sida subditans St.-Hilaire & Naudin, Ann. Sci. Nat. Bot. 18:50. 1842. TYPE: BRAZIL, MINAS GERAES, *Claussen s.n.* (P as photo F-35548).

Sida tenuicaulis Hooker, Trans. Linn. Soc. London 20:232. 1847.

Sida heterocarpa Englemann ex Gray, Boston J. Nat. Hist. 6 (Pl. Lindh. 2):163. 1850. TYPE: TEXAS, HOUSTON, *Lindheimer s.n.* (GH?).

Sida affinis Schmidt, Beitr. Fl. Cap. Verd. Ins. 285. 1852 (non Sprengel, 1826).

Sida spinosa occurs from the central United States to central Argentina and is also known in the Old World. It is a common, often weedy species.

15. *SIDA VIARUM* St.-Hilaire, Fl. Bras. Mer. 1:182. 1827. TYPE: BRAZIL, MINAS GERAES, Comarca do Rio das Mortes, *St.-Hilaire s.n.* (P).

Sida viarum is a South American species that extends northward through Central America as far as southern Mexico.

- SIDA* section *MUTICAE* Presl, Reliq. Haenk. 2:104. 1835. LECTOTYPE (here designated): *Sida aggregata* Presl.

Presl's section is a heterogeneous group of ten species, including species now segregated to genera other than *Sida*. Presl's concept is narrowed by the exclusion of most of his species and is stabilized by the selection of a lectotype species. As here understood, the section is monotypic.

Shrubs to 1.5 m tall, often setiferous. Leaves petiolate, ovate to weakly 3-lobed, serrate, tomentose. Flowers subsessile in spiciform aggregations that are branched to form paniculate inflorescences; calyx prominently 10-angled, usually hirsute; corolla yellow-orange, sometimes with a red center. Mericarps 5–8, submuticous, essentially unornamented.

16. *SIDA AGGREGATA* Presl, Reliq. Haenk. 2:106. 1835. TYPE: MEXICO, *Haenke s.n.* (PR?).

Sida setifera Presl, Reliq. Haenk. 2:105. 1835. TYPE: in terris mexicanis occidentalibus, *Haenke s.n.* (PR?, W as photo F-32642).

Sida arguta Presl, Reliq. Haenk. 2:106. 1835 (non Swartz, 1788). TYPE: MEXICO, ad portum Acapulco, *Haenke s.n.* (PR).

Sida sassanarum K. Schumann, Mart. Fl. Bras. 12(3):308. 1891. TYPE: BRIT. GUIANA, *Schomburgk 819* (B as photo F-9395).

Sida aggregata occurs in Mexico, Central America, the West Indies, and northern South America.

SIDA section **CORDIFOLIAE** (DC.) Fryxell, stat. nov. BASIONYM: *Sida* [subsect.] *Cordifoliae* DC. Prodr. 1:463. 1824. TYPE (Article 22): *Sida cordifolia* L.

Erect shrubs or subshrubs, densely stellate-tomentose. Leaves petiolate, lanceolate to ovate, dentate-crenate throughout (Fig. 4). Flowers solitary in the axils, often aggregated terminally in racemes or panicles; calyx 10-ribbed, tomentose; corolla yellow or yellow-orange, the filaments more or less organized into 5 phalanges. Mericarps usually 7 or more, laterally reticulate, mucous to prominently aristate, the spines often retrorsely barbed.

In addition to the North American species treated here, the section *Cordifoliae* occurs in Australia (*S. roblenae* Domin and *S. atterophora* Domin) and includes a number of South American species, such as *S. angustissima* St.-Hilaire, *S. cerradoensis* Krapovickas, and several others. *Sida cordifolia* is pantropical.

KEY TO THE NORTH AMERICAN SPECIES
OF SIDA SECTION CORDIFOLIAE

- a. Stems and pedicels viscid; corolla yellow-orange, fading rose; mericarps glabrous or sparsely pubescent 23. *S. xanti*
- a. Stems and pedicels stellate-pubescent, not viscid; corolla usually yellow or yellow-orange, sometimes with a red center; mericarps usually pubescent.
 - b. Calyx 7–10 mm long.
 - c. Calyx irregularly 6–9 lobed 17. *S. barclayi*
 - c. Calyx regulary 5-lobed.
 - d. Mericarps mucous 22. *S. tragifolia*
 - d. Mericarps elongated apically, the dehiscent portion ca. half the length of the mericarp, the wall hyaline 19. *S. hyalina*
 - b. Calyx 5–7 mm long.
 - e. Corolla twice length of calyx, with red center 20. *S. maculata*
 - e. Corolla barely exceeding calyx, without red center.
 - f. Flowers and fruits crowded in terminal paniculate inflorescence; calyx prominently 10-ribbed 18. *S. cordifolia*
 - f. Flowers axillary; calyx not prominently ribbed 21. *S. salvifolia*

17. SIDA BARCLAYI E. G. Baker, J. Bot. 30:236. 1892. TYPE: SAN SALVADOR, Gulf of Fonseca, Sierra de Conchagua, *Barclay s.n.* (HOLOTYPE: BM).

Sida anomalouscalyx Fryxell, Syst. Bot. 4:255. 1979. TYPE: MEXICO. CHIAPAS, Mpio. de La Trinitaria, 18 km SW of La Trinitaria, *Breadlow 42230* (HOLOTYPE: DS; ISOTYPES: ENCB, pf).

Sida barclayi is known from southern Mexico (Oaxaca and Chiapas) and Central America (El Salvador, Nicaragua, and Costa Rica).

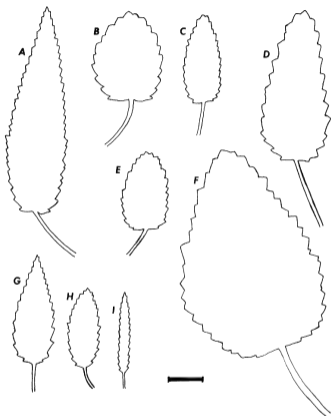


Figure 4. Leaf outlines of *Sida* sect. *Cordifoliae*. A, *S. barclayi*; B-C, *S. xanti*; D, *S. fragifolia*; E, *S. hyalina*; F, *S. cordifolia*; G-I, *S. salvifolia*. [A, Stevens 11108; B-C, Sanders *et al.* 3379; D, Palmer 103; E, Gentry 14301; F, Fryxell 725; G, Fryxell 1155a; H, Koeb & Fryxell 77458; I, Lott *et al.* 1552.] Scale = 1 cm.

18. *SIDA CORDIFOLIA* Linnaeus, Sp. Pl. 684. 1753. TYPE: "cordifolia 4" (LINN-866.12).
Sida micans Cavanilles, Diss. 1:19. t.3.f.1. 1785. TYPE: SANTO DOMINGO, *Jussieu s.n.* (P).
Sida althaeifolia Swartz, Prodr. Veg. Ind. Occid. 101. 1788. TYPE: JAMAICA, *Swartz s.n.* (HOLOTYPE: S). *Sida cordifolia* var. *althaeifolia* (Swartz) Grisebach, Fl. Brit. W. I. 76. 1859.
Sida conferta Link, Enum. Pl. 2:207. 1822 (non Salzmann ex Triana & Planchon, 1862, nec Sessé & Mociño, 1894). TYPE: BRAZIL. *Sida cordifolia* var. *conferta* (Link) Grisebach, Fl. Brit. W. I. 76. 1859.
Sida pellita H.B.K. Nov. Gen. Sp. 5:263 [205]. 1822. TYPE: ad Orinocum prope Angostura, *Humboldt & Bonpland s.n.* (P).
Sida pungens H.B.K. Nov. Gen. Sp. 5:263 [204]. 1822. TYPE: ad Orinocum prope Angostura, *Humboldt & Bonpland s.n.* (B herb. Willd. no. 12176). *Sida aristata* Willdenow ex Sprengel, Syst. 3:116. 1826, pro syn.
Sida bolsonerica Willdenow ex Sprengel, Syst. 3:112. 1826. TYPE: Cumaná, *Humboldt & Bonpland s.n.* (B. herb. Willd. no. 12693).
Sida decagyna Schumacher & Thonning ex Schumacher, Beskriv. Guin. Pl. 307. 1827; Kongel. Danske Vidensk. Selsk. Naturvidensk. Math. Aft. 4:81. 1829. TYPE: *Thonning 119* - "no type specimen traced" (Hepper, 1976, p. 72).
Sida ampla M. E. Jones, Contr. W. Bot. 15:146. 1929. TYPE: MEXICO. NAYARIT, Acaponeta, *Jones 22858* (HOLOTYPE: POM; ISOTYPE: CAS).

Numerous other synonyms are given by Schumann (1891), Kearney (1954), and Borssum Waalkes (1966). *Sida cordifolia* is pantropical and subtropical in distribution.

19. *SIDA HYALINA* Fryxell, *Sida* 7:227. 1978. TYPE: MEXICO. SINALOA, Certos de Navachiste about Bahia Topolobampo, *Gentry 14301* (HOLOTYPE: LL; ISOTYPES: DES, US).

Sida hyalina is known from northwestern Mexico (Sonora and Sinaloa) from the vicinity of Guaymas to the vicinity of Culiacán.

20. *SIDA MACULATA* Cavanilles, Diss. 1:20. t.3.f.7. 1785. TYPE: SANTO DOMINGO, *Jussieu s.n.* (P-JU 12266). *Sida cordifolia* ssp. *maculata* (Cavanilles) Marais, Kew Bull. 38:43. 1983.
Sida subersa L'Héritier, Scrp. Nov. 5:113. t.54. 1789 (non Dietrich, 1847). TYPE: Hort. Paris ex Hispaniola (P?).

Sida maculata occurs in Cuba and Hispaniola. It is questionably distinct from *S. cordifolia*. Marais (1983) cites it from the Mascarenes.

21. *SIDA SALVIFOLIA* Presl, Reliq. Haenk. 2:110. 1835. TYPE: MEXICO, prope Acapulco, *Haenke s.n.* (HOLOTYPE: PR; ISOTYPE: BM). *Sida spinosa* var. *salviaefolia* (Presl) E. G. Baker, J. Bot. 30:237. 1892.
Sida erecta Macfadyen, Fl. Jamaica 1:80. 1837. TYPE: JAMAICA, near Half-Way Tree (lectotype: K).

Sida campestris Benth., Pl. Hartw. 113. 1843. TYPE: ECUADOR. GUAYAQUIL, *Hortus* 634 (OXF).

Sida angustissima var. *moritziana* K. Schumann, Mart. Fl. Bras. 12(3):336. 1891. TYPE: NOV. GRANAT., prope Maracaybo, *Moritz s.n.*

Sida holuayi E. G. Baker & Rose, Contr. U.S. Natl. Herb. 5:176. 1899. TYPE: MEXICO. MORELOS, Cuautla, *Holuay* 3043 (HOLOTYPE: US; ISOTYPES: BM, GH).

Sida salviifolia occurs in Mexico, the West Indies, and parts of South America.

22. *SIDA TRAGIIFOLIA* A. Gray, Boston J. Nat. Hist. 6:164. 1850. TYPE: Cambridge (Mass.) Bot. Gard. ex southern Texas, *Gray s.n.* (HOLOTYPE: GH).

Sida tragiifolia occurs in northeastern Mexico and southern Texas.

23. *SIDA XANTI* A. Gray, Proc. Amer. Acad. Arts 22:296. 1887. TYPE: MEXICO. BAJA CALIFORNIA, Cape San Lucas, *Xantas* 8 (HOLOTYPE: GH; ISOTYPES: K, NY, US).

Sida xanti occurs on the Baja California peninsula and on some of the adjacent islands.

SIDA section MALACHROIDEAE G. Don, Gen. Hist. 1:498. 1831.

LECTOTYPE: *Sida anomala* Sr.-Hilaire (lectotype designated by Fryxell, 1975).

Sida sect. *Pseudomalachra* K. Schumann in Engler & Prantl, Nat. Pflanzenfam. 3(6):43. 1890. TYPE: *Sida ciliaris* L. In generic rank: *Pseudomalachra* (Schumann) Monteiro, Portugal. Acta Biol. B, 12 (1-4): 141. 1974.

Sida [sect.] *Ciliaris* Small, Man. Southeast. Fl. 849. 1933. TYPE: (Article 22): *Sida ciliaris* L.

Perennial herbs or shrubs, the stems prostrate to ascending, stellate-pubescent or scabrous to glabrescent. Leaves short-petiolate, oblong-lanceolate to linear, basally entire, distally dentate (Fig. 1, A-E), in extreme cases entire throughout (Fig. 1, E). Flowers congested at the apices of the branches through abrupt shortening of internodes, the pedicels short, adnate to petioles, crowded with the stipules so as to seem involuclate; petals yellow to rose. Mericarps 5-8, smooth to strongly muricate.

Section *Malachroideae* includes the South American species *S. centuriata* Clements, *S. sarumuensis* Ulbrich, *S. paradoxa* Rodrigo, and *S. plumosa* Cavanilles and the Old World species *S. cuneifolia* Roxb., in addition to the North American species treated here.

KEY TO THE NORTH AMERICAN SPECIES
OF *SIDA* SECT. *MALACHROIDEAE*

- a. Petals 16-23 mm long; leaves 4-10 times as long as broad, entire or obscurely tridentate at apex (Fig. 1, E)..... 24. *S. brachystemon*

- a. Petals 5–13 mm long; leaves generally broader, manifestly dentate at apex (Fig. 1, A–D).
 b. Leaves broadly oblong or obovate, long-hirsute on both surfaces (Fig. 1, A); petals yellow, 12–13 mm long 25. *S. brittonii*
 b. Leaves variable in shape, appressed-pubescent to glabrate (Fig. 1, B–D); petals commonly rose, 5–11 (–13) mm long 26. *S. ciliaris*

24. *SIDA BRACHYSTEMON* DC. Prodr. 1:459. 1824. TYPE: ICON. FL. MEX. s.n. (Torner Collection acc. no. 6331.1803, Hunt Institute).

Sida wendtii Fryxell, Phytologia 46: 393. 1980. TYPE: MEXICO, OAXACA, Mpio. de Santo Domingo Armenta, terracería a Santo Domingo, 29 km al oeste de Pinotepa Nacional, Koch, Fryxell & Wundt 79424 (HOLOTYPE: ENCB; ISOTYPES: BM, BR, CAS, CHAPA, CTES, F, K, MARY, MEXU, MICH, MO, NA, NO, NY, TEX, WIS, XAL, pf).

Sida brachystemon is at present known from isolated collections from Belize, Costa Rica, and Mexico.

25. *SIDA BRITTONII* León, Torreya 19: 172. 1919. TYPE: CUBA, PINAR DEL RÍO, Chirigota, León & Roca 7466 (GH).

Sida brittonii is endemic to Cuba.

26. *SIDA CILIARIS* Linnaeus, Syst. Nat. ed. x. 1145. 1759. TYPE: JAMAICA, Browne s.n. (LINN-866.8). [See comment on type by Clement (1957, p. 24); the type is not 866.6 as stated by Borssum Waalkes (1966).] *Pseudomalachra ciliaris* (L.) Monteiro, Portugal. Acta Biol. B, 12 (1-4):133. 1974.

Sida tridentata Cavanilles, Icon. 4:6. t.312.f.2. 1797. TYPE: in insul. Sancti Dominici, Dupuy s.n. (P-JU). *Pseudomalachra tridentata* (Cav.) Monteiro, Portugal, Acta Biol. B, 12:134. 1974.

Sida muricata Cavanilles, Icon. 6:78. t.597.f.2. 1801. TYPE: Nova Hispania [Vera-cruz?], prope Chalma, Née s.n. (MA as photo F-29779; illustrated by Rodrigo, 1944, plate 3, mislabeled as type of *S. ciliaris* L.).

Sida fulva St.-Hilaire, Fl. Bras. Mer. 1:176. 1827. TYPE: Manguinhos, prov. Rio De Janeiro, St.-Hilaire s.n. (MA as photo F-19684?, P). *Sida ciliaris* var. *fulva* (St.-Hil.) Schumann, Mart. Fl. Bras. 12(3):285. 1891.

Sida anomala St.-Hilaire, Fl. Bras. Mer. 1:177. 1827. TYPE: in prov. Cisplatina, près le village de Sando, St.-Hilaire C212470 (P as photo F-35529 and in Rodrigo, 1944, plate 2). *Sida ciliaris* var. *anomala* (St.-Hil.) Schum. in Engler & Prantl, Nat. Pflanzenfam. 3(6):43. 1890.

Sida anomala var. *mexicana* Moricand, Pl. Nouv. Amér. 36. t.4. 1837. TYPE: MEXICO, near Tampico, Berlandier 66 (BM, G, OXF). *Sida ciliaris* var. *mexicana* (Moricand) Shinnars, Field & Lab 21:94. 1953.

Sida fasciculata Torey & Gray, Fl. N. Amer. 1:231. 1838 (non Willdenow ex Sprengel, 1826). TYPE: TEXAS, Drummond 47 (BM, OXF).

Sida involucreta A. Richard, Hist. Phys. Cuba, Pl. Vasc. 63 (p. 162, French ed.). 1845. TYPE: CUBA, de la Sagra s.n. (F, P).

Sida erosa Salzmänn ex Triana & Planchon, Ann. Sci. Nat. Bot. 17:176. 1862 (non Link, 1822), pro syn.

Malvastrum linearifolium Buckley, Proc. Acad. Nat. Sci. Philadelphia 13:449. 1862. TYPE: N TEXAS, May 1861, Buckley s.n. (HOLOTYPE: PH).

Sida jaliscoensis Gandoger, Bull. Soc. Bot. France 71:629. 1924. TYPE: MEXICO. JALISCO, near Guadalajara, Pringle 4497 (MEXU, MICH, PH, US, VT, pf).

Sida ciliaris occurs in the United States, the West Indies, Central and South America, Africa, southeastern Asia, and Fiji. It is common, often weedy, and highly variable. Consequently it has been handled differently by different authors, sometimes being broken up into several varieties. For example, Clement (1957) recognized five varieties within *Sida ciliaris*. In my experience, the variability in this species is continuous, not discrete, and I am unable to justify or distinguish more than a single taxon, recognizing that it is a highly variable one.

SIDA section **ELLIPTICIFOLIAE** Fryxell, sect. nov. TYPE: *Sida rzadowskii* Fryx.

Suffrutices ascendentes vel erecti, pubescentes vel glabri. Folia breve petiolata, late vel anguste elliptica vel linearia, ubique dentata (Fig. 5). Pedicelli solitarii in axillis foliorum (longissimi vel brevi), secus caulem dispersi vel apicem versus congesti ob internodia abbreviata; corolla flava vel lilacina (centro flava). Mericarpi (5-) 8-11, mutica vel acuta vix spinifera, lateraliter reticulata vel laevia.

Ascending to erect subshrubs, pubescent to glabrate. Leaves short-petiolate, broadly or narrowly elliptic to linear, dentate throughout (Fig. 5). Pedicels solitary in the axils (long or short), scattered along the stem or congested apically through shortened internodes; corolla yellow to rose-lavender with a yellow center. Mericarps (5-) 8-11, mucous to acute but scarcely spined, laterally reticulate to smooth.

KEY TO THE SPECIES OF SIDA SECT. *ELLIPTICIFOLIAE*

- a. Pedicels up to 15 cm long, usually more than twice the length of the subtending leaves.
 - b. Leaves narrowly lanceolate, 7-10 (-15) times as long as wide (Fig. 5, H); calyx 6-7 mm long. 30. *S. longipes*
 - b. Leaves broadly elliptic, 1.2-2 times as long as wide (Fig. 5, I); calyx 9-11 mm long. 32. *S. potosina*
- a. Pedicels no more than 6 cm long, usually shorter than the subtending leaves.
 - c. Calyx 7-10 mm long.
 - d. Pedicels 2-6 cm long, often equaling the subtending leaf. 29. *S. lindbomeri*
 - d. Pedicels less than 2 cm long, shorter than subtending leaf. 28. *S. inflexa*
 - c. Calyx 5-7 mm long.
 - e. Leaves elliptic, 1.5-6 times as long as broad (Fig. 5, L-P).
 - f. Corolla rose or purple (with yellow center); mericarps 8-11; leaves 2-6 times as long as broad; flowers and fruits markedly congested apically. 33. *S. rzadowskii*

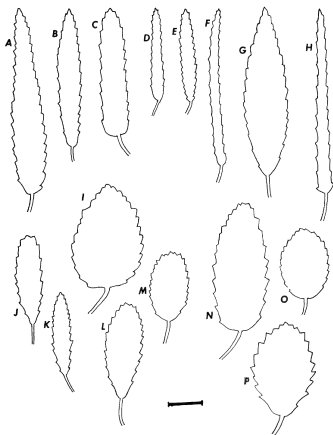


Figure 5. Leaf outlines of *Sida* sect. *Ellipticifoliae*. A-C, *S. lindheimeri*; D-F, *S. eliottii*; G, *S. inflexa*; H, *S. longipes*; I, *S. potanina*; J-K, *S. nomexicana*; L-M, *S. rzadowskii*; N-P, *S. turneroides*. [A, Hill 3353; B, Wilkinson 285; C, Hill 10609; D, Hernández Magaña 5127; E, Donatas & Acosta 2156; F, Hill 5310; G, Fernald & Long 11373; H, Wright 50; I, Purpus 4906; J, Sanders et al. 2970; K, Spellenberg & Soreng 6845; L, Rzedowski 32004; M, Ventura 245; N, Fryxell & Anderson 3613; O, Fryxell 3823; P, Fryxell & Anderson 3644.] Scale = 1 cm.

- f. Corolla yellow; mericarps 5-8; leaves 1.5-3 times as long as broad, sharply serrate; flowers and fruits slightly congested apically 34. *S. sterneroides*
- c. Leaves narrowly lanceolate to linear, 10-20 times as long as wide (Fig. 5, D-F, J-K).
- g. Plants freely branching from the base; flowers and fruits apically congested 31. *S. neomexicana*
- g. Plants few-stemmed; flowers and fruits little if at all congested apically 27. *S. elliotii*

27. *SIDA ELLIOTTII* Torrey & Gray, Fl. N. Amer. 1:231. 1838. BASIONYM: *Sida gracilis* Elliott, Sketch Bot. 2:159. 1822 (non Richard, 1792). TYPE: SOUTH CAROLINA, near Beaufort, *Elliott s.n.* (HOLOTYPE: CHARL).

Sida rubromarginata Nash, Bull. Torrey Bot. Club 23:102. 1896. TYPE: Florida, Tampa, Nash 2472 (GH, MO, NY, US).

Sida leptophylla Small, Bull. Torrey Bot. Club 25:468. 1898. TYPE: ex Torrey herb. coll. 40 (NY).

Sida elliotii occurs in the southeastern United States from North Carolina south to Florida and west to southernmost Missouri, Arkansas, and Texas; it occurs in Mexico from Nuevo León and Tamaulipas south to Veracruz and Chiapas, and extends to Guatemala.

28. *SIDA INFLEXA* Fernald, Rhodora 42:463. 1940. TYPE: VIRGINIA, Southampton Co., near Three Creek, northwest of Carey Bridge, *Fernald & Long 11373* (HOLOTYPE: GH; ISOTYPES: MO, PH, US).

Sida inflexa is confined to the southeast corner of the state of Virginia.

29. *SIDA LINDHEIMERI* Engelm. & Gray, Boston J. Nat. Hist. 5:213. 1845. TYPE: TEXAS, prairies east of the Brazos [River], fascicle I, 1843, *Lindheimer 24* (HOLOTYPE: GH; ISOTYPES: K, OXF). Note: A second collection by Lindheimer, also numbered 24, is part of fascicle II, 1844, and is not type material.

Sida elliotii var. *texana* Torrey & Gray, Fl. N. Amer. 1:681. 1840. TYPE: TEXAS, *Drummond 14* (BM, OXF). *Sida texana* (Torrey & Gray) Small, Fl. Southeast. U.S. 772. 1903.

Sida lindheimeri occurs principally in central Texas and in Louisiana and sporadically in Mexico.

30. *SIDA LONGIPES* A. Gray, Smithsonian Contr. Knowl. 3 (art. 5, Pl. Wright. 1):19. 1852 (non Meyer ex Harvey & Sonder, 1860). TYPE: TEXAS, prairies of Live Oak Creek, *Wright 50* (HOLOTYPE: GH; ISOTYPES: OXF, US).

Sida longipes occurs in Coahuila and western Texas.

31. *SIDA NEOMEXICANA* A. Gray, Proc. Amer. Acad. Arts 22:296. 1887

(non Gandoger, 1924). TYPE: NEW MEXICO, on mountains at the Copper Mines, Wright *s.n.* (PH, US).

Sida elliptica var. *?humilis* A. Gray, Smithsonian Contr. Knowl. 5 (art. 6, Pl. Wright. 2):21. 1853. TYPE: [the same as for *S. neomexicana*].

Sida neomexicana occurs in western Texas, southern New Mexico, Chihuahua, Coahuila, and Durango.

32. *SIDA POTOSINA* Brandegee, Univ. Calif. Publ. Bot. 4:184. 1911. TYPE: MEXICO. SAN LUIS POTOSÍ, Minas San Rafael, *Parpas 4906* (HOLOTYPE: UC; ISOTYPES: MO, US).

Sida potosina occurs in the Mexican states of San Luis Potosí and Tamaulipas.

33. *SIDA RZEDOWSKII* Fryxell, Sida 8:125. 1979. TYPE: MEXICO. HIDALGO, Cerro Ventoso, entre Pachuca y Real del Monte, *Rzedowski 20560* (HOLOTYPE: ENCB).

Sida rzedowskii occurs from Jalisco to Chiapas, at elevations of 2000 to 2700 m, being relatively common in the Valley of Mexico.

34. *SIDA TURNEROIDES* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22:90. 1940. TYPE: MEXICO. TAMAULIPAS, JUMBIVE, SIERRA NEAR SAN LUCAS, *sw Rozynski 514* (HOLOTYPE: P).

Sida turneroides occurs in the Mexican states of Hidalgo, San Luis Potosí, and Tamaulipas.

SIDA section *SIDAE*. Lectotype: *Sida alnifolia* Linnæus.

Erect subshrubs, pubescent or puberulent to glabrate. Leaves short-petiolate, more or less rhombic to lanceolate or elliptic, basally entire, distally crenate-serrate, acute or obtuse (Fig. 6). Pedicels usually solitary in the leaf axils, sometimes aggregated apically, sometimes in axillary pedunculate clusters; calyx prominently 10-ribbed, the ribs often yellowish at base; corolla yellow, with or without a red center. Mericarps 6–13, usually apically 2-spined, laterally reticulate.

Sida sect. *Sidae* includes species from Africa (e.g. *S. drogei* Burt Davy), South America (e.g. *S. glaziovii* Schumann), Asia (e.g. *S. szechuensis* Matsuda), and Polynesia (e.g. *S. fallax* Walpers), in addition to the North American species treated here.

KEY TO THE NORTH AMERICAN SPECIES
OF *SIDA* SECT. *SIDAE*

- a. Leaves and branching pattern distichous; stipules usually falcate, several-veined 35. *S. acuta*
a. Leaves spirally disposed; stipules linear or subulate, usually 1 (-3)-veined.

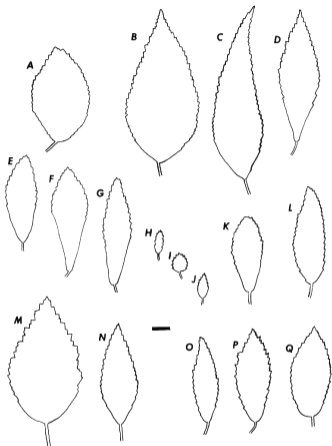


Figure 6. Leaf outlines in *Sida* sect. *Sida*. A, *S. santaremensis*; B-D, *S. setosa*; E-G, *S. collina*; H-J, *S. antillensis*; K-L, *S. rhombifolia*; M-N, *S. buenkeana*; O-Q, *S. acuta*. [A, *Crews & Lindsay* 2271; B, *Gentry et al.* 29193; C, *Dwyer* 10280; D, *Dunn* 22877; E, *Fryxell et al.* 1620; F, *Breedlove & Strother* 46577; G, *Koch et al.* 79469; H, *Hill* 11074; I, *Corrall & Proctor* 48659; J, *Avery* 2020; K, *Fryxell* 2691; L, *Koch et al.* 79329; M, *Koch & Fryxell* 77331; N, *Koch & Fryxell* 77384; O, *Chávez s.n.*; Q, *Breedlove* 20929A; R, *Gandara & Dorantes* 113.] Scale = 1 cm.

- b. Calyx 7–10 mm long; flowers often aggregated apically more or less above the leaves; leaves often loosely pubescent beneath; mericarps mucous.
- c. Corolla yellow with purple center; pedicels twice length of calyx or less; mericarps 6–9 37. *S. collina*
- c. Corolla yellow; pedicels 2–8 times length of calyx; mericarps 8–10 38. *S. baobabiana*
- b. Calyx 3–7 mm long; flowers commonly scattered along the stem; leaves minutely puberulent beneath; mericarps mucous or beaked or aristate.
- d. Mericarps aristate, the 2 aristae capillary, curled, subequal to body of mericarp; flowers sometimes borne in axillary, pedunculate, subumbellate clusters; leaves relatively large (up to 10 cm long or more), lanceolate and sharply acute (Fig. 6, B–D). 41. *S. setosa*
- d. Mericarps mucous to spinose, the spines (when present) less than half the length of mericarp; flowers 1 or more in the leaf axils; leaves seldom more than 6 cm long.
- e. Leaves 0.5–2.5 cm long.
- f. Flowers subsessile in the axils; calyx 5–6 mm long; leaves rotund to elliptic 36. *S. antillensis*
- f. Pedicels 1–2 cm long; calyx 3–4 mm long; leaves oblong or oblanceolate 42. *S. troyana*
- e. Leaves generally 2–6 cm long, more or less rhomboid.
- g. Corolla cream-colored with red center; leaves dentate almost to the base; pubescence (e.g. on petioles) up to 0.5 mm long 40. *S. santarensis*
- g. Corolla yellow without dark center; leaves generally entire in basal third (or more); pubescence never more than 0.1 mm long 39. *S. rhombifolia*
35. *SIDA ACUTA* Burman fil. Fl. Indica 147. 1768. TYPE: PERU (G-Del as photo F-7558); Java, *s. coll. s. n.* (LECTOTYPE: G). Lectotype chosen by Borssum Waalkes (1966). *Sida carpinifolia* var. *acuta* (Burm. f.) Kurz, J. Asiatic Soc. Bengal, Pt. 2, Nat. Hist. 45:119. 1876.
- Sida carpinifolia* Linnaeus fil., Suppl. 307. 1781 (non Miller, 1768). TYPE: MADEIRA, *Masson s. n.* (BM?). *Sida acuta* var. *carpinifolia* (L. f.) Schumann, Mart. Fl. Bras. 12(3):326. 1891.
- Sida frutescens* Cavanilles, Diss. 1:12. *t. 10, f. 1*. 1785. TYPE: ex R. Hort. Paris (P).
- Sida spiraeifolia* Link, Enum. Pl. 2:203. 1822. Based on: *Sida ulmifolia* Willdenow, Enum. Pl. Hort. Berol. Suppl. 49. 1814, nom. nud. TYPE: herb. Willd. no. 12654 (B). *Sida carpinifolia* var. *spiraeifolia* (Link) Millspaugh, Field Mus. Bot. Ser. 2:72. 1900.
- Sida berlandieri* Turczaninow, Bull. Soc. Nat. Mosc. 31:197. 1858. TYPE: MEXICO, *Berlandier 49* (HOLOTYPE: KW).
- Sida carpinifolia* Linn. fil. var. *brevicuspidata* Grisebach, Fl. Brit. W. I. 73. 1859. LECTOTYPE: CUBA, *Wright 1565* (PH). Note: Grisebach did not explicitly cite a type, but later (Grisebach, 1866, p. 24) cites the Wright collection as representing var. *brevicuspidata*, which constitutes a lectotypification.

Note: Borssum Waalkes (1966) cites numerous additional synonyms.

Sida acuta is pantropical in distribution, generally below 1500 m elevation, where it is a prominent component of the weed flora.

36. *SIDA ANTILLENENSIS* Urban, *Symb. Antill.* 5:418. 1908. TYPE: 10 specimens are cited by Urban; lectotypification is needed.

Sida antillensis occurs in the West Indies, southern Florida, and parts of Central America. Many authors have submerged this species in *S. acuta*, but Correll & Correll (1982) maintain it as distinct.

37. *SIDA COLLINA* Schlechtendal, *Linnaea* 11:364. 1837. TYPE: MEXICO [Veracruz], prope Hacienda de la Laguna, Jul 1829, *Schinde s.n.* (HOLOTYPE: HAL; as photo F-9377).

Sida costata Schlechtendal, *Linnaea* 11:365. 1837. TYPE: MEXICO [Veracruz], prope Hacienda de la Laguna, Jul 1829, *Schinde s.n.* (HOLOTYPE: HAL; ISOTYPES: GOET, HAL; as photo F-9377).

Sida corymbosa R.E. Fries, *Bull. Herb. Boissier* 7:988. 1907. TYPE: MEXICO [Veracruz], region d'Orizaba, *Bourgain* 2863 (G, K).

Sida collina occurs in the Mexican states of Sinaloa, Nayarit, Jalisco, Veracruz, and Oaxaca and extends into Central America.

38. *SIDA HAENKEANA* Presl, *Reliq. Haenk.* 2:104. 1835. TYPE: in parte occidentali Mexici, *Haenke s.n.* (HOLOTYPE: PR; ISOTYPE: MO).

Sida woronowii Ulbrich, *Notizbl. Bot. Gart. Berlin* 11:536. 1932. TYPE: MEXICO, Michoacán, prope Uruapan, *Woronow* 2890 (B, LE).

Sida haenkeana occurs at elevations of 1000 to 2800 m in Mexico (Jalisco to Chiapas), Nicaragua, and Costa Rica.

39. *SIDA RHOMBIFOLIA* Linnaeus, *Sp. Pl.* 684. 1753. TYPE: "2 rhombifolia" (LINN-866.3); as photo in Rodrigo (1944, plate 28).

Sida rhomboides Roxburgh ex Flem. *As. Res.* 11:178. 1810; *Hort. Beng.* 501. 1813. TYPE: s. loc., s. coll. 2228 (LECTOTYPE: BR). *Sida rhombifolia* var. *rhomboides* (Roxb.) Masters in Hooker, *Fl. Brit. India* 1:323. 1874.

Sida hondensis H.B.K. *Nov. Gen. Sp.* 5:261 [203]. 1822. TYPE: NOV. GRANAT., prope Honda, *Humboldt & Bonpland* 1709 (P).

Sida ruderata Macfadyen, *Fl. Jamaica* 1:81. 1837. TYPE: JAMAICA.

Sida pringlei Gandoger, *Bull. Soc. Bot. France* 71:631. 1924. TYPE: MEXICO, JALISCO, Rio Honda, *Pringle* 4095.

Sida adusta Marais, *Kew Bull.* 38:42. 1983. TYPE: MAURITIUS, Moka, *Ayres s.n.* (HOLOTYPE: K).

Sida unicornis Marais, *Kew Bull.* 38:42. 1983. TYPE: MAURITIUS, Bouter *s.n.* (HOLOTYPE: K).

Sida rhombifolia is virtually pantropical in distribution and reaches the temperate zones to a limited extent as an annual.

40. *SIDA SANTAREMENSIS* Monteiro, Monogr. Malv. Bras. Fasc. I. Gen. Sida 44. 1936. TYPE: BRAZIL. PARÁ, Santarem.

Sida santarensis is a South American species (Brazil, Argentina, Bolivia) recently discovered in the vicinity of Tampa, Florida (Fryxell et al., 1984).

41. *SIDA SETOSA* Martius ex Colla, Herb. Pedem. 1:416. 1833. TYPE: BRAZIL, Rio Belmonte, Martius s.n. (HOLOTYPE: TO).

Sida kobusiana Presl, Reliq. Haenk. 2:108. 1835. TYPE: IND. OCCID., Martinique, Kobus s.n. (PR).

Sida surinamensis Miquel, Linnaea 22:469. 1849. TYPE: SURINAM, Hostman 1079 (Bas photo F-9396, K, pf).

Sida setosa is a South American species that extends northward into Panama.

42. *SIDA TROYANA* Urban, Symbol. Antill. 5:419. 1908. TYPE: JAMAICA, prope Troy, Harris 8805 (BM?, NY).

Urban (loc. cit.) suggested that this species has its affinity with *S. rhombifolia*, and Fawcett & Rendle (1926) suggested that "it may be perhaps a depauperate form of *S. rhombifolia*." Adams (1972) reduced it to synonym. However, it is sufficiently distinct (cf. key) to be recognized taxonomically, especially in the small calyces, which are this small in only a few other species (e.g. the South American *S. serrata* Willd.).

ACKNOWLEDGMENTS

I am grateful to A. Krapovickas for sharing ideas and clarifying several points concerning species identities and other matters. The responsibility for the interpretations presented here, however, is entirely my own.

APPENDIX I

Species frequently included in *Sida* (Kearney, 1954; Clement, 1957; various floras) that are here excluded

<i>S. acuminata</i> DC.	= <i>Sidastrum multiflorum</i> (Jacq.) Fryx.
<i>S. cuneifolia</i> A. Gray	= <i>Billisturnera helleri</i> (Rose) Fryx.
<i>S. eggerii</i> E. G. Baker	= <i>Abutilon virginianum</i> Krapov.
<i>S. filipes</i> A. Gray	= <i>Meximalva filipes</i> (A. Gray) Fryx.
<i>S. grayana</i> Clem. ex Kearn.	= <i>Billisturnera helleri</i> (Rose) Fryx.
<i>S. boderana</i> (Dougl.) Torr.	= <i>Malsella leprosa</i> (Ortega) Krapov.
<i>S. helleri</i> Rose	= <i>Billisturnera helleri</i> (Rose) Fryx.
<i>S. hilariana</i> Presl	= <i>Alloisidastrum hilarianum</i> (Presl) Krap., Fryx. & Bates
<i>S. integrifolia</i> Sessé & Mociño	= <i>Anoda pentaschista</i> A. Gray
<i>S. interrupta</i> DC.	= <i>Alloisidastrum interruptum</i> (DC.) Krap., Fryx. & Bates

- S. lepidota* A. Gray = *Malvella lepidota* (A. Gray) Fryx.
S. lodigensis E. G. Baker = *Sidastrum lodigense* (Baker) Fryx.
S. mexicana Scopoli = *Anoda cristata* (L.) Schlecht.
S. micrantha Sc.-Hil. = *Sidastrum micranthum* (Sc.-Hil.) Fryx.
S. multiflora Jacquin = *Sidastrum multiflorum* (Jacq.) Fryx.
S. oxyphylla DC. = *Allowisadala seusei* (Lag.) Bates
S. palmieri E. G. Baker = *Maximalva venusta* (Schlecht.) Fryx.
S. physocalyx A. Gray = *Rhynchosida physocalyx* (A. Gray) Fryx.
S. paniculata L. = *Sidastrum paniculatum* (L.) Fryx.
S. pyramidata Cav. = *Alluvidastrum pyramidatum* (Cav.) Krap., Fryx. & Bates
S. quinquerivium Duchass. = *Sidastrum quinquerivium* (Duchass.) Baker
S. sabana Buckley = *Melochia pyramidata* L.
S. sagittifolia A. Gray = *Malvella sagittifolia* (Gray) Fryx.
S. standleyi Clem. = *Krapovickaitia physaloides* (Presl) Fryx.
S. stricta Standley = *Sidastrum strictum* (Standley) Fryx.
S. tehuacanana Brandegee = *Sidastrum tehuacanum* (Brandegee) Fryx.
S. triloba Sessé & Mociño = *Allowisadala seusei* (Lagasca) Bates

APPENDIX II

Species of North America *Sida*
doubtful or inadequately known

- S. amatlensis* Sessé & Mociño, Pl. Nov. Hisp. 110. 1887. [Mexico]
S. anoda Sessé & Mociño, Pl. Nov. Hisp. 109. 1887. [Mexico - *Anoda cristata* ?]
S. bicallota Rafin. Fl. Ludov. 91. 1817. [USA - *Sida spinosa* ?]
S. bicolor Cav. Icones 4:6. t. 311. 1797. [Mexico - *Anoda pentasticha* ?]
S. cardanina Rafin. Fl. Ludov. 90. 1817. [USA - *Sida alliottii* fide Ewan, but flowers too large]
S. carpinifolia Miller, Gard. Dict. ed. viii. no. 2. 1768 [non Linn. f., 1781]
S. deflexa Cav. Anal. Cienc. Nat. 6:337. 1803. [Cuba]
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ACHYRANTHES JAPONICA (MIQ.) NAKAI
(AMARANTHACEAE)
IN KENTUCKY AND WEST VIRGINIA:
NEW TO NORTH AMERICA

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On 26 August 1981 a plant unknown to them was collected by HB and JM on the banks of Tug Fork of the Big Sandy River at Warfield, Martin County, Kentucky (Bryan & MacGregor s.n., DHL). Although identification to family—Amaranthaceae—and genus—*Achyranthes*—posed no problem, the specimens were not convincingly identifiable to species in pertinent eastern North American floristic works (Fernald 1950, Gleason 1952, Gleason and Cronquist 1963, Radford et al. 1968, Robertson 1981, Small 1933, Standley 1917, Steyermark 1963, Strausbaugh and Core 1978.)

According to Robertson, in his account of Amaranthaceae for Vascular Flora of the Southeastern United States (unpublished), *Achyranthes* in the southeast is represented by a single species, *A. aspera*, L., with two subspecies (recognized as two species, under *Centrostachys*, by Standley [1917]). Our specimens did not fit the descriptions of either of these subspecies. We finally concluded, however, that they did fit descriptions of

an Asiatic species, *A. japonica* (Miq.) Nakai (Liu and Kao 1976, Ohwi 1965); they matched the illustration of this species in Liu and Kao (1976). Our tentative identification was verified by comparison with authentic specimens of *A. japonica* from Honshu, Japan, that we borrowed from US. Our specimens (Fig. 1a, b, c) appear to represent var. *hachijoensis* Honda and are, we believe, the first from North America. According to Liu and Kao (1976), *A. japonica*, in addition to its occurrence on Taiwan, is "widely distributed in China, the Ryukyus, Japan and Korea and the temperate and subtropical regions of southeastern Asia."

We have since collected the species in Lawrence County (3 mi S of Louisa, 7 Nov 1982, Medley, Hotchkiss, & Woodward 7160-82, DHL) and Pike County (along Tug Fork in river birch woods, ca 3 miles NW of South Williamson, 9 Sep 1984, Medley s.n., DHL), Kentucky, and in Mingo County, West Virginia (wooded banks of Tug Fork, ca 3 miles S of Kermit, 13 Aug 1982, Medley 6082-82, DHL). It occurs as open colonies of individual plants up to 1.5 m tall on wooded river banks in areas that have an incomplete or light canopy and that are annually flooded. Dominant species in the community at the Martin County site included *Betula nigra*, *Microstegium vimineum*, *Pilea pumila*, and *Boehmeria cylindrica*. This shady habitat of *A. japonica* is in contrast to that of *A. aspera*, which grows in open waste places and on roadsides (Walker 1976).

Dispersal of *A. japonica* in Kentucky and West Virginia appears to be accomplished largely by water. However, at the Lawrence County site in early November, when the infructescences were fully elongated (quite reminiscent of those of *Phryma leptostachya*) and the seeds were mature, the fruiting calyces—each with its accompanying subulate-spinose bracteoles—detached from the plants and clung to clothing, indicating an adaptation to dispersal by animals. (Zoochory, for *A. aspera*, was described by Bullock and Primack [1977].)

The origin of *A. japonica* on Tug Fork is unknown. It was possibly via the major railroad that parallels the watercourse at the site where the species was first found.

This species will probably be found eventually in all Kentucky and West Virginia counties bordering Tug Fork and the lower Big Sandy River; it may ultimately be found along the banks of the Ohio River downstream from the mouth of the Big Sandy. In time it may also move up the tributary valleys of Tug Fork and the Big Sandy via transport by small mammals and fall migrant birds.

The two species of *Achyranthes* now known to occur in the conterminous United States can best be separated on the basis of characteristics of their staminodes, as follows: *A. aspera*—staminodes fimbriate at apex (Fig. 1d);

A. japonica—staminodes entire to denticulate or slightly notched at apex (Fig. 1c).

As an aid to other workers who find *A. japonica* we present the following description of the species, which is based on our Kentucky and West Virginia material.

Herb (reported as perennial; Liu and Kao 1976, Ohwi 1965, Walker 1976). Stem erect or ascending, sometimes becoming decumbent late in the season, 75-150 cm tall, glabrous to lightly pubescent, 4-angled, vertically 12-lined (2 lines per angle, 1 line per face). Leaves simple, opposite, blades oblong-elliptic, 2.5-13.5 cm long, 1.2-6.8 cm wide,



Figure 1. *Achyranthes japonica*. a, upper part of plant, $\times 0.4$; b, inflorescence, $\times 0.4$; c, staminodes and stamens, $\times 14$. *A. aspera*. d, staminodes and stamens, $\times 14$.

pinnately veined (veins opposite to alternate), short pubescent above, pubescent on veins below, apex acute to acuminate, margin entire; petioles 0.4–3.5 cm long. Inflorescence spicate, terminal on main stem and upper branches, erect, many flowered; spikes 2–4 cm long and compact in early flower, elongating to 21 cm and becoming more open, especially proximally, in mature fruit. Flowers perfect, regular, hypogynous, apetalous, sessile, divergent at right angles in anthesis, sharply deflexed in mature fruit, then becoming as much as 1.5 cm apart in lower part of spike; each flower subtended by a membranous bract ca 2 mm long and by 2 rigid, subulate-spinose bracteoles 3–4 mm long, each bracteole with 2 basal, suborbicular, membranous auricles, the bracteoles and the flower falling as a unit; sepals 5, linear-lanceolate, 4–5 mm long, acuminate; stamens 5, alternating and connate below with 5 entire, denticulate, or slightly notched staminodes. Fruit a 1-seeded utricle, oblong, 2.5 mm long, 1 mm wide, tipped by the slender style, this 1 mm long.

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**DRYMARIA VISCOSA (CARYOPHYLLACEAE):
CORRECT AUTHOR CITATION AND
RANGE EXTENSION TO THE UNITED STATES**

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Although cited as *Drymaria viscosa* S. Wats. ex Orc. in both monographs of the genus (Wiggins, 1944; Duke, 1961) and *Index Kewensis* (Durand & Jackson, 1906), the species was neither described by Orcutt nor ascribed to Watson by him. In a narrative of his trip to Baja California, Mexico, Orcutt (1886) merely mentioned the name, creating a *nomen nudum*: "At Socorro we found a few lichens, shells, a young palm tree, and various nice plants of which I will mention *Dalea Seemannii*, *Nemacaulis nuttallii* and a variety, *Aesculus Parryi*, *Euphorbia micromera*, *drymaria* (sic) *viscosa*, n. sp., *Astragalus hornii*, *A. menziesii*, . . . etc."

The specimen collected by Orcutt at "Socono" (Socorro, the handwritten label is easily misread), and cited by Watson (1887:469) with his description of the species, represents the holotype ("C. R. Orcutt, April, 1886" = *Orcutt 1330*, GH!). With regard to *D. viscosa*, Watson makes no other reference to Orcutt. While it is likely that Watson knowingly used and legitimized Orcutt's name for the new plant, he did not give Orcutt credit for the name. Furthermore, because the plant bears an indument of glandular trichomes to which grains of sand adhere, it is equally possible that Watson arrived independently at the epithet *viscosa*.

Articles 46 of the International Code of Botanical Nomenclature (Voss et al., 1983) states that ". . . it is necessary to cite the name of the author(s) who first validly published the name concerned . . ." This is followed by Recommendation 46E. 1. which explains that where an author has validly published a name and ascribed it to another person, "the name of the other person, followed by the word *ex*, may be inserted *before* the name of the publishing author, if desired" (italics ours).

Thus Watson is the author who validly published *Drymaria viscosa* and must be cited. Had Watson ascribed the name to Orcutt, *D. viscosa* Orc. ex S. Wats. would have been the correct option, though opposite the order of authors cited in the monographs (Wiggins, 1944; Duke, 1961) and *Index Kewensis* (Durand & Jackson, 1906). However, because neither Watson nor

Orcutt ascribed *D. viscosa* to the other author, the use of the connector "ex" between their names in either combination is clearly incorrect. As cited in Shreve and Wiggins (1964) and Wiggins (1980) and as suggested in the *Gray Herbarium Card Index* (Harvard University, 1968), but contrary to the monographs, *Drymaria viscosa* S. Wats. is correct and *Drymaria viscosa* Orc. remains a nomen nudum.

DISTRIBUTION

Wiggins (1980) considered *D. viscosa* as endemic to Baja California, occurring in sandy areas from San Quintín to the Cape region. However, Felger (1980) reported the species from the Gran Desierto of northwestern Sonora and there is in CAS a specimen from Sonora collected in 1966 (Ripley 14226). These specimens and others represent a mainland distribution from the region of the Pinacate Lava Flow in Sonora southward along the coast of Sonora nearly to Guaymas.

MEXICO. SONORA: Dunes ca 5 mi NE of Sierra del Rosario, 32°08'N 114°09'W, Felger 20430 *et al.* (ARIZ); Sand desert N of Sierra Pinacate, 0.5 mi S of the San Luis—Sonoita road, Mason 1832 *et al.* (ARIZ); Moon Crater (Cratero Chichi), SW part of the Pinacate region, Felger 19239 (ARIZ); ca 1 mi S of Moon Crater, 31.7°N 113.6°W, Felger 19095 & Hanson (ARIZ); ca 6 mi S of Moon Crater, 31.6°N 113.6°W, Felger 19034 & deRosa (ARIZ); Dunes 0.2 km S of Hwy 8, ca 29 km SW of Sonoita, Borges 4761 (ARIZ); 7.2 mi from cabin 245 at Choya, Burch *s.n.* (ASU); La Mancha Blanca, N side of Cerro Tepopa 29°24'N 112°24'W, Felger 20850 *et al.* (ARIZ); Sand dunes, Puerto Kino, 15 Feb 1966, Ripley 14226 (CAS); High beach dunes ca 1 mi NW of village of Tastiata, 28°20'N 111°30'W, Felger 20881 *et al.* (ARIZ, GH); Coastal sand dunes S of Moro (Morro) Colorado, 5 mi SSE of Estero Tastiota, Copp 70-3 (CAS).

Thus although not previously reported for the United States, the occurrence of *Drymaria viscosa* from the United States portion of the Pinacate region is not as unusual as Wiggins' (1980) report of endemism in Baja California would suggest. One specimen is now known from the U.S.A.: Arizona, Yuma Co., eastern edge of the Pinacate Lava Flow, along the Camino del Diablo, Cabeza Prieta Game Range, occasional on sand dunes with *Triteliopsis palmeri*, ca 900 ft elev., 17 Apr 1983, Hodgson 2080 & Engard (DES).

This species may be distinguished from other Arizona species of *Drymaria* by its occurrence below 1000 ft elev.; the others occur above 4000 ft (Kearney & Peebles, 1960). Because the leaves are several per node it most strongly resembles, and keys with, *D. molluginea* (Lagasca) Didr. but is heavily glandular pubescent with smooth, tan seeds.

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NOTES

THEMEDA QUADRIVALVIS (L.) KUNTZE (POACEAE) IN LOUISIANA.—*Themeda quadrivalvis* (L.) Kuntze was first reported from the United States from St. Landry Parish, Louisiana, based on several collections from populations established on agricultural lands (Brown 1945). Since the time of Brown's report *Themeda* has apparently not been recollected in Louisiana, and publications citing the name with reference to the Louisiana flora contain no new information on the status of *Themeda* in Louisiana (Allen 1980; Thieret 1972; Thomas & Allen 1984). We report here that populations of *T. quadrivalvis* still thrive in Louisiana in St. Landry Parish based on our field observations of it in September 1984 (Figs. 1–4). Anthesis had begun on 6 September, when we first located stands of *Themeda* in the field, and grains had begun to develop a week later when we discovered additional stands.

Dr. Brown's original description of *Themeda's* habitat in Louisiana is still accurate for the stands we recently observed: "Dense stands were found on the headlands of cultivated fields, along fence rows, and along the ridges of cultivated fields outside the influence of the last cultivation. In places the stand of this grass was so thick that the usual weeds of these sites were excluded." From our observations *Themeda* appears to be in no danger of dying out in Louisiana in spite of intensive cultivation of soybeans in the areas in which the grass grows. In fact, because *T. quadrivalvis* is an annual, it probably could not persist without maintenance of favorable sites for it through agriculture. The most robust plants we saw were in a large fallow field dominated by *Ambrosia trifida* and *Setaria* sp. where there were several small colonies of *Themeda*, widely separated from one another, and including some very tall culms to 2.62 m. The plants in this fallow field were much larger on average, and more mature, than those growing around fields actually under current cultivation. Presumably the plants in the fallow field grew so well because they were able to get an early start and were not knocked down or otherwise disturbed by agricultural practices. In well-tended soybean fields, in which the headlands and field edges were kept mowed, *Themeda* was lacking. It is apparently not able to grow right out in the field among the soybean plants as some other grasses—*Sorghum halepense* for example—do so successfully. In the United States *T. quadrivalvis* is also known from Manatee County, Florida, where it is said to be an escape from cultivation (Wunderlin 1982). Specimens of our recent collections of *T.*



Figure 1. Typical habitat of *Themeda quadrivalvis* in St. Landry Parish, Louisiana; fencerow indicated by trees at right, soybean field at left, *Themeda* growing between the fencerow and the soybeans.

Figure 2. Site similar to that shown in Fig. 1 but lacking *Themeda* because field edges are kept mowed.



Figure 3. Stand of *Themeda quadrivalvis* in a fallow field with *Setaria*, sp. and *Ambrosia trifida*. Tallest culms of *Themeda* here were over 2.6 m.

Figure 4. Inflorescences of *Themeda quadrivalvis*.

quadrivalvis, in addition to those at LAF, are being distributed to GA, GH, IBE, KNK, LSU, LTU, MICH, MO, NATC, NCU, NLU, NO, NY, SMU, TAES, US, and VDB.

We thank John W. Thieret for suggesting that an attempt be made to relocate *T. quadrivalvis* in Louisiana, and Debra Waters for participating in the field work.—William D. Reese and Garrie P. Landry, Biology Department, University of Southwestern Louisiana, Lafayette, LA 70504, U.S.A.

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CAMPANULA RAPUNCULOIDES (CAMPANULACEAE) NEW TO TEXAS—On June 9, 1984 I collected a single plant of *Campanula rapunculoides* L. (Brown 7507, SMU) in a woodland of *Quercus glaucooides* on a rocky limestone slope above the Sabinal River in Lost Maples State Park north of Vanderpool in Bandera County. This native of Europe is reported by Fernald (FERNALD, Gray's manual, 1950) to be naturalized in eastern North America south to Indiana, Illinois, and Missouri.—Larry E. Brown, Houston Community College, 726 Horncastle St. Channelview, TX 77530, U.S.A.

NOTES ON TWO TEXAS PLANTS—*JUNCUS CAPITATUS* Weigel (Juncaceae) was first reported for Texas by Gould in 1962 [1963] from Walker County. This collection by S. R. Warner was annotated as a new species (COTYPE: SMU) by Tharp & Barkley. A literature search indicates the name was never published. Since then the species has been determined as *J. capitatus*—an introduction from the Old World—now scattered over the southern United States. Two new locations are here reported for the state.

Collection data: Walker Co.: Rock Springs Church, 3 May 1944, S. R. Warner *s.n.* (SMU). Bandera Co.: first low water crossing on FM 187 N of Utopia ca 5 mi S of Vanderpool, 2 May 1984, T. M. Kewey 3876 (SMU, UVST); same locality, 6 May 1984,

3878 (UVST); same locality, 8 May 1984, 3879 (UVST). Uvalde Co.: sandy soil, Frio River bed NW of Knippa, 11 May 1985, Keeney 4493 (SMU, UVST).

VERONICA AMERICANA (Raf.) Schwein. (Scrophulariaceae) was first reported for Texas based on a single collection from Kendall County in the Edwards Plateau (Correll & Johnston, 1970; Correll & Correll, 1972). A recent collection of this aquatic is apparently the first for the state since 1961.

Collection data for the two known locations are: Kendall Co.: gravelly stream along Ranger Creek, ca 4 mi NW of Boerne, 11 Jul 1961, K. I. & L. W. Miller 975 (SMU). Kerr Co.: in Verde Creek ca 300 yds E of bridge over Verde Creek at Camp Verde on Hwy 173, 6 Oct 1984, T. M. Keeney 4099 (SMU, UVST).

—Tony M. Keeney, Herbarium, Southwest Texas Junior College, Uvalde, TX 78801, U.S.A. and Barney L. Lipscomb, Herbarium, Southern Methodist University, Dallas, TX 75275, U.S.A.

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SCAEVOLA SERICEA VAHL VAR. *TACCADA* (GAERTN.) THIERÉT & LIPSCOMB, COMB. NOV. (GOODENIACEAE)—Based on *Lobelia taccada* Gaertn., Fruct. Sem. Pl. 1:119, t. 25, fig. 5. 1788. *Scaevola sericea*, a widely distributed Indo-Pacific strand plant, is grown as an ornamental and has escaped in southern Florida. It has been called *S. taccada* (Gaertn.) Roxb. in some recent floras, but C. Jeffrey has shown (Kew Bull. 34:537–545. 1979) that *S. sericea* Vahl is the correct name. Two variants of the species occur in Florida—as “on many other tropical shores” (H. St. John, Proc. Biol. Soc. Washington 88:73–75. 1975): one with sericeous leaves, *S. sericea* var. *sericea*, and one with glabrous leaves, for which the above new combination is made.—John W. Thierét, Dept. of Biological Sciences, Northern Kentucky University, Highland Heights, KY 41076, U.S.A.; Barney L. Lipscomb, Southern Methodist University Herbarium, Dallas, TX 75275, U.S.A.

REVIEWS

INDICES TO THE MICROFICHE OF THE TYPES AND SPECIAL COLLECTIONS (FLOWERING PLANTS AND FERNS) OF THE HERBARIUM OF THE ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA. James A. Mears. 274 pp. 1984. Meckler Publishing, 11 Ferry Lane West, Westport, Connecticut 06880. \$350.00

The thorough title tells it all. Two copies of this clothbound set of indices are included in the \$3700 purchase price for the complete microfiche collection. The volume is available separately, however, for anyone (or, more likely, any institution) desiring it. This work alone will give some clue as to whether a type may be in the Philadelphia Academy, and thus can be useful even without the microfiche (or herbarium itself)—and it contains some useful historical information besides. But the phrase "special collections" is an important part of the title.

This is not an index to verified types. Many of the PH collections date from before the type method. The major portion of this volume (185 pp.) covers the "Collection of Types and Early Authenticating Specimens," and the latter phrase includes a multitude of specimens possessed or annotated by authors of species names or simply by important early botanists. Even the verified types are not designated as such in this index. Collectors' names but, strangely, not their numbers are given and so are geographic sources, presumably whenever known (which is sometimes not often); but the index does not reveal, and makes it difficult to determine without examination of the specimen or photograph, whether any specimen is in fact a type. Perhaps this is good—it encourages checking the original data—but it does reduce the usefulness of the index.

Shorter indices cover the G. H. E. Muhlenberg Herbarium, the B. S. Barton Herbarium Fragment, the A. B. Lambert Herbarium Fragment, the Lewis & Clark Collection, and specimens of various other notables. The verified types from some of these, however, are listed in the initial index to types and early authenticating specimens and *not* with the collection in which they are in fact filed (e.g., Barton, Muhlenberg). Some specimens which borrowers did not return for this project did not get photographed at all (but may be indexed), and "many type specimens (particularly unlabeled isotypes)" are "still in the general and local herbaria of the Academy." An introduction to each of the indices explains the origin of the particular collection and the sequence of names (Muhlenberg following his Catalogue, Barton with families after the Bessey system, Lambert alphabetical by species as named in Pursh, the initial index after Dalla Torre & Harms, etc.). All this apparent chaos is partly alleviated by a concluding index to all pages on which specimens of each family are listed.

The broad scope of this work greatly enhances its usefulness—not alone the generous definition of "special collections" besides types, but also the inclusion of specimens from collections on indefinite loan to the Academy, such as those of the

American Philosophical Society and the University of Pennsylvania. Many botanists may be pleasantly surprised to learn that the PH collections—well known as an extraordinarily rich source of early North American specimens—include so much Old World material (with some even from Linnaeus himself).

I am unable to say how many specimens are indexed. An advertisement states that there are 454 microfiche each with a maximum of 60 plants. Slightly less than 300 of the fiche cover the herbarium of "types and early authenticating specimens"—which are said to number about 40,000 vascular plants. Perhaps less than half of these *are* photographed—or does the apparent contradiction in numbers merely mean there is an average of two collections per photo?—*Edward G. Voss, Herbarium, University of Michigan, Ann Arbor, MI, 48109, U.S.A.*

METHODS IN PLANT VIROLOGY. 1984. Hill, Stephen A. *Methods in Plant Pathology* Vol. 1. Blackwell Scientific Publications, Ltd., Oxford, London, Edinburgh, Boston, Palo Alto, Melbourne. 167 pp. + viii. Paper, \$24.00.

The volume concentrates on the methods for virus diagnosis. The beginning student of plant virology should learn the basic techniques and gradually evolve into the more sophisticated techniques. The techniques are sequential and may provide a route to virus characterization. The Chapters are 1) Introduction, 2) Histological and other Basic Methods, 3) Basic Virus Characterization and Storage, 4) Transmission Tests (Sap, graft, and vector transmission), 5) Serological Techniques (Precipitation and agglutination tests, labelled antibody techniques), 6) Electron Microscopy (Quick methods for sample preparation and immuno electron microscopy).

By grouping the basic methods of characterization into one volume, the author has produced a valuable handbook that not only describes the concept of each method but also lists the materials required and proceeds in a step by step cookbook fashion. The text was written for senior undergraduates and researchers in plant pathology and plant virology and is recommended not only for its total contents but for the brief, concise individual nature of each recipe.—*Wm. F. Mabler, Southern Methodist University Herbarium, Dallas, TX 75275, U.S.A.*

INTRODUCTION TO MODERN MYCOLOGY. 1984. Deacon, J. W. *Basic Microbiology Series* Vol. 7. Blackwell Scientific Publications, Ltd., Oxford, London, Edinburgh, Boston, Palo Alto, Melbourne. 167 pp. + viii. Paper, \$24.00.

The text is an introduction to the biology of the fungi and deals with their structure, function, and some aspects of their life history. The Chapters include topics on structure and fine structure, growth, differentiation, nutrition, metabolism, environmental conditions for growth, genetic systems, spore dispersal, the role of fungi as saprophytes and parasites (plant and animal), and on prevention and control of fungal growth.

From an educational viewpoint, this text is recommended after a solid foundation in the "modern" taxonomic and life cycle concepts has been achieved in order to permit the student to attain the proper perspective of the whole while studying various detailed aspects. This text on the biology of the fungi is an excellent one for the second course in a two course sequence of an "Introduction to Mycology."—*Wm. F. Mabler, Southern Methodist University Herbarium, Dallas, TX 75275, U.S.A.*

PLANT PATHOLOGY & PLANT PATHOGENS. 1982. Dickinson, C. H. and J. A. Lucas. Basic Microbiology Series Vol. 6. Blackwell Scientific Publications, Ltd., Oxford, London, Edinburgh, Boston, Palo Alto, Melbourne. 2nd ed. 229 pp. + viii. Paper, \$19.75.

In the Preface, the authors state that the "aim in this book is to provide a balanced treatment of all aspects of disease caused by microbial agents" with an emphasis on the host-pathogen complex and the development of general principles. The Chapters cover the concept of disease, the microbial pathogens, pathogen structure and function, infection and colonization, host-pathogen interaction at the population, whole plant, cellular, and molecular levels, host-pathogen specificity and disease control. An annotated list of pathogens and the diseases they cause comprise the Appendix.

The text achieves the aims of the authors and covers the basic concepts concerned with plant diseases caused by microbial agents and the appendix is especially useful for quick reference.—*Wm. F. Mabler, Southern Methodist University Herbarium, Dallas, TX 75275, U.S.A.*

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SYSTEMATICS OF *LEUCOPHYLLUM* AND *EREMOGETON* (SCROPHULARIACEAE)

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ABSTRACT

Leucophyllum and *Eremogeton* were placed in Leucophylleae series Pseudosolaneae by Bentham and in Verbasceae by Wettstein at the base of Scrophulariaceae. The two genera have been considered somewhat anomalous in Scrophulariaceae because of their woody habits and other features. Recent comparisons have shown similarities with woody Myoporaceae but the woody habit of *Leucophyllum* appears to be derived: this and comparisons of ovary structure show relationships are clearly with Scrophulariaceae. Data from comparative anatomy and morphology of leaves, stems, flowers, and trichomes, from chromosome number, and from phytogeography suggest recognition of 12 species of *Leucophyllum* including *Faxomanthus* as a monotypic subgenus. The species range from Puebla north through arid portions of Mexico into southern Texas. *Leucophyllum langmaniae* and *L. ultramonticola* are described as new. *Eremogeton*, retained as a monotypic genus related to *Leucophyllum*, is endemic to Central America.

INTRODUCTION

Since its inception, *Leucophyllum* has been placed in Scrophulariaceae, however, its position within the family has varied. Bentham (1846), in de Candolle's *Prodromus*, placed the genus in his suborder (subfamily) Antirrhinideae, tribe Gratiroleae, subtribe Aptosimeae, next to the Old World genera *Aptosimum* Burchell, *Peliosotomum* E. Mey., *Anticharis* Endl., and *Doratantbera* Benth. ex Endl. (= *Anticharis*).

Later, Bentham (1876) in his *Genera Plantarum* treatment, placed *Leucophyllum* along with *Gbiesbrachtia* Gray (= *Eremogeton* Standl. & Williams) and *Heterantbia* Nees & Mart. (a monotypic Brazilian genus now placed in Solanaceae) in his series Pseudosolaneae (with alternate leaves, simple centripetal inflorescences, corolla with posterior lobes external in bud), tribe Leucophylleae (corolla tubes campanulate), at the base of the family next to the South African Aptosimeae (with *Aptosimum*, *Plisotomum*, and *Anticharis*) and the Old World Verbasceae (with *Verbascum* L., *Celsia* L., and *Staurophragma* Fisch. & E. Mey.).

Wettstein (1891), in Engler and Prantl's *Natürlichen Pflanzenfamilien*, placed *Leucophyllum* and *Gbiesbrechtia* in the series Pseudosolanaceae, tribe Verbasceae (again next to Aptosimeae) and emphasized the multicellular, branched trichomes, mostly axillary flowers with actinomorphic or zygomorphic corollas with short, campanulate tubes and 5 stamens with anther thecae united at the tip or throughout. Within the tribe the New World genera were separated from the Old World *Verbascum*, *Celsia*, and *Staurophragma* on the basis of campanulate corolla tubes, anther sacs united at tips only, and solitary, axillary flowers.

Flyr (1970) suggested that *Leucophyllum* may best be placed in Myoporaceae. In an analysis of pollen, Niezgodna and Tomb (1975) showed that, unlike most Scrophulariaceae, *Leucophyllum*, *Faxomanthus* (here treated as a subgenus of *Leucophyllum*), and *Eremogeton* have distinctive, prolate or oblate—spheroidal, 3-colpate, diorate pollen, characterized by two elliptical apertures on each colpus, one at each side of the equator, a condition also found in the three genera of the Myoporaceae: *Bontia* L., *Eremophila* R.Br., *Myoporum* Soland. ex Forst.f. As noted by Niezgodna and Tomb (1975), however, the same pollen type is present in *Capraria* L. (Scrophulariaceae). Argue (1980) noted similar pollen in sections *Mimulus* and *Erythranthe* of *Mimulus* L., in several genera of the Gratiolieae (*Lancea* Hook.f. & Thoms., *Artanema* D. Don. and *Conobea* Aubl.), in *Penstemon* Mitch. of the tribe Cheloneae, and in *Celsia* of Verbasceae. On the basis of pollen data, Niezgodna and Tomb (1975) suggested the tribe Leucophylleae be transferred to the Myoporaceae as a subfamily. However the paper by Argue (1980) weakens their argument. Tomb (pers. comm. 1984) has recently found similar 3-colpate, diorate pollen in Bignoniaceae.

Karrfalt and Tomb (1983) suggested ontogenetic similarities between the epithelium-lined secretory cavities of *Bontia* (Myoporaceae) and the larger, non-lined air cavities in leaves of selected leucophyllums noting that scattered cells surrounding the air cavities in *Leucophyllum* have epithelial-like expansions. They also cited the occurrence of branched multicellular trichomes on vegetative buds on *Bontia*, the co-occurrence of isobilateral leaf structure in *Leucophyllum* and some species of *Eremophila* and *Myoporum*, and noted the similarity in habit between the shrubby, gray-leaved *Leucophyllum* and some *Eremophila*.

In spite of these and other similarities, there exist strong differences between *Leucophyllum* and Myoporaceae, particularly in gynoecial and fruit characters. As noted by Karrfalt and Tomb (1983), the 2-carpelled, 2-loculed, superior ovaries with axile placentas, many ovules, and septicial capsules that also open loculicidally at the tip that characterize *Leucophyllum* and *Eremogeton* are typical of Scrophulariaceae but unlike the conditions

found in Myoporaceae. To this we may add that the campylotropous ovules and seed structure of *Leucophyllum* and *Eremogeton* are also identical to that of Scrophulariaceae.

While Myoporaceae also tend to have 2-carpelled ovaries with placenta oriented in a manner similar to that of Scrophulariaceae (i.e. with enlarged placenta intruding into the locules perpendicularly from the ovary septum) the placentae in Myoporaceae often extend all the way to the outer ovary wall forming false and incomplete septa that effectively divide each carpel into 2 locules. In some species placentae are not so well developed and carpels are unilocular. Ovaries of *Myoporum*, in contrast, typically are divided into 2-4 (-up to 12 in *Myoporum sandwicense* A. Gray) (Webster 1951) uniovulate compartments and this has been interpreted as consisting of 2 carpels divided by supernumerary partitions (Cronquist 1981) or it could possibly be a multicarpellate ovary with up to 6 carpels. Ovules are few in number, typically 1-3 (very rarely 4) pair per carpel, and when consisting of 2 or more pair per carpel, the ovules are superimposed in the narrow locules bordering the intruded placentae. Unlike the Scrophulariaceae or Leucophylleae ovules are pendulous, anatropous with micropyles superior (Wettstein 1895; Chinnock pers. comm. 1984).

Differences also occur in stigma structure. In the Leucophylleae style tips are expanded, flattened, rounded to acute and stigmatic along the somewhat thickened distal margins. In Myoporaceae style tips are either capitate (*Myoporum*) or more often slender with stigmatic surfaces restricted to a notch at the slender tips, with this rarely expanded into a slightly bifid tip (Chinnock idem.).

Unlike the Scrophulariaceae and Leucophylleae mature fruit of Myoporaceae are indehiscent and can be dry or drupaceous. The endocarp of the fruit walls can be thickened and sclerified or thin and rather cartilaginous (Chinnock idem.). The exocarp can be dry and papery and separable from the endocarp by breakdown of the mesocarp. The mesocarp is often dry, pithy or firmly pithy. These dry fruit are indehiscent but there may be some disintegration of tissue near the top of the ovary and carpels may separate slightly (Chinnock idem.). In *Myoporum* and some species of *Eremophila* the mesocarp is thickened and fleshy and the fruit are considered drupaceous though there may be several seeds from more than one carpel inside the hardened endocarp (Chinnock idem.). As ovule number in Myoporaceae typically ranges from 1-3 pair per carpel, fruit have only 1-8(-12) seeds and these are much larger than in the Leucophylleae measuring 2-3.5 mm in length with testa surfaces smooth or faintly reticulate (Chinnock idem.). Unlike the Scrophulariaceae and Leucophylleae seeds have scanty or no endosperm.

While Myoporaceae appear to be uniformly woody, data presented here indicate that *Leucophyllum* may be secondarily woody, i.e., derived from herbaceous ancestors. Woody growth habits, of course, also occur in other tribes of the Scrophulariaceae.

Species of *Leucophyllum* are very similar vegetatively to some species of *Eremophila*. As they both occur in semiarid and arid habitats, this to some degree may be convergence. They both have dorsi-ventral to isobilateral leaves, and can be pubescent to densely canescent often with dendritically-branched hairs. In both, corollas can be weakly zygomorphic, though *Eremophila*, with 140 species (Chinnock idem.), exhibits considerably more diversity with corollas ranging from nearly actinomorphic to strongly zygomorphic, with some species having 4 posterior corolla lobes and solitary anterior lobes. The corolla and androecium of *Leucophyllum* strongly resemble those of some species of *Myoporum* (e.g. *M. laetum*) even down the surface texture of the corolla trichomes and in the arrangement of the anther sacs. However, many of these characteristics occur throughout both families. There, however, remain significant differences between the families in gynoecial features, and chromosome numbers etc.

While *Leucophyllum* and *Eremogeton* may constitute a somewhat discordant element within Scrophulariaceae, they are strongly discordant in Myoporaceae and their inclusion in that family would completely go against the few (mostly gynoecial) characters that distinguish Myoporaceae from Scrophulariaceae. On the other hand, there are so many characteristics in common between Myoporaceae and Scrophulariaceae that recognition of Myoporaceae as a distinct family could be questioned.

In the paragraphs below we present data on morphology, anatomy, and cytology of *Leucophyllum* and *Eremogeton* and wherever possible we comment on characteristics found in other Scrophulariaceae and/or Myoporaceae. The picture that emerges is that in many features *Leucophyllum* and *Eremogeton* are similar to both families and in other features (some critical) they are more similar to Scrophulariaceae. These data plus phylogenetic considerations, discussed below, support retention of *Leucophyllum* and *Eremogeton* in the tribe Leucophylleae, series Pseudosolaneae, at the base of the Scrophulariaceae along with other Old World tribes as initially suggested by Bentham (1876).

MORPHOLOGY AND ANATOMY

HABIT: *Leucophyllum* species are mostly small- to medium-sized, rounded shrubs 0.5 – 2.5 m tall with divaricately branching stems. Branching may be ascending or divergent. In some species, dead branches persist and give the plants a thorny aspect. The habit of *L. pringlei* differs from others in its

basal woody burl from which arise several, slender, erect stems that branch only in the distal portion. *Eremogeton*, which neither of us has seen, is apparently a taller, branched shrub to small tree 1.5–8 m high (*fade* labels). **YOUNG STEMS:** Young stems of *Leucophyllum* are terete and vestitured. The nodes develop distinct, persistent protuberances, and long-shoot leaves abscise just above the swollen bases. Anatomically, young stem pith initially consists of large parenchyma cells that develop into lignified brachysclereids within the first year. Vascular tissue develops in a continuous ring, i.e., not broken by medullary rays (see xylem description below). A continuous ring of primary phloem fibers to 0.06 mm thick in *Leucophyllum*, to 0.2 mm thick in *Eremogeton*, occur outside the non-lignified phloem. This cylinder of fibers is broken apart as stems increase in diameter. In some species the areas between the primary phloem fibers develop brachysclereids. The cortex is parenchymatous, the outer portion consisting of chlorenchyma and later storing starch. A phellogen develops in the outermost cortex layer immediately beneath the epidermis. Periderm (phellem) cells do not collapse radially, and the cork is often soft and thickened. In several species (e.g., *L. revolutum*, *L. pruinatum*, *Eremogeton*, and probably others), the tangential pockets of radially thickened, elongate secondary phloem fibers eventually are included in the periderm. In some species certain phellem cells develop into brachysclereids.

XYLEM: Data on xylem anatomy of *Leucophyllum* kindly have been provided in part by David Michener, whose interest in *Leucophyllum* was sparked by previous studies of woods of shrubby Scrophulariaceae, namely *Keckiella* (Michener 1981). A full report on comparative xylem anatomy of *Leucophyllum* will be presented elsewhere by Michener. His data provide evidence that the woody habit of *Leucophyllum* may be secondarily derived from herbaceous ancestors.

The data on xylem anatomy were obtained from standard transverse, tangential, and radial sections and macerations from samples of each of the eight *Leucophyllum* species native to Coahuila, Chihuahua, Nuevo León, Tamaulipas, and Texas. The following summary constitutes a generic description of the xylem of *Leucophyllum*. Woods of *Eremogeton* have not been studied.

Xylem of *Leucophyllum* has both distinct and indistinct growth rings even in one stem reflecting periodic growth flushes probably tied to rainfall. Vessel elements are aggregated and widest in the initial portion of a growth ring; they continue across the growth increment as narrow elements, mostly loosely aggregated in meandering to radial chains associated with paratracheal axial parenchyma. The growth ring terminates in a narrow band of very narrow vessel elements ($\pm 12-15 \mu\text{m}$ in diameter) that can be

distinguished from fibers in cross section by their pitting. Occasional elements in this zone do not develop perforations and thus constitute vascular tracheids. Vessel elements have simple perforations. The wider elements frequently have narrow tails at one or both ends and perforations are oblique to transverse. Narrower vessel elements tend to have more oblique to nearly lateral perforations. Intervascular pitting is of alternate, circular-bordered pits. Prominent tertiary helical thickenings are frequent both in wide and narrow vessel elements. Vessel elements are short (mean lengths range from $158 \pm 41 \mu\text{m}$ to $238 \pm 51 \mu\text{m}$) and narrow to very narrow (mean diameters range from $40 \pm 17 \mu\text{m}$ to $24 \pm 9 \mu\text{m}$) in species studied.

Axial parenchyma is paratracheal, confluent, associated with the radial chains and initial aggregations of vessel elements at the beginning of the growth ring. Successive growth rings and minor growth flushes are separated by 1-celled bands of axial parenchyma. Axial parenchyma is commonly once-divided transversely and constitutes parenchyma strands.

The ground matrix of the xylem consists of masses of narrow, moderately thick-walled fiber-tracheids with distinct outer pit apertures. In the one specimen of *L. frutescens* in which they were measured they had an average length of $427 \mu\text{m}$ with a maximum length of $550 \mu\text{m}$, minimal length of $220 \mu\text{m}$ with average length 2.25 times that of the average vessel element length for the same collection.

Both uniseriate and multiseriate rays are present. Uniseriate rays are usually short, 2–3 cells tall (to 10 cells tall in *L. zygophyllum*). Multiseriate rays are 2–3 cells wide and usually less than 12 (rarely 18) cells tall. Ray cells are primarily procumbent; erect to square cells occur at the zone between successive growth increments.

Analysis of ontogenetic development of the vascular cambium of a collection of *L. frutescens* (Miebener 4308) showed a drop in vessel-element length from metaxylem into the first four increments of secondary xylem. The mean vessel element length in late metaxylem was $396 \mu\text{m}$, for the metaxylem-secondary xylem transition area, $307 \mu\text{m}$, and for the first through fourth years of secondary growth, 187, 134, 163, and $137 \mu\text{m}$ respectively. The drop in vessel-element length reflects subdivision of cambial initials and the failure of the initials to elongate during secondary growth. This pattern is considered by Carlquist (1962, 1975) to be paedomorphic, and this pattern is considered characteristic of plants that are secondarily woody and derived from herbaceous ancestors. If this is the case in *Leucophyllum* the shrubby habit of *Leucophyllum* need not be considered such an anomaly in Scrophulariaceae nor indicative of relationship to the woody Myoporaceae.

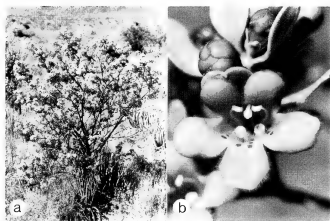


Figure 1. *Leucophyllum frutescens*. a. Habit. b. Face view of flower showing orientation of stamens, style, and spot pattern on floor of corolla throat. Note trichomes on corolla lobes, throat, and orientation of lobes in upper buds (Henrickson 19694).

LEAVES: Leaves are alternate, occasionally subopposite (when crowded), in a $2/5 - 5/13$ phyllotaxy in all species except *L. zygophyllum*, in which they are opposite, and *L. candidum*, in which they are mostly alternate but tend to be subopposite to opposite on uppermost stems. Leaves are borne only on long shoots, axillary short-shoot spurs do not form. However, axillary shoots with crowded leaves may develop in *L. minus* and *L. laevigatum* var. *griseum*. Leaves are simple, oblanceolate, obovate to orbicular, acute to rounded, emarginate at tip, narrowly to broadly cuneate or rounded at base, entire, sometimes undulate, revolute in *L. revolutum*, (fig. 2 a), toothed in *Eremogeton*, (fig. 21), flat, or conduplicately folded along the midrib in *L. zygophyllum* and *L. frutescens*, soft, pliable, mostly equally, often densely, tomentose on both sides with dendritic trichomes or less strongly vestitured on the upper surface (*L. revolutum*, *L. frutescens*) to nearly glabrous (*L. laevigatum* var. *laevigatum*, *L. langmaniae*). Stipules are absent.

Leaves of most species are isobilateral, as noted by Karrfalt and Tomb (1983), with palisade layers 2 - 5 cell layers thick on both surfaces (fig. 2 c-d), though often less well developed on the lower surface. Leaves of the bicolored *L. revolutum* and *L. frutescens* (fig. 2 a - c), as well as *Eremogeton*,

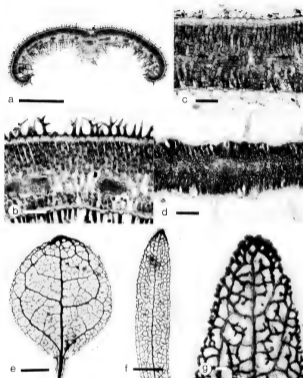


Figure 2. Leaf anatomy of *Lewophyllon*. a. Cross section of leaf of *L. revolutum* showing revolute margins and longer vestiture on adaxial surface. b. Same leaf showing short trichomes on upper surface and dorsal-ventral mesophyll structure. (Henrickson and Heis 19074). c. *L. frutescens*. Leaf cross section showing unequal development of palisade and dorsal-ventral leaf structure (Henrickson and Heis 19054). d. *L. pruninum*. Leaf cross section showing equal development of palisade in an isobilateral leaf; note also base of trichome (Henrickson and Heis 19117). e. *L. nims*. Cleared leaf with venation stained. Note venation pattern and concentration of sclerified elements near the tip. Leaf is 3.6 mm wide (Goutry 605). f.-g. *L. pringlei*. f. Cleared leaf with venation stained. g. Terminal portion of same leaf as in f enlarged, showing marginal and terminal sclerified bundle-sheath elements (tracheids) characteristic of leaves of all species (Prigge 3239). Scales in b, c, d, g = 0.1 mm; in a, e, f = 1 mm.

have a dorsi-ventral structure. The mesophyll of many species has poorly to well developed air spaces (Karrfalt and Tomb 1983, figs. 16 d, 10 a). These are lacking in *L. ambiguum*, *L. pruniosum*, and *L. pringlei*. Stomata have anisocytic subsidiary cells; some anomocytic arrangements were observed along with the anisocytic ones in *Eremogeton*. Leaves receive a single trace from a unilacunar, 1-trace node.

Cleared leaves show venation to be pinnate, camptodromous, and brochidodromous (Dilcher 1974; fig. 2 e, f, g). Secondary veins are few (2-3), abruptly curved upward near margins adjoining superadjacent secondary veins at right angles, sometimes the lowermost pair, however, do not join. Tertiary veins form orthogonal reticulacae with veins diverging at right angles from secondary and midveins. Areoles are well developed, small to medium sized (Dilcher 1974), mostly (3-)/4(-5)-angled, without or with simple, linear, rarely curved veinlets (fig. 2e-g). Leaf venation is distinguished by development of groups of enlarged sclerified xylem tracheids located at tips of veinlet endings in areoles of some species and the development of larger, more conspicuous, sometimes continuous, aggregations of similar sclerified elements along the distal leaf margin, with greatest development at the leaf tip in all species. These more massive groups of sclerified cells consist of xylem tracheids and adjacent sclerified bundle-sheath elements with somewhat elongated, fully bordered pits. In some leaves layers of leaf mesophyll cells are also sclerified and exhibit small non-bordered pits. Development of marginal and terminal sclerified elements appears identical to that found in leaves of Fouquieriaceae (Henrickson 1972), where they were designated water-storage tracheids. Lersten and Carvey (1974) questioned their function in water storage in Fouquieriaceae and referred to them as sclerified veinlet elements. Their role in water transport-storage is unknown.

VESTITURE: Vestiture provides important and useful taxonomic characteristics in *Leucophyllum* and *Eremogeton*. Trichomes cover the leaves, young stems, petioles, calyces, in some species the ovary and fruit apex, style base, and various portions of the corolla. Several types of trichomes occur together in any one species.

All species have short, stipitate glands in the understory of the longer trichomes on both leaf surfaces, on calyces, and occasionally, on the stems (fig. 3 c, f, i). The trichome stalks are uniseriate, consisting of one slightly elongated or short, thick-walled cell topped with a thin-walled short cell immediately beneath the gland (fig. 3 c, i). The gland in most species of *Leucophyllum* and *Eremogeton* consists of 2 or 4 to 7 vertical cells. In *L. pringlei* the trichome gland is considerably larger and is divided vertically into 10-15 cells; the glands appear to be "sessile" but are actually short-stalked,

sunken into the leaf surface. Cronquist (1981) noted that glands divided by vertical walls are characteristic of Myoporaceae. However, nearly identical stipitate glands with glands vertically divided into 2 cells occur in *Verbascum* and other genera in Scrophulariaceae.

In *Eremogeton* trichomes on vegetative portions of the plants are uniseriate, multicellular, mostly unbranched, and typically antrorsely curved (figs. 3 g-h, 20 d). Occasional trichomes are branched and one branch may terminate with a gland (fig. 3 h). In dried specimens the thin, transparent walls of individual cells are often collapsed.

In *Leucophyllum* trichomes are once dendritically branched and consist of a uniseriate, multicellular central axis bearing 1-4 lateral, divergent, single-cell radii or "branches" at each "node" or cell junction of the central axis of trichomes in all species (fig. 3 b) except *L. pringlei*, which has multicellular lateral radii (fig. 3 d, e). Interspecific trichome variation involves the relative elongation and numbers of central-axis and branch cells. The trichomes may be very short, with short, tapering radii (*L. langmaniae*, *L. minus*, *L. laevigatum*, and some *L. frutescens*) or tall, with slender radii to 3(-5) mm long (*L. ambiguum*, *L. pruinosum*, *L. ultramonticola*) or they may have an elongate central axis with short radii (*L. candidum*). Constituent cells have clear, transparent, smooth walls that may be relatively firm and remain terete at maturity or they may be thin and collapse upon drying. The central axis may be straight or may zig-zag at the junction of each cell. Commonly tall, much-branched trichomes have no lateral branches on the lower portion of the axis (fig. 16 d). Trichome radii typically are of equal length along the axis as in the "bottle brush" trichomes on the young stems of *L. candidum* (fig. 16 ac). Occasionally, however, in *L. candidum* and others, radii on the distal portion of the trichome as distinctly shorter.

In many species young leaves are densely woolly-tomentose but vestiture is reduced in stature and density in mature leaves. This occurs partly due to the increases size of mature leaves but it is mostly because of weathering of terminal portions of individual trichomes. In instances where the more distal radii are shorter and proximal radii longer, the change in vestiture pattern, from one high stature with short radii to one of low stature with long radii on older leaves, can be considerable (fig. 16 c).

The most dramatic change in vestiture in young to old leaves is seen in *L. laevigatum* in a taxon described as *L. virescens* (= *L. laevigatum* var. *griseum*) in which young leaves are white with densely-crowded trichomes with short radii. Older leaves have a sparse vestiture of trichomes with much longer radii to 0.3(0.5) mm long (fig. 14 a, b). This apparently is not due to loss of the distal trichome radii, but, it appears that trichome radii development

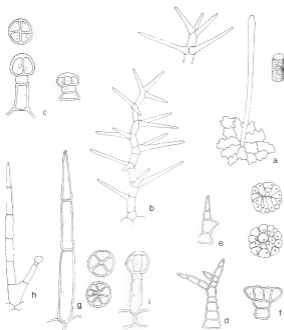


Figure 3. Trichome structure in *Leucophyllum* and *Eriogonon*. a-b. *Leucophyllum frutescens*. a. Unicellular trichome from inner floor of corolla tube. Note somewhat claviform shape, sculptured outer surface indicated in section at right. Note undulate pattern of adjacent inner corolla epidermal cells. b. Long dendritically branched trichome with 2 radii per "node" showing multicellular nature of central axis. Other trichomes may have 3-several radii per node (Henrickson and Hes 1969:4). c. *L. revolutum*. Glandular trichomes from leaf (left) and calyx (right). Note each consists of 2 stalk cells, the lower with thickened walls, the upper with twin walls and glandular contents. Head of glands throughout the two genera have only vertically-arranged cells, 2-15 in number. Note top view of gland with 4 cells on upper left (Henrickson and Hes 1967:4). d-f. *L. pringlei*. d. Branched trichome from stem showing multicellular structure. Note multicellular radii. e. Trichome with lateral protuberance accounting for branching. f. Leaves have shorter, tack-shaped glands with 2 stalk cells and multicellular heads with 10-15 vertical cells arranged as shown in circular drawings above (R. Cruz C. 2008). g-i. *Eriogonon grandiflorus*. g. Stem, leaves have multicellular trichomes that typically curve distally and have collapsed walls (See fig. 20 d). h. Variation with branched trichome, one branch gland-tipped. i. Glandular trichome. Glands have 4-7 cells. Scale = 0.1 mm.

may be dependent on environment with leaves developing after rains having longer radii than those produced later in the season when conditions are drier.

Trichomes of *L. minus* (fig. 14 e, f) appear stellate but actually are only compressed dendritic with several broad, thin-walled radii extending from the tip of the central axis. Other trichomes have radii extending from the top few "nodes" of the central axis. Often in this species the terminal cells of the axis may die before differentiating and thus create a darkened, gland-appearing point at the trichome tip.

In *L. pringlei*, nonglandular trichomes are reduced and occur primarily on the stem, petioles, and occasionally along basal portions of the leaf midrib. The trichomes are uniseriate and multicellular and may be either simple or distally forked or branched (fig. 3 d, e). Trichome branching occurs either through multicellular radii or from lateral protuberances of individual cells (figs. 3 d, E; 20 c). Cell walls in this species are firm and do not collapse.

These trichome differences provide useful taxonomic characters. Trichomes of most species are illustrated with scanning electron micrographs (figs. 8, 9, 10, 13, 14, 16, 20).

INFLORESCENCES: Flowers are solitary in axils of upper leaves on terete, ascending, slender pedicels 1–5(-9) mm long in *Leucophyllum* and 2–3.5 cm long in *Eremogeton*. Pedicels are usually vestitured as the stems. In *Eremogeton*, pedicels are strongly accrescent and 4–6 cm long in fruit. Bracts and bracteoles are absent.

Leucophyllum is noted for its showy, though brief, display of flowers after rains in late summer but species occasionally flower at any time of the year. The brief display of flowers in some instances may effectively isolate sympatric species, however, simultaneous, syntopic flowering of some species can occur when the first summer rains are very late.

CALYCES: Calyces are divided into 5 lobes to or almost to the base. The tube, when present, is broadly campanulate. Calyx lobes are oblong, oblong-lanceolate to -oblanceolate, acute to obtuse at the tip, entire, slightly accrescent in *Leucophyllum*, with sessile or stipitate glands and various other vestiture (sometimes less than the subtending pedicels) abaxially and to some extent on the distal adaxial surface. Sepals of *Eremogeton* are large, oblong-oblanceolate, green, leafy, vestitures as the leaves, and accrescent.

COROLLAS. Corollas in *Leucophyllum* are sympetalous, horizontally oriented, slightly zygomorphic, (4-)5(-6)-lobed. Corolla lobes are orbicular or broader than long, mostly emarginate to rounded, entire, occasionally erose. The posterior 2 lobes are external in bud (fig. 1 a) and reflexed at anthesis. The anterior 3 lobes are spreading to reflexed-recurved with the

medial lobe larger than the lateral two and all are slightly larger than the posterior two. Externally corollas may be glabrous to sparsely stellate or stipitate-glandular. Inner corolla surfaces may have short to long, tangled, unicellular trichomes 0.2–3 mm long with blunt, rounded tips and warty surfaces (fig. 3a) located on the throat floor, sometimes also on the throat roof, and sometimes extending to lobes; in some specimens they are restricted to the lobe margins.

Corollas range from lavender, pinkish, violet to white (albino), and most have a white patch on the floor of the throat beset with irregular rows of yellow to yellow-brown spots (fig. 1 b), or they may be of a solid color or with a white patch with dark purple-violet spots. The spots apparently serve as nectar guides.

Corollas of *Eremogeton* are very large (6–7 cm long), 5-lobed (fig. 21); the lobes are oblong with the posterior 2 lobes united nearly to the obtuse to acute tips. The posterior 3 lobes are reflexed to spreading. Corollas are stipitate-glandular outside and weakly so inside. The lobes are ciliate with long, crinkled trichomes. The corollas are thick and whitish; according to label data, they open in the evening.

ANDROECIA: *Leucophyllum* typically has 4 didynamous (rarely 3 or 5) stamens. Rarely a medial, posterior staminode is present. Filaments are adnate to the corolla tube for one-fourth to one-third their total length. They may be glabrous or pilose at the base but are glabrous and whitish where free above. In the species descriptions the filament lengths recorded are measured from the base of the corolla to the anthers because insertion is often variable even in an individual flower. Filaments of the posterior stamens extend along the upper margin of the tube-throat and abruptly turn inward just below the anther; the anthers are positioned along the roof of the mouth (fig. 1b). The relatively shorter filaments of the anterior stamens extend along the margin of the corolla tube floor and turn inward just below the anthers, which are then situated at the floor of the corolla mouth (figs. 1 b, 19 d). Anthers are white to yellowish, glabrous, birchecial but 3-locular (fig. 5 q), with the inner 2 locules shorter and distinct while the outer anther sac is longer, confluent across the anther tip. Dehiscence occurs between the inner and outer anther locules, and after anthesis the anther sacs are explanate, divergent 120–180 degrees (fig. 5 q).

Eremogeton, in contrast, has only the two anterior stamens, (the two posterior stamens are sometimes represented as filamentous staminodia) with glabrous, whitish filaments inserted at the base of the corolla tube and anther sacs exerted and situated below the two posterior corolla lobes. The whitish anthers sacs are similar to those of *Leucophyllum* but are divaricate only 30–40 degrees after pollen release.

Pollen in all species is distinctive, 3-colporate, diorate, with mesocolpia reticulate, tectate, and exhibits some variation in sculpturing (Niezgoda & Tomb 1975). Pollen grains of *Leucophyllum* range from 21–26 μm in equatorial diameter, 19–30 μm in polar diameter (Niezgoda & Tomb 1975). Those in *Eremogeton* are similar but slightly larger (30.6–31.6 μm).

GYNOECIA: Ovaries are superior, 2 (rarely 3)-carpelled, 2(-3)-loculed, with expanded, axile, medially-furrowed placentae (figs. 4 c, d; 5 q). Ovules are numerous in each locule, borne on the expanded placentae, campylotropous (fig. 5 n), tenuinucellar, and unitegmic. The styles are terminal, cylindrical, and glabrous or variously vestitured at the base. The style tip expands into a slightly flattened, acute to rounded, mostly rhomboid, thickened tip that is papillate and stigmatic across the distal margin (or margins when acute). There is some interspecific variation in stigma structure; some species have blunt tips, others have more elongate, acute tips that sometimes fold back upon drying.

FRUITS: Fruits are woody capsules that dehisce septically to the base and part way to the base loculicidally. The outer 3–5 layers of the fruit wall consist of soft cells; the inner 3–4 layers consist of radially oriented lignified sclereids with the innermost sclerified layer parallel to the inner carpel wall surface (fig. 4 d, e). Fruits are contained within the persistent, slightly accrescent calyx and may be glabrous or glabrate or persistently beset with dendritic trichomes near the tip. Capsule structure is basically identical to that found in *Penstemon* (Scrophulariaceae).

SEEDS: Seeds are small, often somewhat flattened, angular, in *Leucophyllum frutescens* 1–1.3 mm long, 0.5–0.7 mm wide, mostly 0.2–0.5 mm thick with shape affected by the close packing of the seeds between the expanded axile placentae and the ovary wall (fig. 4 f). Testa are brown to gray with a reticulate pattern formed as tangential walls collapse between erect radial walls (fig. 4 g). The embryo occupies about 80 percent of the seed, is 0.8–1.1 mm long, flattened, and has two oblong cotyledons that are rounded at the tip and are about equal in length to the hypocotyl. Endosperm is about 0.1–0.15 mm thick and consists of 3–5 layers of cells with unevenly thickened walls. Both endosperm and embryo contain oil droplets that stain with Sudan IV. Seeds are identical to those sampled in *Penstemon* and *Verbascum* except for the convoluted external sculpturing in the latter. Seeds of *Eremogeton* are similar in structure but slightly larger.

FLOWER VASCULARIZATION: Flower vascularization of *Leucophyllum* was studied from serial sections and clearings of whole flowers (figs. 4 b–d, 5 a–p). Pedicels contain a continuous cylinder of vascular tissue (fig. 5 a). Ten vascular traces emerge in one series in the receptacle; five medial sepal

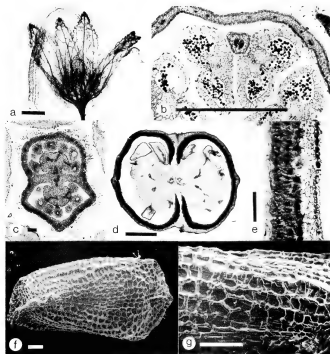
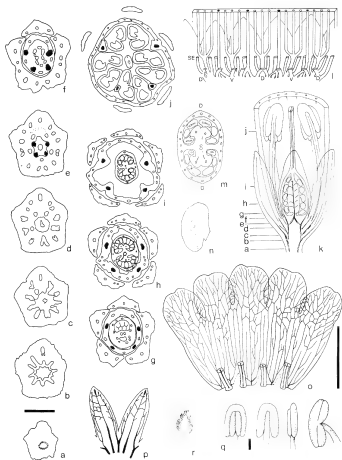


Figure 4. Floral, fruit, and seed structure of *Lanophyllum*. a. *L. frutescens*. Cleared flower, note vascularization and sclerified elements at tip of sepals (Henrickson and Hess 19054). b. *L. pennisium*. Cross section of anther below attachment of filament showing 4 locules, corolla (Henrickson and Hess 19117). c. *L. revolutum*. Cross section of ovary showing axial placentation. Ovary is 1.26 mm long (Henrickson and Hess 19074). d-e. *L. frutescens*. d. Cross section of fruit note locatin of sclerenchyma in fruit wall and axial placentae with few developing seeds. Ovary is 4 mm long. e. Enlargement of fruit wall showing epidermis, (on right), few parenchyma layers and (on left) inner layer of 3 radial and innermost tangentially-elongated sclerenchyma cells. Structure is identical to that found in Scrophulariaceae (Henrickson and Hess 19054). f-g. *L. frutescens*. f. SEM of seed, note surface sculpturing. g. Enlarged view of seed surface showing reticulate pattern developed by collapse of tangential epidermal walls (Henrickson and Hess 19301). Scales in a, b, d = 1 mm; in c, e, f, g = 0.1 mm.

traces alternate with five petal-sepal traces. The petal-sepal traces soon branch off two lateral traces, one going to each adjacent sepal as lateral sepal traces. The remaining adaxial vascular tissue then continues as the petal trace (fig. 5 b-d, 1). Each sepal then receives three separate traces (fig. 5 p) that branch and anastomose distally in the lobes. They are associated with sclerified bundle-sheath cells similar to those in the leaves (figs. 4 a, 5 p). Similar thickenings also occur along the thickened basal portions of the sepal traces (figs. 4 a, 5 p). The remaining five petal traces each branch into three traces at the base of the corolla tube and continue to branch and anastomose further up the corolla tube and into the lobes (fig. 5 o). After the sepal and petal traces diverge, the remaining receptacular vascular tissue forms into a cylinder giving rise to the four stamen traces (shown in black in fig. 5 g-j). These merge into the corolla, eventually becoming free some distance above the corolla base. The remaining vascular tissue organizes into the ovary traces. That portion of the vascular tissue that would have gone to the posterior or fifth stamen develops into the dorsal trace of the posterior carpel thus affecting the vertical orientation of the ovary. The remaining vascular tissue forms into the other dorsal, ventral, and lateral traces, with the dorsal traces continuing into the style (fig. 4 a). The pattern illustrated in fig. 5 a-1 was found in all flowers of *Leucophyllum* studied, except in one flower of *L. frutescens* in which the lateral sepal traces of two sepals developed from the medial sepal trace rather than the alternate petal traces. The vascularization pattern was identical to that found in both

Figure 5. Flower vascularization and structure of *Leucophyllum*. a-j. Diagrams of vascular system as seen in serial cross sections of *L. prinosum* at levels indicated in k. Stamen traces are indicated by black circles. Note sepals receive 3 traces, medial traces directly from receptacle, lateral traces branch from adjacent petal traces. Also note origin of stamen traces (Henrickson and Hess 1917). k. Cutaway longitudinal diagram of flower showing patterns of vascular bundles in receptacle and approximate levels of sections a-j. l. Two-dimensional diagram of vascular system as seen from inside flower cut between anterior lobes, with lowest, innermost series of traces going to ovary (D = dorsal traces, V = ventral traces), second series to sepals (SE), note medial trace develops directly, lateral sepal traces develop with petal traces. Petal traces branch at corolla base, stamen traces terminate with black circles. m-r. *L. frutescens*. m. Cross section of ovary showing 2 carpels, dorsal traces (D), expanded axile placentae, ovules. n. Camplyotropous ovule (diagramatic). o. Vascular system of corolla as seen from adaxial surface cut between 2 posterior lobes. Note basal branching of initial 5 petal traces and basal portion of 4 stamens. p. Vascular system of mature calyx showing 3 traces, distal trace branching and location of sclerified elements near sepal tip. q. Anther structure as seen from adaxial (left), and abaxial side views and after anthesis (right). Note outer thecum is continuous around 2 inner locules. r. Style tip showing marginal papillate thickened stigmatic portion (m-r from Henrickson and Hess 19074). Scale above a = 1 mm holds for a-j; in o = 1 cm; in q = 1 mm.



Penstemon and *Myoporum laetum* except for the 3-carpelled gynoecium and reduced ovule number in the latter. Vascularization of flowers of *Eremogeton* was not studied as no material was available.

CYTOLOGY

Flyer (1970) reported one unvouchered chromosome count for *Leucophyllum* ($n = 15$, for *L. minus*). He noted that meiosis apparently is very rapid in pollen parent cells, for, despite numerous attempts, no stages between prophase and the tetrad stage could be seen with this one exception. The number $\bar{n} = 16$ may reflect $\bar{x} = 8$; $\bar{x} = 8$ has been reported for other Scrophulariaceae (e.g., some species of *Verbascum* and *Mimulus* and throughout the genera *Antirrhinum*, *Pedicularis*, and *Penstemon*). Myoporaceae has $\bar{x} = 18$ in *Eremophila*, (Barlow 1971) and $\bar{x} = 27$ in *Myoporum* (Hair and Beuzenberg 1959).

SPECIES RELATIONSHIPS

Various phenetic and cladistic analyses were performed on character data obtained from *Leucophyllum* species. Problems arose with characters involving vestiture. Plants with dense stem-leaf vestiture had an uneven and apparently meaningless, though species-specific, continuation of vestiture onto various floral features. Certain species, however, grouped together in most analyses, including: (1) *L. ambiguum*, *L. ultramonticola*, *L. pruinosum*; (2) *L. laevigatum*, *L. griseum*, *L. minus*; and (3) *L. zygophyllum*, *L. candidum*. *Leucophyllum pringlei* usually did not group closely with other species. The positions of *L. frutescens*, *L. revolutum*, *L. langmaniae*, and particularly *L. flyrii* were very variable. Use of different or reduced data-sets gave variable results but from this came a synthesis of data resulting in a tentative tree (fig. 6), derived by applying the method of grouping of species by shared derived character states (synapomorphies). This is presented in the form of a cladogram to facilitate representation of character states in relation to proposed relationships. The basic structure of the tree was derived from a reduce data-set using only 11 characters but these characters are considered to be significant. Relationships at some upper points of the tree were resolved through other data-sets. Attempts to apply the outgroup method (Stevens 1980) of character polarization were largely unsatisfactory. Relationships undoubtedly lie within Scrophulariaceae but exactly where is not known. However, as all species of *Leucophyllum* are woody, have some form of branched, dendritic vestiture, have glands with 2 stalk cells and multicellular gland heads with vertically-oriented cells, have bractless, ebracteolate flowers with 5 subequal corolla lobes, (the posterior 2 lobes external in bud), and have 4 anthers with continuous outer thecae and bicarpellate

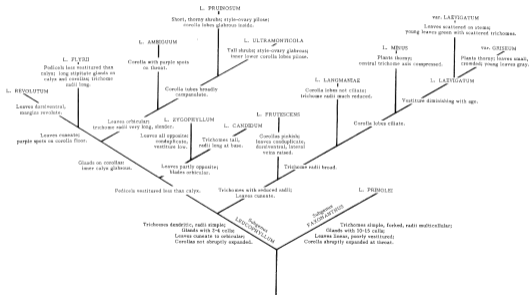
ovaries with axial placentae, etc., these characters are considered to be primitive (plesiomorphic) for the genus. Factors such as thorny, reduced habit and degrees of vestiture development are considered to be highly variable and poor characters for estimating (guessing at) phylogeny. The pattern that emerges from phytogeographic evidence (see below) is that *Leucophyllum* may be an old group that has been in existence in the altiplano of Mexico in arid and semiarid habitats since perhaps the late Eocene (Axelrod 1979) and its history may be marked by hybridization (as is occurring today) with derivatives recombining characteristics and thus its phylogenetic history may include reticulations between major lines.

In figure 6, trichomes of moderate stature with single-celled, moderate-lengthed radii, cuneate, alternate leaves, and yellow corolla-throat spots are considered plesiomorphic. From these states, opposite, linear or orbicular leaves with either very long or reduced vestiture with very long and slender or short radii and development of purple or no corolla throat spots are considered derived. Vestiture types appear to have evolved more than once. Vestiture varies throughout the range of *L. frutescens* from very tall to highly reduced and obscure. In its reduced state the vestiture is very similar to that found in *L. langmaniae*, which we do not, however, consider to be closely related. Corolla throat spotting varies throughout the range of *L. ambiguum*. Most populations have no corolla spots but collections near Meztitquitlan in Hidalgo have yellow corolla-tube spots—is this an atavistic or apomorphic feature? Data summarized in fig. 6 must be considered tentative but reflective of possible relationships of the taxa of *Leucophyllum*. Our biggest questions concern relationships of *L. flyrrii*. It is similar to *L. revolutum* in its cuneate leaves and purple corolla spots but, unlike *L. revolutum*, its leaves are isobilateral not dorsi-ventral. It also shares characteristics with members of the *L. ambiguum-pruinatum* complex, which can also have purple spots on the corolla floor, isobilateral (but orbicular) leaves, and long trichome radii.

Eremogeton, with its large, toothed leaves and large white, more strongly zygomorphic flowers with only 2 stamens, is considered to be distinct from the hypothetical ancestor of *Leucophyllum*. It is not included in this discussion. Because of the large number of apomorphic features that distinguish *L. pringlei*, it is here considered as a distinct subgenus.

PHYTOGEOGRAPHY

Leucophyllum is one of several genera endemic to the arid and semiarid regions of Mexico and adjacent United States (Rzedowski 1962, 1973). Axelrod (1979) considered *Leucophyllum* among those genera that evolved autochthonously in this region, perhaps from ancestors present during late Cretaceous-Paleocene times (50–60 mybp) that initially adapted to local



semi-arid sites and became adapted to the more arid climate that arose in late Eocene and later times. A possible scenario for development of the genus involves the development of arid zones in central Mexico from Tertiary onward. In early Tertiary local dry sites were scattered all across central Mexico in the lee of mountains allowing plants to gradually adapt to these sites (Axelrod 1979). During Eocene, the uplift of the Sierra Madre Oriental and other parallel ranges in central Mexico (the Hidalgoan Orogeny of de Cserna; see de Cserna 1960; Guzman, and de Cserna 1963) and additional volcanism resulted in a more widespread development of arid sites throughout Mexico. Much later in Miocene-Pleistocene, development of the igneous-rock Sierra Madre Occidental caused still further expansion of these arid and semi-arid zones throughout central Mexico and allowed taxa to adapt to arid- and semi-arid habitats to spread throughout the expanded dry zone that extended from Puebla to northern Mexico. Vegetation in the Miocene and early Pliocene in central Mexico, which according to Axelrod (1979) probably was warmer and had higher precipitation than today, may have consisted of dry tropical forests and woodland with thorn scrub and drier edaphic and lee-slope-habitats supported semi-arid taxa. During late Pliocene to Recent time extensive volcanic activity formed the trans-volcanic belt (Guzman and de Cserna 1963) which isolates the Pueblan arid zone (present home of *L. pringlei*) from those in the north; later uplifting and volcanic activity isolated the Hidalgoan arid region from that of the Chihuahuan Desert Region in the north (Axelrod 1979). While the southern Puebla arid regions were protected from cold winter northern fronts by the trans-volcanic belt, species diversity in the northern Chihuahuan Desert was impoverished by increasingly colder climates particularly during Quaternary glacial periods. During the Quaternary these semi-arid and arid zones were alternately reduced and expanded during pluvial and interpluvial periods. Van Devender (1977) noted that during the latest pluvial period pinyon-juniper-oak woodland vegetation extended into the areas now occupied by the northern Chihuahuan Desert, which expanded to its present conformation only within the last 8000 (-4000) years.

With the absence of fossil evidence it is not possible to know exactly how *Leucophyllum* and *Eremogeton* fit into such a scenario. Consideration that the nearest relatives of these genera of Scrophulariaceae have always been considered to be Old World herbaceous and suffrutescent genera implies that *Leucophyllum* and *Eremogeton* may be New World vicariants or at least

Figure 6. Diagram of an intuitive phylogeny of the species of *Leucophyllum*. See text for explanation.

New World survivors. Michener's xylem ontogeny data indicate that the shrubby habits of our taxa may be a derived condition. *Leucophyllum* particularly appears to be well adapted to arid and semi-arid habitats in central Mexico exhibiting a number of xeromorphic features and, undoubtedly, a number of physiological features that allow it to survive in these environments.

The present distribution of taxa appears to fit well into a vicariance model. The distinctive *Eremogeton* is geographically well isolated from the more northern species of *Leucophyllum*. *Leucophyllum pringlei*, which here is considered to be the sole member of a separate subgenus, occurs in Puebla and Oaxaca, south of the late-Pliocene-Recent Trans-volcanic belt. The other species of *Leucophyllum* occur north of this volcanic axis, one in Hidalgo-Querétaro, the others in or around the Chihuahuan Desert. These eleven species show various distribution patterns in related lines. The three species with long trichome radii (*L. ambiguum*, *L. pruinosum*, and *L. ultramonticola*) seem to form a related group and are widely disjunct: *L. ambiguum* occurs in the southern disjunction of the Chihuahuan Desert in Hidalgo and Querétaro, *L. pruinosum* in basins in southern Nuevo León and adjacent Tamaulipas and San Luis Potosí, and *L. ultramonticola* in an arid pocket along the Río Atengo in Southeast Zacatecas (fig. 16). Their present ranges probably reflect their respective refugia during the past pluvial period. It is of course attractive to propose that they may have been one widespread species during the previous interpluvial period and that subsequent isolation of refugial populations resulted in the differentiation of these three closely related vicariant species.

Many of the present day species of *Leucophyllum* occur in a Chihuahuan Desert scrub, mostly in a mixed desert scrub association above the *Larrea* zone up to the *Yucca-Dasyliirion*-dominated zones; their ranges were probably restricted during the latest pluvial period, or at least they were restricted to arid habitats within the presumed dominant woodland communities. The presumed bottlenecks in population size could well provide for more rapid character differentiation that is reflected in today's more expanded populations. At present, populations of *L. candidum*, *L. minus*, and, particularly, *L. frutescens* seem to be expanding their ranges. The latter species appears to be expanding northward from a potential refugium east of the Sierra Madre Oriental into southern Texas and spilling over into the Chihuahuan Desert. The occurrence of three species of *Leucophyllum* in the basins around southern Nuevo Leon separated from the main mass of the Chihuahuan Desert by series of low mountains is of considerable interest. This area may well have served as a refugium during the past pluvial period:

it is the present-day home of *L. prinosum*, *L. revolutum*, and *L. zygophyllum*. Many other endemics also occur in this area.

Three species of *Leucophyllum* appear to be relictual and occur only in reduced populations. *Leucophyllum langmaniae* occurs in isolated arid pockets in the woodlands in canyons between Monterrey, Nuevo León, and Saltillo, Coahuila. The geographical extent of this species is not known. *Leucophyllum flyrii* is known only from two populations, one near Laguna Seca (Gral. Candido Navarro) and one in the adjacent sierras in central San Luis Potosí. The extent of *L. ultramonticola* in southwestern Zacatecas is unknown.

ECONOMIC USE

Leucophyllum frutescens is commonly cultivated and is known as cenizo, ceniza, Texas silverleaf, Texas ranger, purple sage, and, less frequently, barometer bush, liar bush, ash bush, Texas rain sage (Texas Agricultural Experiment Station Tract L-2058). The species has been widely cultivated in south-central Texas and is becoming popular throughout the Southwest in relatively frost-free, arid regions. The plants can, however, tolerate light to moderate frost. The species is popular because of its white-gray foliage, rounded habit, and great show of pink-purple flowers after rains in late summer-fall. According to the Texas Agricultural Experiment Station, the plants prefer open sun and alkaline soils with good drainage. Recently the Texas Agricultural Experiment Station has made available a white-flowered, gray-leaf cultivar 'White Cloud,' and a green-leaved, purple-flowered cultivar 'Green Cloud' of *L. frutescens*, and a deep violet-flowered, gray-leaved cultivar of *L. candidum* under the name 'Silver Cloud.' Plants are propagated by cuttings. Flowering plants may be produced from seeds in about two years.

TAXONOMIC TREATMENT

- A. Corollas 60–70 mm long, white, posterior 2 lobes united to near tip, erect, anterior 3 lobes oblong-ovate, spreading, 25–33 mm long, 13–15 mm wide; calyx lobes 2–3.6 mm long, 4–7 mm wide; stamens 2; trichomes multicellular, tapering, antrorsely curved; leaves 4–12 cm long; México (Chiapas) and Guatemala II. *Erevogeton*. *E. grandiflorus*
- AA. Corollas 8.5–28 mm long, lavender, violet, pinkish, rarely white (albino), often with white on floor of tube marked with yellow or purple dots, lobes all orbicular to broadly oblong, subequal, 3–10 mm long and wide; calyx lobes 5–10 mm long, 0.7–1.5 mm wide; stamens 4, didynamous; trichomes multicellular, erect, stellate or dendritic or forked distally; leaves 6–35 mm long; México (Oaxaca) to sw. U.S. I. *Leucophyllum*
- B. Leaves linear-lanceolate, 6–12 mm long, 1.2–2.2 mm wide, crowded, glabrous except for sessile glands; young stems with erect,

- tapering or distally forked trichomes 0.1–0.25 (–0.4) mm long; Puebla and Oaxaca. 12. *L. pringlei*
- BB. Leaves oblanceolate, obovate to orbicular, mostly 2.5–12(–22) mm wide, tomentose or with scattered stellate or dendritic trichomes; young stems canescent to tomentose with stellate to dendritic trichomes; Hidalgo and northward.
- C. Leaves bicolorous, upper leaf surfaces more green with slightly to much-reduced vestiture (be sure to look at both surfaces of one leaf).
- D. Leaf blades oblanceolate, 2–4(–5) mm wide, at margins distinctly revolute, often inrolled towards leaf base; corollas violet with dark violet spots inside on floor of tube; sw. Tamaulipas to adjacent n. San Luis Potosí. 7. *L. revolutum*
- DD. Leaf blades obovate to oblong-obovate, (4–)6–16 mm wide, margins flat or variously undulate, not revolute; corollas pinkish to lavender, with yellow spots inside on floor of tube; w. central Texas s. to e. central Coahuila, Nuevo León, s. Tamaulipas. 1. *L. frutescens*
- CC. Leaves concolorous, upper and lower surfaces equal in vestiture and color (although sometimes more strongly vestitured along midrib beneath).
- E. Vestiture of leaves and young stems densely and closely silver-gray canescent, trichomes crowded, overlapping, appearing stellate, radii broad, translucent to whitish, to 0.1 mm long, radiating from a central, often gland-tipped, axis (use 30 X magnification); leaves small, crowded at nodes; thorny shrubs from sw. New Mexico through Trans-Pecos Texas to e. Chihuahua, s. to about 50 km ne. of Saltillo, Coahuila. 3. *L. minus*
- EE. Vestiture of at least young stems and often of lower leaf margins of dendritic trichomes, this often of an uneven stature, or if not, then either older leaves greenish or trichome arms slender, longer.
- F. Leaf-blades mostly ovate-orbicular, abruptly narrowed at base; petioles usually conspicuous; leaves silver-gray.
- G. Leaves all opposite, usually conduplicately folded along midrib; leaf-blades commonly orbicular or nearly so, closely vestitured; s. Nuevo León, sw. Tamaulipas and adjacent San Luis Potosí. 6. *L. zygophyllum*
- GG. Leaves mostly alternate, occasionally some leaves opposite or sub-opposite, seldom conduplicately folded; leaf-blades orbicular or not, with dense, thick vestiture.
- H. Corollas uniformly violet to purple throughout, occasionally with white along very base of tube but without colored dots in lower tube; Hidalgo to Querétaro. 11. *L. ambiguum*
- HH. Corollas lavender to violet but with lighter or white patch on floor of tube marked with yellow or deeper violet spots; plants of more northern distribution.

- I. Dendritic trichomes of young stems and leaf blades long and slender, mostly 0.1–0.5 mm in diameter with radii 0.1–0.25 mm long, only a few times longer than the thickness of the trichome axis; compact shrubs of Brewster Co., Texas, s. through central Coahuila to Zacatecas, e. Durango, central Chihuahua. 5. *L. candidum*
- II. Dendritic trichomes of stems and leaf-blades 0.3–1.5 mm in diameter, with radii (0.1–) 0.2–0.5(–8) mm long, many times longer than the thickness of the axis; shrubs from s. Nuevo León to Zacatecas.
- J. Style, ovary, and capsule tip glabrous or with few glands; corolla lobes pilose inside; sw. Zacatecas. 10. *L. ultramonticola*
- JJ. Style, ovary, and capsule tip pilose to densely pilose; corolla lobes glabrous inside; s. Nuevo León, adjacent Tamaulipas, San Luis Potosí. 9. *L. pruinatum*
- FF. Leaf-blades obovate-oblongate, cuneate, gradually narrowed to base; petiole (if present) not conspicuous; leaves green or not.
- K. Calyx lobes with scattered long-stipitate glands extending well above the vestiture; corolla with dark purple (not yellow) dots on floor of tube inside; leaves permanently gray-canescens; ne. of city of San Luis Potosí. 8. *L. flyrii*
- KK. Calyx lobes lacking long-stipitate glands; corollas with yellow dots on floor of tube inside; mature leaves often greenish.
- L. Leaves appearing glabrous but uniformly covered with relatively dense, but minute trichomes to 0.05 mm wide on both surfaces; radii about as long as central trichome axis; corolla lobes not ciliate; local between Monterrey, Nuevo León, and Saltillo, Coahuila. 2. *L. longianis*
- LL. Leaves with scattered to dense, stellate trichomes 0.1–0.2 (–0.8) mm broad, radii mostly 2 times longer than trichome axis; leaves either green or the youngest leaves (occasionally all) gray; corolla lobes distinctly ciliate; plants from Chihuahua and Coahuila, to San Luis Potosí, Durango, and Zacatecas. 4. *L. laevigatum*

I. LEUCOPHYLLUM Bonpl. in Humb. & Bonpl., Pl. Aequinoct. 2:95. 1812. TYPE: *Leucophyllum ambiguum* Bonpl. in Humb. & Bonpl.

Terania Berlandier, Mem. Com. Limit. Mier y Terán 4. 1823. TYPE: *Terania frutescens* Berlandier.

Rounded to rhomboid, moderately to strongly branched, evergreen to semi-deciduous, silvery-gray to greenish shrubs; young stems subterete, uniformly to irregularly tomentose to canescent with stellate to dendritically-branched, rarely forked, spreading trichomes, in age more uniformly tomentose-canescens due to weathering, eventually glabrate;

older stems with dark to light gray or reddish-brown, smooth or vertically fissured bark; older dead stems sometimes persisting as thorns. Leaves alternate, subopposite to opposite, simple, often crowded or sometimes also in reduced subfasciculate, axillary shoots, oblanceolate, obovate, elliptical, orbicular to ovate-orbicular, obtuse, rounded to acute or emarginate, with midrib continuing as a blunt, sometimes reflexed apiculation at tip, cuneate, sessile or subsessile to abruptly cuneate-rounded and distinctly petiolate at base, entire to revolute, often somewhat conduplicate folded along midrib or otherwise undulate, soft, pliable but usually thickish due to thick indumentum, silvery-gray to greenish, densely tomentose to canescent or sparsely vestitured with dendritically-branched or stellate trichomes, rarely glabrous. Trichomes uniform on both surfaces or shorter or more sparse above, consisting of a series of long, slender or short, tapering, straight or wavy simple radii extending from a short to elongated multicellular central axis that may fragment causing a reduction in vestiture stature through a season, mostly with sessile to stipitate glands in understory, with midrib and sometimes secondary veins raised beneath, abscissing above prominent, usually persistent leaf bases. Flowers 1(-2) in axils of leaves, mostly produced in abundance after rains; bracts, bracteoles absent; pedicels ascending, vestitured as young stems; calyces divided to near base into 5 lobes, lobes lanceolate to oblong-ovate, acute to attenuate, valvate in bud, tomentose, canescent as leaves or young stems or with a diminished vestiture, obscurely glandular, rarely long stipitate-glandular outside, glabrous, glandular or sericeous or sparsely stellate except a tip inside; corollas showy, lavender, light violet to pink-lavender, blue, violet, rarely white, mostly with one or more white patches on floor of tube marked with rows of yellow-brown to orange dots, or of a solid color marked with dark purple-violet spots, zygomorphic, funnellform to campanulate, tube gradually to abruptly ampliate, usually slightly to moderately dorsiventrally compressed, lobes (4-)5(-7), shorter than tube, imbricate in bud, spreading, posterior two sometimes more reflexed than anterior three, often with long, slender, tangled unicellular trichomes on floor of tube and on lower throat, with straight, erect, slightly clavate, colored hairs on throat and often on inner surface and margins of lobes, glabrous to sparsely glandular-pilose, rarely sparsely stellate outside; stamens (3-)4(-5), didynamous, included or the longer, posterior pair slightly exerted; filaments adnate to base of corolla tube for one-fourth to one-third length, glabrous or pilose near base, cylindrical to slightly compressed, whitish above, posterior pair spreading, inwardly curved at tip, anterior pair upwardly curved at tip; anthers white to yellowish, glabrous, anther sacs becoming widely divaricate ($120-180^\circ$), outer locules confluent, inner locules distinct, dehiscent across continuous end, promixal anthers oriented parallel to tube axis, anterior pair oriented nearly perpendicular to floral axis; ovary superior, ovoid, glabrous or pilose or loosely stellate at tip, 2-loculed; placentae oblong, attached medially along septum; ovules many;

styles terminal, cylindrical, glabrous to sparsely pilose, straight, extending to posterior corolla tube-throat, sometimes slightly exerted, decurved at tip, flattened, stigmatic along distal margin of terminal, obtuse to somewhat acute tip. Fruit of dark brown, woody, ovoid, apiculate capsules, these dehiscent first septically to near base, then loculicidally half way to base, enclosed in slightly accrescent calyx; seeds 15–25 per locule, small, irregularly ovoid, yellowish-brown, minutely reticulate, smooth to somewhat angled. Chromosome number $n = 16$ (one species).

LEUCOPHYLLUM Bonpl. in Humb. & Bonpl. subgen. **LEUCOPHYLLUM**.

Trichomes dendritic, with unicellular radii; glandular trichomes with 2–7 cells in head; leaves oblanceolate, obovate to orbicular, mostly covered with trichomes on both surfaces.

Distribution: Texas, adjacent New Mexico, south from Chihuahua and Tamaulipas to San Luis Potosí and Zacatecas, also in Hidalgo and Querétaro. (Species No. 1–11).

LEUCOPHYLLUM Bonpl. in Humb. & Bonpl. subgen. **Faxonanthus** (Greenman in Sargent) Henrickson & Flyr, comb. et stat. nov. *faxonanthus* Greenman in Sargent, *Trees & Shrubs* 1:23. pl. 12. 1902. TYPE: *Faxonanthus pringlei* Greenman in Sargent.

Trichomes simple or distally forked, with multicellular radii; glandular trichomes with 10–15 cells in head; leaves linear-lanceolate, glabrous except for sessile glands.

Distribution: Southern Puebla and adjacent Oaxaca. (Species No. 12)

1. **LEUCOPHYLLUM FRUTESCENS** (Berlandier) I. M. Johnston, *Contr. Gray Herb.* 70:89. 1924. *Terania frutescens* Berlandier Mem. Com. Limit. Mier Y Teran 4. 1832. TYPE: MÉXICO. NUEVO LEÓN: Monterrey, *Berlandier 1406* (LECTOTYPE: BM!; ISOTYPE: OXF!)

Leucophyllum texanum Benth. in DC., *Prodromus* 10:344. 1846. TYPE: TEXAS. WEBB CO.: "Laredo," *Berlandier 2070* (LECTOTYPE: here designated K!).

Leucophyllum frutescens (Berlandier) I. M. Johnston forma *albiflorum* Clover, *Madroño* 4:97. 1937. TYPE: TEXAS. STARR CO.: Roma, *Clover 492* (HOLOTYPE: MICH!)

Leucophyllum frutescens (Berlandier) I. M. Johnston forma *albivinum* Lundell, *Contr. Univ. Mich. Herb.* 8:86. 1942. TYPE: TEXAS. CAMERON CO.: 8 mi W of Boca Chica, 12 Mar 1942, C. L. Lundell and A. A. Lundell 10699 (HOLOTYPE: MICH!; ISOTYPES: LL!, TEX!).

[*Leucophyllum frutescens* (Berlandier) I. M. Johnston var. *floribunda* R. A. Vines, *nov. nod.* *Trees, shrubs, and woody vines of the southwest* p. 920. 1960.]

[*Leucophyllum frutescens* (Berlandier) I. M. Johnston var. *glaucom* R. A. Vines, *nov. nod.* *Trees, shrubs, and woody vines of the southwest* p. 920. 1960.]

Erect, rounded, alternately-branched shrubs 0.5–2(-3) m tall; young stems densely tomentose with conical to cylindrical, dendritic trichomes

0.1–0.3 mm long with short tapering radii 0.05–0.1 mm long, tardily glabrate; older stems with reddish-brown to light-gray bark. Leaves alternate, rarely opposite, obovate, oblong-obovate, to obovate-orbicular, 10–25(-35) mm long, (4-)6–16 mm wide, obtuse, rounded, often bluntly apiculate at tip, cuneate to petiole 1–2 mm long at base, at margins entire, sometimes slightly revolute, usually conduplicateley folded along midrib, mostly silvery-gray, tomentose on both surfaces but with shorter, more open vestiture and more gray-green to green above, upper surface with dendritic trichomes 0.1–0.3 mm high or mixed dendritic and shorter stellate trichomes or rarely of reduced, scattered stellate trichomes to 0.1 mm long, sometimes appearing nearly glabrous except for glands, lower surface mostly densely, irregularly tomentose with dendritic trichomes 0.2–0.3(-1.0) mm high, radii mostly straight, slender, 0.1–0.2 mm long, midvein and secondary veins raised beneath. Flowers with tomentose pedicels 1–4 mm long; calyces 5–7 mm long, lobes oblong-lanceolate, 3–5 mm long, 1.3–2.1 mm wide, acute, densely tomentose with dendritic trichomes as on stem outside, more glabrous, strigose slightly glandular in lower half inside, to 6 mm long, 2.5 mm wide in fruit; corollas rose-lavender, light violet, rose-pink to reddish-pink (rarely white), with white patch marked with gold-brown dots on floor of tube, 18–26 mm long, tube ampliate, to 7–12 mm wide at throat (pressed), lobes 5(-7), oblong to reniform, reflexed-spreading, 8–10 mm long, 6–9 mm wide, emarginate, sparsely pilose on floor of tube, more densely pilose at throat with straight trichomes 0.5–2 mm long, lower lobes pilose and ciliate, upper lobes ciliate only, corolla glabrous throughout outside; stamens (3-)4(-5), anther glabrous, posterior filaments 5–11 mm long, anterior filaments 4–7 mm long, glabrous; styles 9–14 mm long, glabrous; ovaries glabrous. Capsules 3.5–4.5 mm long, glabrous.

Leucophyllum frutescens (figs. 1, 7–10) is characterized by its relatively large shrub habit (1–3 m tall), moderately large, obovate, cuneate-based, bicolored, dorsiventral leaves with both mid and major lateral veins raised beneath, and the relatively large, mostly pinkish to lavender (rarely white) corollas.

The species exhibits considerable variation in leaf vestiture over its range. In all instances, vestiture is less well developed on the upper surface than on the lower surface. At one extreme, generally in plants in the northern portion of the range, both upper and lower leaf surfaces are covered with erect, dendritic trichomes generally 0.1–0.3 mm tall on the upper surface and 0.2–0.5(-1.0) mm tall on the lower surface (fig. 8 c-d). On both surfaces the horizontal radii are 0.06–0.15(-0.2) mm long. Upper leaf surfaces may appear grayish-white or greenish when vestiture is diminished through time.

In other plants (fig. 9 a–d) throughout this northern range the upper leaf surface vestiture is somewhat reduced and consists of a mixture of dendritic trichomes, sometimes with the more distal radii shorter than the



Figure 7. Line drawings of *Leucophyllum frutescens*. a. Stem showing orientation of leaves and flowers. b. Lateral, frontal, cutaway side views of flowers. Note orientation of longer, posterior and shorter, anterior stamens. c. Mature fruit showing characteristic sepicidal and loculicidal dehiscence. (From cultivated material in Austin, Texas). Scales = 1 cm.

basal radii on a trichome, and shorter stalked or sessile stellate trichomes (basically reduced dendritic trichomes), or only of stellate trichomes mostly with radii 0.06–0.15(–0.2) mm long. In contrast, the lower leaf surface has a taller, more dense vestiture of dendritic trichomes 0.2–0.5 mm tall again with radii 0.06–0.2 mm long. In these plants upper leaf surfaces often appear green in living plants while the lower surface is distinctly whitish.

The diminution of vestiture continues in the southern portion of the range in Nuevo León and Tamaulipas with upper leaf surface vestiture consisting of often more widely scattered, reduced stellate trichomes sometimes mixed with widely scattered dendritic trichomes but with radii mostly only 0.02–0.06 mm long and occasional radii to 0.1 mm long. Lower leaf surface may consist of dendritic trichomes to 0.2 mm tall with

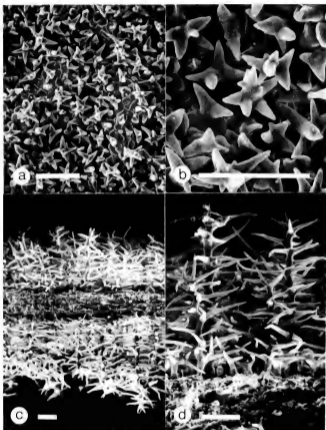


Figure 8. Leaf vestiture of *Lycopodium langmaniae* and *L. frutescens*. a–b. *L. langmaniae*. Species characterized by uniformly short trichomes with very reduced radii on both leaf surfaces. a. Mature leaf, abaxial surface. b. Trichomes enlarged (*LeSueur 435*). c–d. *L. frutescens*. c. Strongly vestitured leaf showing longer trichomes on abaxial surface. d. Expanded view of lower surface vestiture (shown here downside up). Note each "node" of central axis has 2 or 3 radii. (Compare with fig. 3 b for internal structure). (*Clark et al s.n.*, s. of Sabinas, Coahuila). Scales = 0.1 mm

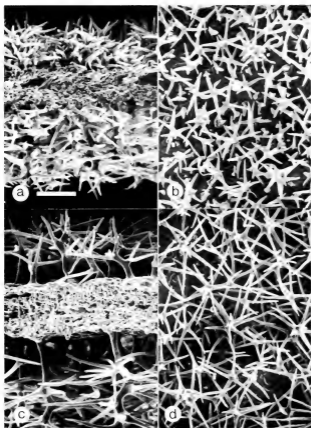


Figure 9. Leaf vestiture of *Lencophyllum frutescens*. a. Cross section of leaf showing shorter vestiture than in fig. 8 c, note also trichomes of lower surface are longer than those of upper surface. b. Surface view of adaxial vestiture, Note moderately spaced trichomes (*Henrickson and Hess 19052*: 20 km sse of Montemorelos, Nuevo León). c. Cross section of leaf showing unbranched base of trichomes and long radii. d. Surface view of adaxial vestiture, note long radii (*Lewis l.n.*: near Amistad Dam, Pecos County, Texas). Scale in a = 0.1 mm; holds for b–d.

radii to 0.2 mm long or only of stellate trichomes with reduced radii similar to those present on the upper surface but still more dense than on the upper surface.

This series culminates in plants with leaves that appear nearly glabrous on the upper surface (fig. 10 a-b, d) but have small, well-spaced, highly reduced stellate and short dendritic trichomes to 0.05 mm tall with radii to 0.02 mm long on the upper surface, and to 0.07 mm tall with radii to 0.04 mm long on the lower surface (fig. 10 c, e). As the branched trichomes are reduced in density, the underlying gland-tipped trichomes, (which are present in leaves of all the species), become more conspicuous.

In Flyr (1970), plants with such reduced vestiture from southern Nuevo León and Tamaulipas were recognized as a distinct variety but the pattern of variation is *clinal* with a general reduction in stature and density of trichome observed in populations from the north into southern Tamaulipas. However, even in these southern populations there is a variation in leaf vestiture: some plants have reduced stellate trichomes with short radii and others have a mixture of stellate and larger dendritic trichomes with longer radii similar to those found in northern populations. Also, occasional plants from Texas such as *McKinney 039* (LL) from native habitats in Austin (fig. 10 d, e) and *Johnston 53257.6* (TEX) from Star County have leaf vestiture comparable to that of populations in Tamaulipas and Nuevo León. The only effective way to separate these northern and southern population series would be on the basis of upper leaf surface trichome size with the northern populations having radii mostly 0.06–0.15(–0.2) mm long, those in the southern populations having shorter radii mostly 0.02–0.06 mm long.

Although the trend of diminished vestiture is generally recognizable, the interpopulational variation, the minute nature of the vestiture differences (effectively observed only with magnifications of 30 power or more), the lack of correlated characteristics, makes recognition of varieties along this clinal variation gradient both arbitrary and difficult. Therefore, no infraspecific taxa are recognized.

From a viewpoint in Texas one tends to consider that the species is typically rather strongly vestitured and that the reduced vestiture in southern populations is a derived feature. But paleobiogeographic considerations tend to support the idea that populations with reduced or diminished vestiture in the south may be relictural from pluvial times and that the taxon has been spreading northward and spilling over into the Chihuahuan Desert with more densely vestitured populations.

On the other hand it is hardly defensible to say that the highly reduced vestiture found in some southern populations (fig. 10 a–c) is pleisomorphic because the vestiture is so obviously reduced from a more dendritic

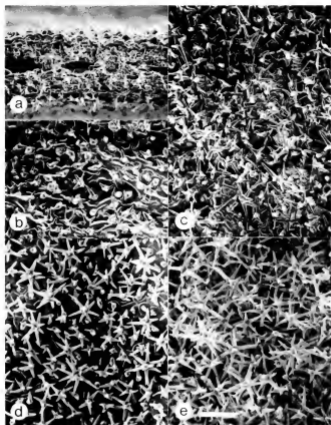


Figure 10. Leaf vestiture of *Lemnophyllum frutescens*. a. Cross section of leaf with very reduced vestiture on both surfaces. Compare with fig. 8 c, 9 a, c. Note air lacunae in mesophyll. b. Surface view of adaxial vestiture. c. Surface view of abaxial vestiture, both surfaces are green in color (*Graham and Johnston 440*: 17 mi S of Victoria, Tamaulipas). d. Surface view of adaxial vestiture. e. Abaxial vestiture of plant from Barton Springs, Austin, Texas, showing similar diminished vestiture (*M. Krony 039*). Scale in e = 0.1 mm; holds for a - d.

type. It is more probable that selection has been occurring in both directions over time.

Leucophyllum frutescens is the widest ranging species in the genus and occurs from Trans-Pecos Texas (Brewster Co.) east through the southern Edwards Plateau to the south Texas plains south through Coahuila, north central Nuevo León to southern Tamaulipas (fig. 11) where it occurs mostly in limestone, calcareous, sandy to clay plains and hills from Chihuahuan Desert to Tamaulipan Thorn Scrub habitats from 5 to 1200 m. The species is commonly cultivated in Texas and over much of the southwestern United States. It is quite cold hardy and can withstand moderate frosts.

2. *LEUCOPHYLLUM langmaniae* Flyr, sp. nov.

A speciebus altis foliis concoloribus, pubescentiis densis, trichomatibus stellato-dendriticis, radiis 0.01–0.04 mm longis differt.

Erect, alternately-branched shrubs 0.6–2.5 m tall; young stems closely, sometimes irregularly tomentose-canescens with dendritic trichomes 0.04–0.2 mm long, 0.04–0.1 mm wide with blunt, short radii 0.2–0.05 mm long, tardily glabrate; older stems light brown; internodes 1–7 mm long. Leaves alternate, crowded near tips of branches, oblanceolate to spatulate-obovate, 10–8 mm long, 4–9 wide, obtuse, rounded, rarely acute, usually bluntly apiculate to retuse at tip, narrowly cuneate at base, obscurely petiolate, greenish, concolorous, both faces with fairly dense, reduced stellate to stellate-dendritic trichomes 0.03–0.1 mm long and wide, radii very short, sometimes scarcely developed 0.01–0.04 mm long, mixed with scattered glands, trichomes more dense along raised midvein beneath and on petioles. Flowers on slender pedicels 3–8 mm long, calyces 3.5–4.5 mm long, lobes linear-lanceolate to obovate, 3–4 mm long, 1–1.2 mm wide, greenish, closely vestitured as leaves, slightly less than pedicels, greenish, sparsely pilose inside except near tip; corollas lavender-blue, with yellowish dots in floor of tube, 12–26 mm long, tube ampliate to 4–9 mm wide at throat (pressed), lobes obovate, reniform, 4–8(-10) mm long, lower medial lobe emarginate, 5–12.5 mm long, others slightly smaller, all undulate at margin, tube moderately pilose inside with tangled trichomes 1–2 mm long, pilose with shorter hairs at base of lobes near throat, otherwise glabrous, not ciliate, corollas glabrous outside; stamens 4, anthers glabrous, posterior filaments 5–10 mm long, anterior filaments 3–7.5 mm long, glabrous; style 5.6–10.5 mm long, sparsely pilose; ovary sparsely pilose. Capsules 4.5–5 mm long, 3–3.5 mm wide, pilose at tip.

TYPE: MÉXICO. NUEVO LEÓN: hills near Monterrey, 1700 ft, 31 Aug 1903, C. G. Pringle 11656. (HOLOTYPE: SMU!; ISOTYPES: F!, GH!, LL!, MEXU (2 sheets!), MICH!, PH!, US!).

Additional collections: MÉXICO. NUEVO LEÓN: Obispado near Monterrey, Feb 1909, *Abbot s. n.* (PH); Huasteca Canyon near Monterrey, Aug 1938, *LeSueur 435* (TEX); 17.2 mi w of Santa Catarina, 3420 ft, 8 Aug 1959, *Youngpeter and Cobb 62* (MICH) and 9 Aug 1959, *Youngpeter and Cobb 80* (ENCB, MICH); ca 1 mi from entrance of Huasteca Canyon, 2 Aug 1972, *McGill, Brown, and Pinkava 9734*. (ASU, ENCB), Huasteca Canyon, 0.1 mi below Pozo No. 17, ca 850 m, 12 Aug 1985, *Prigge and Muhlenb 5311* (RSA, TEX).

Leucophyllum langmaniae is characterized by its oblanceolate, greenish, isolateral leaves covered with a close vestiture of closely-spaced, stellate-dendritic trichomes with very short radii 0.01–0.04 mm long (fig. 8 a, b). In its uniformly short leaf vestiture it differs from all other species in the genus though a similar vestiture occurs on the upper leaf surfaces of some *L. frutescens* from Nuevo León and Tamaulipas, however, in the latter species, leaves are bicolorous, with dorsiventral structure and the lower leaf surfaces have denser dendritic trichomes. This similarity in vestiture caused Flyr (1970) to consider relationships with *L. frutescens*. Relationships appear to lie with *L. laevigatum* var. *laevigatum*, which also has greenish leaves equally vested on both sides, but with fewer, larger trichomes. In both *L. langmaniae* and *L. laevigatum* var. *laevigatum* newly formed leaves are also green, i.e., the leaves are not covered by a dense layer of trichomes that eventually fall away giving rise to a more open vestiture. They differ, however, in a number of floral features. Their similarity may be entirely due to their shared reduction in vestiture. *Leucophyllum langmaniae* appears to be restricted to the canyons of the Sierra Madre Occidental in Nuevo León between Monterrey and Saltillo (fig. 18); an area of considerable endemism.

The new species is named for Ida K. Langman, author of the monumental guide to the literature of the flowering plants of Mexico.

3. *LEUCOPHYLLUM MINUS* A. Gray in Torrey, Bot. Boundary Surv. 115. 1859. TYPE: TEXAS. PECOS CO.: rocky hills of the Pecos, 4 June 1851, *Wright 1481* (field number 345) (lectotype: here designated GH!; isotypes: GH!, MO!, NY!).

Leucophyllum minus A. Gray forma *argenteo* Pennell, Proc. Acad. Nat. Sci. Philadelphia 92:295. 1940 [8 Apr 1941]. TYPE: TEXAS. BREWSTER CO.: Persimmon Gap area, 21 Aug 1939, *O.E. Sperry 1518* (holotype: PH!; isotype: TAES!).

Intricately, alternately-, divaricately-branched shrubs 2–8(-15) dm tall, often rather thorny due to persistence of young dead branches; young stems closely canescent-tomentose with appressed stellate trichomes 0.1–0.2 mm in diameter with rather thick, tapering radii, these tardily glabrescent; older stems reddish-brown to light, rarely dark, gray: internodes 0.5–10 mm long. Leaves alternate, crowded in axillary fascicles or on compressed lateral shoots, oblanceolate or spatulate, to obovate-orbicular, typically small, (2-)3–10(-16) mm long, 1.8–5(-10) mm wide, obtuse to acute, often apiculate at tip, gradually cuneate (sometimes in small or broader leaves abruptly cuneate) to a petiole (0.5-)1–3(-4) mm

long, both surfaces equally silvery-gray, uniformly canescent-tomentose with short dendritic to "stellate" trichomes 0.1–0.2 mm in diameter with radii often appearing to originate from a gland-like umbo, radii broad, tapering, thick- or thin-walled, variously twisted, 0.05–0.1 mm long, occasionally some marginal trichomes more dendritic, midrib slightly raised beneath. Flowers on slender tomentose pedicels 1–3(–5) mm long; calyces 2.8–4.5 mm long, lobes oblong, oblong-lanceolate, (2.2–)3–4.4 mm long, 1–4(–1.9) mm wide, acute, strongly canescent-tomentose as stem outside, glabrous, sparsely glandular inside except at tip; corollas light purple, lavender, rarely pink, white, with white patch marked with yellow-brown dots in floor of throat, 12–18(–24) mm long, tube rather abruptly ampliate 1–3 mm above base, to 6–7 mm wide at throat (pressed), slightly compressed, lobes subequal, orbicular-reniform, obovate, reflexed, 3–7.5 mm long and wide, often emarginate, sparsely pilose in tube with tangled hairs to 2 mm long, more pilose in throat, lobes mostly glabrous to sparsely pilose, distinctly ciliate with hairs 0.2–0.5 mm long, corolla glabrous outside; stamens 4, anthers with short hairs at tip, posterior filaments 5–11.5 mm long, anterior filaments 3–8.5 mm long, glabrous to pilose; style (6–)8–12 mm long, glabrous to sparsely pilose. Capsule usually glabrous, rarely pilose, 4–5 mm long, 2.3–3 mm wide. Chromosome number $n = 16$.

Leucophyllum minus (figs. 15 c, 13 e, f) is characterized by its low, intricately-branched habit with many old stems persisting as thorns, by its small, concolorous, silver-gray leaves crowded on short, lateral shoots and particularly by its distinctive "stellate" vestiture with thick, tapering, broad-based, but thin-walled radii extending from a central stalk (fig. 14 e, f) best seen under 30 X magnification. The vestiture has been described best by Johnston (1941:120): "in *L. minus* the indument is very dense and close and almost suggests a coating of aluminum paint. The very numerous small white trichomes are flat and stellate. The primary axis of the trichomes is extremely shortened and its top appears as a small dot or knob at the center of the radially arranged arms." Actually, the trichomes are not stellate but compressed-dendritic with radii extending from several levels but typically with one series of radii at the top. The terminal, sometimes darkened, trichome tip is not always conspicuous. In young leaves scattered marginal trichomes are clearly dendritic but they weather away and shorten with age. Corollas are typically light purple, usually small, and the lobes are distinctly ciliate.

Leucophyllum minus may occur sympatrically with *L. frutescens* and *L. candidum* in Trans-Pecos Texas and adjacent México (figs. 11, 17, 18). Fly

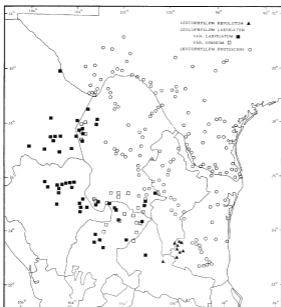


Figure 11. Distribution of *Leucophyllum revolutum*, *L. laevigatum* var. *laevigatum*, *L. laevigatum* var. *griuon*, and *L. frutescens* in Texas and northern México.

(1970) presented evidence of hybridization between *L. minus* and *L. frutescens* in a population in Big Bend National Park.

Leucophyllum minus occurs in rocky limestone to igneous-rock hills, plains, and canyons in *Larrea*, Mixed Desert Scrub, Izotal, and Chaparral in the Chihuahuan Desert region from southeastern New Mexico through Trans-Pecos Texas into northeastern Chihuahua and Coahuila (fig. 18) from 700 to 1700 m.

4. *LEUCOPHYLLUM LAEVIGATUM* Standley

Erect to strongly, alternately-branched shrubs (3-35 - 15(-20) dm tall, stems erect or not, sometimes thorny from persistence of old stems; young stems closely tomentose-canescens with irregular stellate and dendritic

trichomes 0.1–0.2 mm high, radii very short, tapering, 0.02–0.1 mm long, vestiture weathering in time, tardily glabrate; old stems with dark gray to black bark; internodes 1–8(-11) mm long. Leaves alternate, borne on erect long shoots or sometimes in compressed axillary clusters, oblanceolate, obovate (3-)5–18(-27) mm long, (1.3-)3–8(-10) mm wide, obtuse, rounded to truncate, often bluntly apiculate to emarginate at tip, narrowly cuneate to a petiole 1–3.5 mm long as base, at margins entire or variously folded, greenish to canescent-tomentose when young, sparsely to densely vestitured equally on each surface with low stellate to dendritic trichomes 0.1–0.3 mm high, 0.1–0.2(-0.8) mm in diameter with tapering, thin-walled radii 0.02–0.15(-0.2, rarely to 0.5) mm long, but more concentrated along midveins, often gradually glabrate and scattered with interlying glands visible on each surface in mature leaves, mature leaves then green (drying dark brown) but petioles vestitured as stems. Flowers with pedicels (1-) 2–5(-9) mm long, vestitured as stems; calyces 2–5 mm long, lobes linear-lanceolate, (1.5-)2.5–4 mm long, to 5.2 mm long in fruit, 0.6–1.2 mm wide at base, acute, sparsely to moderately vestitured with stellate to dendritic trichomes, often with very short radii, with underlying glands often visible, glabrous to glandular inside; corollas lavender-purple, violet, light lavender-violet, rarely blue, white, or purple with whitish patch marked with yellow-brown spots on floor of tube, (10-)14–20(-28) mm long, tube gradually ampliate, slightly compressed, lobes subequal, broadly obovate-orbicular, 4–6.5(-11) mm long and wide, emarginate; tube and throat with tangled hairs 0.5–2 mm long, lobes strongly ciliate, often pilose with shorter trichomes 0.2–0.7 mm long at least on lower lobes inside, corolla glabrous to sparsely stellate, rarely with stipitate glands outside; stamens 4, anthers glabrous or pilose below; styles 4–10 mm long, mostly glabrous to sparsely pilose below; ovaries glabrous or pilose at tip. Capsules oblong in outline, 4–7 mm long, 2.5–3.7 mm wide, glabrous or pilose at tip.

Leucophyllum laevigatum (fig.s 12, 13, 14) is characterized by its small shrub habit with either erect, straight stems or of a more gnarled habit with some old stems persisting as naked thorns, by its alternate, often fasciculate, concolorous, obovate-oblancoate, cuneate-based, typically green or grayish leaves with a vestiture of open or crowded stellate or mixed stellate-dendritic trichomes 0.1–0.3(-0.8) mm in diameter. Flowers have lavender to purple-violet or blue corollas 10–24 mm long with a yellow-to brownish-spotted whitish patch on the bottom of the throat. Corolla lobes are distinctly ciliate and calyx lobes are linear, usually sparsely vestitured. Two varieties are recognized, separable by the following key:

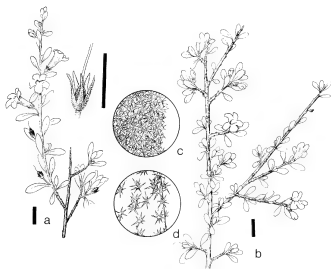


Figure 12. Line drawings of *Leucophyllum laevigatum*. a. *L. laevigatum* var. *laevigatum* stem with characteristic scattered leaves and (in this specimen) large flowers. Note long pedicels, enlarged immature fruit and calyx (upper right) (Chiang, Wendt and Johnston 9041). b-d. *L. laevigatum* var. *griseum*. Stem with characteristic thorny branches, more crowded, smaller leaves. Circular inserts indicate variation of vestiture in young, grayish leaves (c) and mature, more green leaves (d). Scales = 1 cm; c, d circles measure ± 1 mm in diameter.

- A. Young and older leaves both green, thichomes in both typically well-spaced, not or slightly overlapping, radii short, 0.02–0.07(–0.15) rarely to 0.3 mm long; leaves typically (5–)10–18(–27) mm long, borne along erect stems; stems seldom persisting as thorns. . . 4a. *L. laevigatum* var. *laevigatum*
- AA. Young leaves gray, canescent-tomentose with crowded trichomes, mature leaves either gray, with a dense mat of trichomes with radii 0.03–0.16 mm long, or more green with trichome radii overlapping, 0.1–0.5 mm long; leaves 3–10(–15) mm long, crowded into fascicles; plants often thorny with old leafless stems persisting as thorns. . . 4b. *L. laevigatum* var. *griseum*

4a. *LEUCOPHYLLUM LAEVIGATUM* Standley var. *LAEVIGATUM*, *Contr. U.S. Natl. Herb.* 23:1305. 1924. TYPE: MÉXICO. Durango: between Ramos and Inde, 11–14 Aug 1898, E. W. Nelson 4689 (G, GH, NY, US; BOITYPIC: GH!, K!, PH!).
Leucophyllum laevigatum Standley var. *caubuleusis* Kiger, *Rhodora* 74:347. 1972. TYPE:

MÉXICO. COAHUILA: Caneros Pass area, along México Hwy 54, about 23 mi S of Saltillo, 5 Aug 1971, J. L. Reveal, W. H. Hess, and R. W. Kiger 2617 (HOLOTYPE: US!; ISOTYPES: LL!, and elsewhere).

Erect-stemmed shrubs 5–15(-20) dm tall, seldom with old stems persisting as thorns. Leaves alternate, sometimes also in axillary fascicles, (5-)10–18(-27) mm long, (2.5-)4–8(-10) mm wide, green when young and at maturity, trichomes stellate to dendritic-stellate, radii 0.2–0.8 (-0.15, rarely to 0.3) mm long, trichomes mostly well-spaced on mature leaves except along midvein; pedicels 3–9 mm long; ovary and style mostly glabrous.

In *Leucophyllum laevigatum* var. *laevigatum* (fig. 12 a) both young and mature leaves are green with moderately- to well-spaced, stellate to stellate-dendritic trichomes with short, rather thickish, tapering, translucent radii 0.2–0.8(-1.5) mm long (fig. 13 a–d). Similar but much more crowded trichomes cover young stems and this denser vestiture extends onto petioles and often along the midribs of both leaf surfaces. This vestiture pattern is found throughout the range of the taxon, except in eastern Durango and west-central Coahuila where plants tend to have some leaves with larger trichomes with radii to 0.3 mm long (fig. 13 a, b). The variety also tends to have a more erect habit with stems bearing alternate leaves.

Corolla color varies and Kiger (1972) described a new variety from the Caneros Pass area in southeastern Coahuila with strong blue corollas.

This variety occurs in limestone, caliche hillsides and alluvial fans in the Chihuahuan Desert from southeastern Chihuahua, western and southeastern Coahuila, and eastern Durango to Zacatecas, and San Luis Potosí (fig. 11) from *Larrea*, Mixed Desert Scrub to Izotal zones from 1200 to 2200 m.

4b. *LEUCOPHYLLUM LAEVIGATUM* Standley var. *griseum* (I. M. Johnston)

Henrickson comb. et stat. nov. *Leucophyllum griseum* I. M. Johnston, J. Arnold. Arbor. 22:119. 1941. TYPE: MÉXICO. COAHUILA: foothills of the Sierra Planchada, 6 mi N of Esmatada, 16 Aug 1940, I. M. Johnston and C. H. Mueller 341 (HOLOTYPE: GH!; ISOTYPE: LL!).

Leucophyllum virens I. M. Johnston, J. Arnold Arbor. 21:253. 1940. TYPE: MÉXICO. DURANGO: near La Loma valley of the Rio Nazas, 4900 ft, 22 Aug 1939, F. Sbray 9191 (HOLOTYPE: GH!)

Low, rounded shrubs 3–10(-18) dm tall; typically with old naked branches persisting as thorns. Leaves alternate and crowded in axillary fascicles in distal 2–5(-12) cm of branches, 3–10(-15) mm long, 1.3–5(-7) mm wide; young leaves gray, densely covered with a close vestiture of stellate, stellate-dendritic to dendritic trichomes, older leaves gray, densely vestitured or green with a sparse vestiture, trichome radii

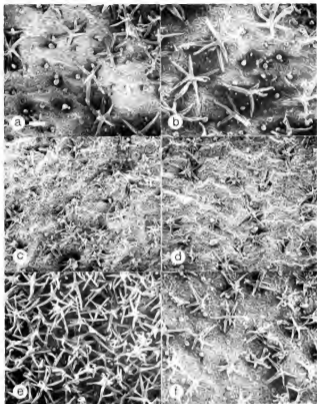


Figure 13. Leaf vestiture of *Leucophyllum laevigatum*. a-b. *L. laevigatum* var. *laevigatum*. In typical variety, both young (a) and old (b) leaves are green, with scattered, well-spaced trichomes. Note sessile glands (adaxial surfaces) (Flyr 672a; near Pedricena, Durango). c-d. *Laevigatum* var. *laevigatum*. Phase with smaller well-spaced trichomes equally distributed in young (c) and mature (d) leaves (abaxial surfaces) (Correll and Johnston 20238; 11 mi E La Zarca, N of Durango). e-f. *L. laevigatum* var. *griseum*. In this variety young leaves are gray with dense vestiture (e), mature leaves may be gray or green (f) with sparse vestiture, (abaxial surface) (Johnston and Mueller 341; isotype of *L. griseum* from N of Esmaralda, central Coahuila). Scale in a = 0.1 mm, holds for b-f

(0.03–)0.1–0.16(–0.3, rarely to 0.5) mm long; peduncles 1.5–5 mm long; ovary and styles mostly pilose.

Leucophyllum laevigatum var. *griseum* occurs in west-central and southern Coahuila and adjacent northern Zacatecas and San Luis Potosí (fig. 11). In several areas it is sympatric and appears to intergrade with *L. l.* var. *laevigatum*. In Flye (1970) *L. laevigatum* and *L. griseum* were recognized as distinct species distinguished in the key by habit with *L. griseum* having persistent, leafless, short, lateral branches giving the plants a thorny appearance while *L. laevigatum* characteristically had longer, leafy shoots and specimens lacked such short, lateral branches unless the plants had been browsed (Flye 1970). While such habit differences can be recognized in most specimens, they are not consistent and certainly can be influenced by environmental conditions.

Vestiture differences tend to correlate with habit. In the more openly-branched variety *laevigatum* both young and mature leaves are green, with an open, typically non-overlapping vestiture of trichomes typically with short radii. In the more tightly-branched variety *griseum* with shorter, more crowded leaves, the young leaves are gray with a dense, low vestiture and mature leaves may either retain this dense gray vestiture or the vestiture may thin; the mature leaves are then green. In many southern Coahuila, Zacatecas, and San Luis Potosí populations of variety *griseum* both young and mature leaves are gray, covered with a dense to moderately dense vestiture of stellate or a mixture of stellate and short-dendritic trichomes with short radii 0.02–0.08(–0.15) mm long, basically with trichomes with short radii similar to those of variety *laevigatum* but very crowded.

In specimens of variety *griseum* from west-central Coahuila (including the type of *L. griseum*), young leaves tend to be gray, densely vestitured with stellate and dendritic trichomes, however, as the leaves mature, dendritic trichomes with short radii tend to fall away and the remaining stellate, stellate-dendritic trichomes are more dispersed, though typically with overlapping radii (fig. 13 c, f). They also tend to have longer radii, 0.1–0.2 mm long, similar to the longer-trichome radii found on leaves of variety *laevigatum* in that region. In some specimens trichomes on young leaves have long radii at the base and short radii in distal portions and as leaves mature the distal portions of the trichomes fall away leaving the larger basal radii. A similar pattern is seen in some specimens of variety *griseum* in northern Zacatecas.

This trend reaches its extreme in southwestern Coahuila and adjacent Durango, where in some specimens, young leaves are gray with a dense, close vestiture of trichomes with short radii (fig. 14 a) and older leaves are greenish, with moderately dense, typically overlapping, large trichomes

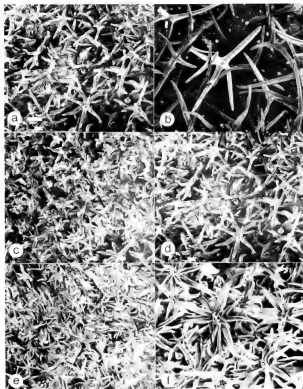


Figure 14. Leaf vestiture of *Lycopodium laevigatum* var. *griseum* and *L. minus*. a–b. *L. laevigatum* var. *griseum*. Vestiture similar to that of type of *L. virescens*; young leaf has dense, short vestiture (a); mature leaves have very sparse vestiture with radii to 0.4 mm long (b), (abaxial surfaces) (Chang, Woodl. and Johnson 9550, near Sierra Jimulco, Coahuila). c–d. *L. laevigatum* var. *griseum*. In S Coahuila, Zacatecas, vestiture of both young (c) and mature (d) leaves is dense and both young and mature leaves are gray (adaxial surfaces) (Saxford, Retherford and Northcott 157; S of Párras, Coahuila). e–f. *L. minus*. Both young and old leaves have dense vestiture of "stellate", actually short dendritic trichomes. e. Mature leaf, abaxial surface (McGill and Keil 7626). f. Enlarged view showing broad, flat radii. Base at radii at trichome tip often darken giving appearance of a terminal gland (Engard and Gentry 605). Scale in a = 0.1 mm, holds for a–e, f = 0.1 mm.

with radii 0.13–0.5 mm long (fig. 14 b). In some specimens trichome radii vary among adjacent leaves on a stem; some leaves have trichome radii 0.13–0.2 mm long, others have radii 0.2–0.5 mm long, indicating that trichome radii development may be influenced by environmental conditions.

A specimen with this type of long-rayed trichomes similar to that shown in fig. 14 b was designated the type of *L. virescens* by I. M. Johnston (1940), who emphasized the short trichome radii on young leaves in contrast to the long radii on trichomes of old leaves. However, the specimen appears to be completely referable to variety *griseum* and differs only in its very long trichome radii. Additional specimens bridge the gap between this specimen and typical *griseum*. Flyr (1970) considered *L. virescens* to be a hybrid between *L. laevigatum* and *L. candidum* because specimens referable to these two taxa were the only plants found during two searches at the type locality of *L. virescens*. The occurrence of trichomes with long-basal radii and short distal radii and others with only short radii is reminiscent of those of *L. candidum* but the specimen exhibits no other features of *L. candidum*.

Whether *L. l.* var. *griseum* merely represents a more xeromorphic derivative of *L. l.* var. *laevigatum*, i.e., with a reduced, more thorny habit, more strongly vestitured leaves, or presents intergradation with *L. candidum*, or other more densely vestitured species, is not known. Specimens available indicate a continuum of variation between the two varieties. The line between the two taxa must be drawn arbitrarily. Distinction on the basis of habit (sensu Flyr, 1970) versus vestiture (emphasized here) gives a slightly different assignment of specimens that have long, erect stems (as in variety *laevigatum*) but dense vestiture on young leaves (as in variety *griseum*).

The younger epithet *griseum* (Johnston 1941) is recognized at the varietal level over the older *virescens* (1940) because the type of *griseum* is more representative of the taxon and *griseum* has been more widely used than *virescens*.

Leucophyllum l. var. *griseum* grows on limestone and calcareous hillsides from *Larrea*- to *Yucca*-dominated zones to chaparral from 1400 to 2400 m (fig. 14).

5. *LEUCOPHYLLUM CANDIDUM* I. M. Johnston, J. Arnold Arbor. 22:120. 1941 [15 Jan 1941]. TYPE: MÉXICO. COAHUILA: between Carrizo and Carricito on (gypsaceous?) ridge, 11 Aug 1940, I. M. Johnston and C. H. Mueller 160 (HOLOTYPE: GH!; ISOTYPE: LL!).

Leucophyllum violaceum Pennell, Proc. Acad. Nat. Sci. Philadelphia 92:295. 1940 [8 Apr 1941]. TYPE: TEXAS. BREWSTER CO.: frequent on flats from Lone Mountain to

Nugent Mt., Chisos Mt. area, 2 Aug 1937, B. H. Warnock 1124 (HOLOTYPE: US!;
ISOTYPES: GH!, PH!, SRSC, TAES!, TEX!).

Compact, divaricately, alternately-branched, rounded to erect shrubs 3–10(-15) dm tall; young stems densely, unevenly tomentose with spreading dendritic trichomes, the longer 0.2–0.7 mm long, 0.15–0.3 mm in diameter, these eventually weathering to a more uniform stature and eventually glabrate; older stems red-brown to light or dark gray. Leaves alternate to subopposite, often opposite near tip of stem, often with reduced

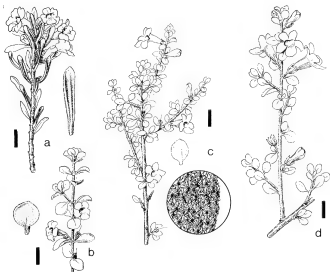


Figure 15. Line drawings of *Leucophyllum* species. a. *L. revolutum*. Stem showing characteristic orientation of leaves, flowers. Note swollen residual leaf bases at nodes. Leaf in abaxial view shown to right (Johnston, Wendt and Chiang 11181). b. *L. zygophyllum*. Stem, note opposite, conduplicate leaves and flowers leaf in adaxial view at left (Correll and Johnston 19860). c. *L. minus*. Stem showing characteristic thorny habit, small, crowded leaves, flowers. Circular insert represents vestiture consisting of low, dense "stellate" trichomes that tend to develop darkened dots at tips (Chiang, Wendt and Johnston 7703). d. *L. candidum*. Stem, note leaves and large flowers. The species is characterized by mostly alternate leaves and dendritic trichomes (Warnock 257). Scale = 1 cm, separate leaves shown 2 x larger. Circle with vestiture measures ± 1 mm in diameter.

leaves in axillary shoots, mostly broadly obovate to obovate-orbicular, reniform, occasionally some ovate, 6–10(-16) mm long, 3.5–7(-10) mm wide, rounded, obtuse, occasionally acute, often bluntly apiculate or appearing emarginate by recurving of midrib tip, rounded, abruptly, occasionally gradually, cuneate at base above a petiole 1–3(-6) mm long, at margins entire, rarely revolute, initially densely, equally gray-tomentose (often turning tan in herbarium specimens) on both faces with uneven tapering-cylindrical dendritic trichomes 0.15–0.6 mm long, 0.1–0.3 mm wide, with slender, tapering radii 0.05–0.2 mm long, longer trichomes somewhat weathering in time and vestiture more uniform in height and exposing longer basal radii 0.1–0.3 mm long. Flowers on densely tomentose pedicels 1–4.5 mm long; calyces 4–7(-9) mm long, lobes oblong, oblong-lanceolate, 2.5–5(-6) mm long, 0.7–1.7(-2.5) mm wide, densely tomentose with elongate cylindrical dendritic hairs as on young stems outside, glabrous, gland-dotted except at tip inside; corollas dark to light violet-purple, with white patch marked with orange to yellow-brown dots on floor of tube, (10-)12–22(-25) mm long, tube ampliate, somewhat compressed, 5–8 mm wide at throat (pressed), lobes subequal, suborbicular, emarginate, 3–7(-11) mm long and wide, strongly to moderately long-pilose inside lower tube with tangled hairs 0.5–2 mm long, pilose with shorter, often blue-tipped, wavy hairs 0.2–0.7 mm long inside and on margins of lobes, corollas loosely stellate to glabrous outside; stamens 4, anthers with stellate tuft at tip, posterior filaments 5–10.5 mm long, anterior filaments 5–7 mm long, glabrous to pilose; styles 6–9.5 mm long, sparsely pilose in lower half to glabrous; ovaries pilose above. Capsules 4–5 mm long, pilose at tip.

Leucophyllum candidum (figs. 15 d, 16) is characterized by its mostly low, densely-branched habit, by its mostly alternate or partially opposite, crowded, often small, broadly obovate, suborbicular, non-conduplicately folded leaves with a well-developed layer of dendritic trichomes 0.2–0.5 mm thick on both faces with radii 0.05–0.25 mm in length. It can be distinguished from the closely related *L. zygophyllum* because the latter more consistently has opposite, conduplicately folded leaves with a close vestiture. In contrast leaves of *L. candidum* are flatish or variously undulate-crisped with a thicker vestiture.

Trichomes of young stems and leaves are dendritic, rather cylindrical, 0.2–0.6 mm tall with slender, wavy radii 0.1–0.2(-0.3) mm long at the base but only 0.05–0.1(-0.2) mm long in the upper two-thirds. In young leaves and stems, vestiture is quite thick and uneven with scattered, longer, cylindrical hairs apparent particularly on the stems and lower leaf margins.



Figure 16. Leaf vestiture of *Lasophyllum candidum*. a - b. Young stems and leaves have dense vestiture; scattered trichomes have long, narrow, terminal portions and these often fall away in time to expose basal, longer radii (Henrickson 120886). c. In this specimen, terminal portions of trichomes were much reduced (aborted); note longer basal trichome radii (Chiang, Wendt and Johnston 12098). d. Cross section of leaf showing trichomes of both faces. Note also air lacunae in leaf mesophyll and lack of radii on basal portion of trichomes (Henrickson 6093). Scales = 0.1 mm.

However, as the hairs weather away, the longer basal radii are exposed resulting in an apparent change in vestiture to one with longer radii (fig. 16).

There exists a rather perplexing variation pattern within the species. Plants from eastern Durango and central Chihuahua, and some from

Brewster Co., Texas, have corollas, 17–27 mm long versus 9–15(–16) mm for other specimens. These longer-flowered populations also tend to have, on the average, longer trichome radii (0.1–0.2 mm long for upper radii and 0.1–0.3 mm long for the lower radii) as compared to more eastern populations with upper radii 0.05–0.1(0.15) mm long and lower radii 0.1–0.25 mm long. Many specimens from Brewster Co., Texas, also have longer calyces, 6.5–9 mm versus 4–6 mm long in Durango-Chihuahua collections. Because of their geographical separation it is tempting to recognize these western populations as distinct at least at the varietal rank, and there are many botanists who need less than that to describe a new taxon. However, field observations in the Big Bend area of Texas show that these large-flowered plants are probably hybrids with *L. frutescens* rather than a distinct taxon. Similar long-flowered populations occur in *L. minus* in the same area and occur scattered throughout the range of *L. laevigatum*. Field observations indicate that some genetically controlled variation in total corolla length is the norm for certain species of *Leucophyllum*. Though the occurrence of populations with large corollas in Durango and central Chihuahua may represent a monophyletic group, the occurrence of specimens with long corollas in the Big Bend area where short corollas are the norm probably represents an independent evolution of the trait and makes any taxon based on corolla length polyphyletic. Collections of these eastern Durango populations were annotated *L. violaceum* by Flyr but reduced to synonymy under *L. candidum* in Flyr (1970). *Leucophyllum violaceum* is a direct synonym of *L. candidum* and represents the short-flowered populations.

Over its range *L. candidum* occurs sympatrically with *L. frutescens*, *L. laevigatum* var. *laevigatum*, and *L. l.* var. *griseum* (Flyr 1970; Johnston 1941). It ranges from Big Bend area of Trans-Pecos Texas south to central Chihuahua (at La Bufa near Batopilas) and south through Coahuila to eastern Durango and northern Zacatecas (fig. 17) mostly on limestone hillsides, plains in *Larrea*. Mixed Desert Scrub to *Izotal* vegetations from 800 to 1500 m.

6. *LEUCOPHYLLUM ZYGOPHYLLUM* I. M. Johnston, J. Arnold *Arbor.* 21:263. 1940. TYPE: MEXICO. NUEVO LEÓN: Puerto de Pastores, SE of Galeana, 2 Aug 1934, C. H. and M. T. Mueller 1299 (HOLOTYPE: A!; ISOTYPES: GH!, MICH!, TEX!).

Erect, oppositely- to alternately-branches shrubs 2–10(–20) dm tall; young stems densely, unevenly silver-gray tomentose with longer conical, dentic trichomes 0.1–0.5 mm long, 0.1–0.2 mm in diameter with short tapering radii, vestiture weathering in time, tardily glabrate; older

stems with gray to tan bark; internodes (2-)5-10(-15) mm long. Leaves opposite, occasionally subopposite, broadly ovate to broadly obovate to orbicular, 4-13(-17) mm long, 3.5-11(-13) mm wide, rounded, bluntly apiculate at tip, rounded to broadly cuneate to a 1-1.5 mm long petiole at base, mostly conduplicately folded, often strongly reflexed at petiole, thick, silver-gray, equally, irregularly, densely tomentose on both sides, longer dendritic trichomes (0.1-)0.2-0.4 mm long, 0.1-0.2 mm in diameter, radii short, tapering, 0.02-0.1 mm long, trichome axis not straight, longer trichomes often along raised midrib beneath and along margins, these weathering and vestiture more uniform in older leaves. Flowers with tomentose pedicels 1.5-3(-5) mm long; calyces 3.5-5 mm long, lobes oblong-lanceolate, 3-3.5 mm long, 0.7-1.1 mm wide, acute, slightly less strongly vestitured than pedicels with dendritic trichomes to 0.2 mm long, glabrous except for stipitate glands below tip inside; corollas purple to light violet with a white patch with gold-brown dots on floor of tube, 11-15(-17) mm long, tube campanulate-funnelform, to 3-6 mm wide at throat (pressed), lobes obovate to orbicular, subequal, 3-7 mm long and wide, wavy, emarginate, tube and throat with sparse to dense, tangled hairs 0.5-1.5 mm long inside, lower lobes often densely pilose with often violet-tipped hairs 0.2-0.5 mm long, corolla glabrous outside; stamens 4, anthers with short hairs at tip, posterior filaments (4-)5-7 mm long, anterior filaments (4-)5-6 mm long, slightly pilose; styles 5-8 mm long, slightly pilose near base; ovary pilose with branched trichomes. Capsules 3-5 mm long, 2.5-3 mm wide, sparsely vestitured with dendritic hairs near tip, trichomes with long radii, sparsely glandular below.

Leucophyllum zygophyllum (fig. 15 b) is a strongly-branched, rounded shrub characterized by opposite, broadly ovate to orbicular, abruptly cuneate to rounded-based, petiolate leaves that are densely, equally tomentose on both surfaces. Typically the leaves are conduplicately folded along the midrib and may be ascending or more frequently divergent or reflexed beyond the recurving petiole. Leaves are often small, but when larger (as in *F. Medellin Leaf 1557* and *F. Gonzalez M. 9066*, both MEXU), leaves may be alternate, flattened with raised lateral veins and vegetatively approach *L. ambiguum*. These plants also tend to have longer trichomes as in *L. candidum*. Whether these plants came from shaded habitats is not known. Flowers in this species are dark purple to violet with yellow spots in the tube and have a slight lavender odor.

Leucophyllum zygophyllum appears to be most closely related to *L. candidum* differing mainly in the opposite, conduplicately-folded leaves and the closer vestiture. It may occur sympatrically with *L. pruinatum* and *L. revolutum* on

rocky limestone, and caliche, rarely gypseous habitats in mesquital to chaparral, oak-pine forests in southern Nuevo León, southwestern Tamaulipas, and adjacent San Luis Potosí (fig. 17) from 1200 to 2100 m.

7. *LEUCOPHYLLUM REVOLUTUM* Rzedowski, *Ciencia* 15:94. 1955. TYPE: MEXICO. SAN LUIS POTOSÍ: E of Nunez, km 84 on highway from San Luis Potosí to Antigua Morelos, 18 Nov 1954, *Rzedowski 5611* (HOLOTYPE: MEXU!; ISOTYPE: SLP!)

Erect, alternately-, rather closely-branched shrubs 5–25 dm tall; young stems densely tomentose with erect, conical, dendritic trichomes 0.05–0.3 mm long, radii tapering, 0.05–0.1 mm long, trichomes tardily glabrate; older stems light gray with corky periderm. Leaves alternate, crowded in terminal 5–15 cm of stems, with internodes 1–2(-5) mm long, ascending, oblanceolate, 10–26 mm long, 2–4(-5) mm wide, obtuse, bluntly apiculate at tip, cuneate to base, at margins entire but distinctly revolute, sometimes inrolled in lower half, bicolored, greenish, closely tomentulose with stellate-dendritic trichomes 0.05–0.1 mm long above, densely white tomentose with dendritic trichomes 0.1–0.3 mm long, 0.1–0.2 mm wide, with slender radii 0.05–0.1 mm long beneath. Flowers with tomentose pedicels 1.5–2.5 mm long; calyces 4.2–5.5 mm long, lobes oblong-ovate, 2.5–3.5 mm long, 1.2–1.4 mm wide, acute to obtuse at tip, densely tomentose with conical, dendritic trichomes 0.1–0.2 mm long outside, more glabrous, glandular inside; corollas violet to purple, with white or whitish-purple patch on floor of throat marked with dark violet spots, yellow at very base, 10–18(-20) mm long, tube amplify to campanulate, dorsiventrally compressed, to 6–8 mm wide at throat, lobes orbicular-obovate, emarginate, spreading, 4–8 mm long and wide, anterior 3 larger than posterior 2, tube rather densely long pilose with tangled trichomes to 2 mm long inside on floor, lobes glabrous, corolla sparsely glandular-pilose outside; stamens 4, anthers with a tuft of hairs at tip or glabrous, white or suffused with purple, posterior filaments 6–9 mm long, anterior filaments 6–7 mm long, pilose; styles 7–12 mm long, pilose; ovaries pilose at tip. Capsules 4 mm long, 2 mm wide, pilose near tip.

Leucophyllum revolutum (figs. 15, 2 a, b) is a very distinct species readily distinguished by its oblanceolate, distinctly bicolored, revolute to inrolled-margined, ascending leaves that are usually crowded along the distal portions of the stems. The violet corollas are distinctive due to their dark purple spots on the floor of the tube and throat.

The relationship of this species within the genus is uncertain. Its leaves are bicolored as in *L. frutescens* but phenetically it tends to cluster with *L. flyrii*. The species occurs sympatrically with *L. zygothyllum* and *L. prinosum*

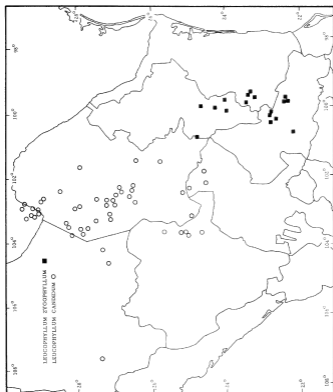


Figure 17. Distribution of *Leucophyllum zygophyllum* and *L. candidum* in southern trans-Pecos Texas and northern México.

on rocky hillsides from *Larrea* scrub to chaparral or submontane scrub in southwestern Tamaulipas near Miquihuana and Bustamente and adjacent northern San Luis Potosí east of El Huizache Junction (fig. 11) over an elevational range of 1600 to 2200 m.

8. *LEUCOPHYLLUM FLYRII* B. L. Turner, Sida 5:54. 1972. TYPE: MÉXICO. SAN LUIS POTOSÍ: 4.4 mi NE of Laguna Seca (Gral. Candido Navarro), 29 Jul 1966, D. Flyr 1113 (HOLOTYPE: TEX!).

Strongly, alternately-branched, rounded shrubs 5–16 dm tall, often rather thorny due to persistence of young dead branches; young stems densely, unevenly, silvery-gray tomentose with dendritic trichomes 0.2–0.4 mm long, 0.2–0.3 in diameter, radii wavy, slender, 0.1–0.2 mm long, trichomes weathering, vestiture more uniform in time, tardily glabrate; older stems with dark gray bark; internodes 2–8 mm long. Leaves alternate, oblanceolate to obovate-spathulate, broadest in distal one-fourth, 10–22(-27) mm long, 4–9(-11) mm wide, obtuse, sub-rounded, bluntly apiculate at tip, tapering to a cuneate base, true petiole not discernible, at margins entire, densely unevenly gray (slightly tan in herbarium specimens) tomentose on both faces with dendritic trichomes 0.1–0.4 mm long, radii wavy, slender, 0.1–0.2 mm long, trichomes diminishing in stature through weathering; midrib raised beneath. Flowers with tomentose pedicels 1–3 mm long; calyces 5–6.5 mm long, lobes lanceolate, 4.5–5.5 mm long, 1.1–1.5 mm wide, acute-attenuate, sparsely beset with dendritic hairs and slender, spreading, stipitate-glandular trichomes 0.1–0.3 mm long, glabrous inside except for stipitate glands; corollas purple to light violet with small dark purple spots throughout lower tube, yellow only at very base, (16-)19–21(-25) mm long, tube broadly ampliate, slightly compressed, to 8 mm wide at throat (pressed), lobes obovate, subequal, 5–7 mm long and wide, emarginate, tube sparsely pilose on floor inside with crinkled hairs 1–2 mm long, lobes nearly glabrous inside, not ciliate, corolla sparsely stipitate glandular outside; stamens 4, anthers glabrous, posterior filaments 8–10.5 mm long, anterior filaments 6–9 mm long, glabrous; styles 10–12 mm long, sparsely pilose near base; ovaries sparsely pilose, stipitate-glandular at tip. Capsules dark brown, 5–6 mm long, 3–4 mm wide, pilose near tip.

Leucophyllum flyrii is distinguished by its somewhat thorny habit, oblanceolate to obovate, cuneate-based leaves that are equally tomentose on both sides with dendritic trichomes with moderately long wavy radii. In addition the calyces, unlike any other species in the genus, have an overstory of slender stipitate glands on the outer surface and are less strongly vestitured than the pedicels. The corollas have broadly ampliate tubes, with dark purple dots to 1 mm wide on the floor of the tube. It is known from a few localities northeast of Ciudad San Luis Potosí in the southernmost margin of the Chihuahuan Desert and in the adjacent Sierra San Pedro (fig. 18) from 1800 to 2200 m.

9. *LEUCOPHYLLUM PRUINOSUM* I. M. Johnston, J. Arnold Arbor. 22:119. 1941. TYPE: MEXICO. SAN LUIS POTOSÍ: 11 mi S of Marehuala, 10-11 Sep 1938, J. M. Johnston 7569 (HOLOTYPE: GH!).

Strongly, alternately-branched shrubs sometimes somewhat thorny due to persistence of old stems, (3-)8-15(-26) dm tall; young stems loosely tomentose with dendritic trichomes 0.3-0.8 mm long, with long, slender, wavy radii 0.1-0.5 mm long, vestiture tardily glabrescent; old stems with gray to brownish bark. Leaves alternate, orbicular to broadly ovate, rarely broadly elliptical, 8-16(-27) mm long, 6-13(-17) mm wide, rounded, obtuse, often obscurely apiculate at tip, rounded to abruptly cuneate above petiole 1-3.5(-6) mm long at base, at margin entire to crisped-undulate or variously folded, densely but loosely gray tomentose on both faces (sometimes slightly tan in herbarium specimens) with elongate dendritic trichomes 0.4-0.8 mm long with slender, wavy radii 0.1-0.3(-0.5) mm long, trichomes often more dense along raised midvein beneath. Flowers on tomentose pedicels 1.5-3 mm long; calyces 4-6.5 mm long, lobes oblong-lanceolate, 3-5 mm long, 1-1.7 mm wide, acute to attenuate, often unequal, densely tomentose outside and near tip inside as young stems, sparsely to moderately pilose, glandular inside; corollas dark purple to violet with a reddish tinge, with a large white patch with gold dots in floor of tube inside, with grape odor, 8.5-11(-14) mm long, tube broadly campanulate, abruptly expanded above base, (5-)7-9 mm broad at throat (pressed), lobes orbicular, obovate, subequal, 3-5 (-6.5) mm long and wide, sometimes crisped, often emarginate, tube long pilose only in the tube base and lower throat, lobes mostly glabrous, ciliate with shorter hairs, corolla stipitate-glandular outside; stamens 4, anthers pilose at tip, posterior filaments 5-9 mm long, anterior filaments 3-4.5 mm long; styles 5-9(-11) mm long, sparsely pilose; ovaries densely pilose and stipitate-glandular at tip. Capsules 3.5-5 mm long, 2.3-3 mm wide, pilose at tip.

Leucophyllum pruinatum (fig. 19 a) can be distinguished by its distinctive vestiture of large dendritic trichomes with slender radii 0.1-0.5 mm long; the consistently longest trichome radii found in the genus (fig. 20 b), the orbicular to suborbicular, petiolate leaves usually with finely crisped to undulate-folded margins, and the relatively short corollas with the distinctive campanulate tube that abruptly increases in diameter above the base. It is most similar to *L. ultramonticola* as discussed under that species. It differs from *L. ambiguum* in the conspicuous yellow-spotted white patch on the corolla-tube floor. Niezgodna and Tomb (1975) noted this was the only species of *Leucophyllum* with rugulate rather than reticulate pollen sculptur-

ing. Tomb (pers. comm. 1984) noted differences also occur in seed sculpturing. The species can occur sympatrically with *L. revolutum* and *L. zygophyllum* but no hybrids have been observed. *Leucophyllum pruinosum* occurs on rocky limestone slopes and alluvial fans in *Larrea* to Mixed Desert Scrub from southern Nuevo León, southwestern Tamaulipas, and eastern San Luis Potosí (fig. 18) from 1000 to 1600 m.

10. *LEUCOPHYLLUM ultramonticola* Flyr sp. nov.

A *L. pruinosum* ovaris et stylis glabris non pilosis, corollas lobis inferis pilosis non glabris, foliis orbicularioribus, distributione in Zacatecas meridio-occidental differt.

Alternately- rather openly-branched, erect shrubs 10–17 dm tall; young stems irregularly, densely gray-tomentose (turning brown in herbarium specimens) with cylindric, dendritic trichomes (0.1–)0.3–0.7 mm long with slender, wavy radii 0.1–0.2 mm long, tardily glabrate, older stems light gray, often remaining as coarse thorns; internodes 1–10 mm long. Leaves alternate, crowded, broadly ovate-orbicular to broadly elliptical, 10–25 mm long, 8–25(–30) mm wide, obtuse to rounded, occasionally retuse or bluntly apiculate at tip, abruptly cuneate-rounded at base above a tapering petiole 2–5 mm long, at margins entire, undulate, densely gray to rather greenish (turning brownish in herbarium specimens), tomentose on both faces with dendritic trichomes (0.1–)0.2–0.4(–0.7) mm long, radii slender, straight or wavy (0.1–)0.2–0.4 mm long, trichomes weathering, becoming more uniform in age, midvein and in larger leaves basal, lateral veins prominent beneath. Flowers with tomentose pedicels 3–3.5 mm long; calyces 5.5–8(–9.2) mm long, lobes oblong to oblanceolate, 4.2–7 mm long, 1.3–2.1 mm wide, obtuse-acute, densely tomentose as stems outside and inside at tip, moderately sericeous-pilose inside, glabrous, sparsely glandular near base inside; corollas purple-violet, with a large yellow patch marked with red-brown spots on tube floor inside, 12–16 mm long, tube broadly campanulate, to 6.5–8.5 mm broad at throat (pressed), lobes obovate, 4–5 mm long and 3.5–4.5 mm wide, truncate to emarginate at tip, undulate, short ciliate, tube with long tangled hairs 1.5–2 mm long on basal floor, lobes pilose with shorter, wavy hairs 0.3–0.5 mm long, to 1.0 mm long near throat; corolla glabrous to very sparsely stipitate-glandular outside with hairs 0.1–0.2 mm long; stamens 4, posterior filaments 8.5–10 mm long, anterior filaments 5–6.5 mm long, glabrous; styles 9–10 mm long, glabrous; ovaries glabrous. Capsules 4.5 mm long, 2.5 mm wide, glabrous except for some stipitate glands near base.

TYPE: MÉXICO, ZACATECAS: San Juan Capistrano, 21 Aug 1897, J. N. Rose 2452 (HOLOTYPE: US!).

Additional collections: MÉXICO. ZACATECAS: 9 mi W of Huanquilla El Alto, 8.8 mi E of Rio Atengo on sandy tuffs, 17 July 1984, *Michener, Prigge and Meyer* 4465 (A, MEXU, TEX).

Leucophyllum ultramonticola is clearly related to *L. pruinosum* with which it shares the distinctive broadly campanulate corolla tube, leaf shape, vesti-

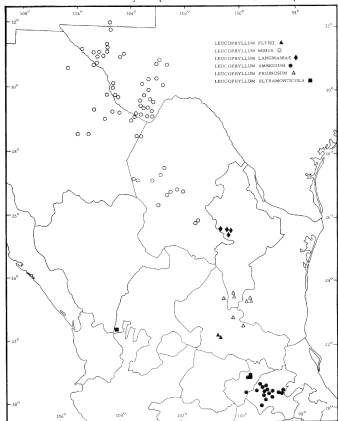


Figure 18. Distribution of *Leucophyllum flyrii*, *L. minus*, *L. langhamae*, *L. ambiguum*, *L. pruinosum* and *L. ultramonticola* in Trans-Pecos Texas, adjacent New Mexico to Querétaro and Hidalgo in central México.

ture, and texture, and openly branched habit. The new species differs from *L. pruinatum* in its nearly glabrous (not densely pilose) ovary and style base, in its more strongly vestitured (not glabrous) inner lower corolla lobe surfaces, the orange-brown rather than yellow spots on the corolla floor, its slightly larger flowers, generally larger stature with larger, more often orbicular leaves, and its distribution on the Pacific drainage in extreme southwestern Zacatecas (fig. 16). All evidence indicates that it is a rather recent vicariant of *L. pruinatum* of southern Nuevo León, adjacent Tamaulipas, and San Luis Potosí (fig. 18). The new species also shares many characters with *L. ambiguum* of Hidalgo and Querétaro, but the latter has narrower corolla tube-throat, typically lacks yellow-brown spots on the corolla tube floor, and has densely pilose ovary and style bases.

Rose's type specimen collected in 1897, was for a long time the only known collection of *L. ultramonticola*. It has been recently recollected by Michener, Prigge, and Meyer near the type locality where it is locally common on xeric, well-drained, sandy, whitish and reddish volcanic tuffs in association with *Fouquieria splendens*, *Agave*, *Opuntia*, *Jatropha*, *Hyptis*, *Acacia*, *Prosopis* and other leguminaceous shrubs and trees along the road between Huejaquilla El Alto and the Rio Atengo from 1000 to 1500 m elevation just east of San Juan Capistrano in an area that apparently has been very poorly collected.

11. *LEUCOPHYLLUM AMBIGUUM* Bonpl. in Humb. & Bonpl. Pl. Aequinoct. 2:95, pl. 109. 1812. TYPE: MÉXICO. HIDALGO, prope Actopan, 1050 hex., *A. Humboldt & A. Bonpland s. n.* (HOLOTYPE: [Microfiche of Humboldt and Bonpland Herbarium?]).

Leucophyllum campanulatum Miers. Ann. Mag. Nat. Hist. 5:254. 1850. TYPE: Coulter 1271 (HOLOTYPE: BM!; ISOTYPES: GH!, K!, NY!, PH!).

Leucophyllum altamirani Urbina, Anales Inst. Méd.-Nac. México. 8:275. 1906. TYPE: MÉXICO. QUERÉTARO: Del Ciervo al cerro de la Mesa, 20 Aug 1905, *Altamirano 1557* (HOLOTYPE: unknown).

Strongly, alternately-branched, rounded shrubs 0.6–1.5(-20) dm tall, sometimes somewhat thorny due to persistence of old stems; young stems irregularly, densely gray-tomentose (or brown in herbarium specimens) with cylindrical, dendritic trichomes 0.2–0.6 mm long, (0.1-)0.2–0.4 mm in diameter with slender, wavy radii (0.06-)0.1–0.25 mm long, tardily glabrate; old stems light gray to reddish-brown; internodes 1–10(-14) mm long. Leaves alternate, rarely some opposite, sometimes crowded on compressed lateral shoots, broadly ovate to orbicular, rarely broadly elliptical, 8–22(-40) mm long, 5–15(-27) mm wide, often variable on same plant, obtuse-rounded, bluntly apiculate at tip, abruptly cuneate to rounded at base above a broad, 1.5–7 mm long petiole, entire to undulate



Figure 19. Line drawings of *Leucophyllum pruinosum* and *L. pringlei*. a. *L. pruinosum*. Stem with leaves and flowers. Corolla in side view (lower right) shows characteristic expanded tube (Flyr 564c). b-e. *L. pringlei*. b. Stem with crowded, overlapping leaves and flowers. c. Enlargement of stem and leaves. Note expanded leaf bases and branched trichomes at lower right. d. Transparent view of corolla as seen from above, note relative position of stamens. e. Immature fruit enclosed in persistent calyx and topped with style (R. Cruz C. 2089). Scales = 1 cm.

at margins, densely, irregularly gray (or brownish in herbarium specimens) tomentose on both faces with dendritic trichomes 0.2–0.6 mm long, radii slender, straight or wavy (0.1–)0.2–0.4 mm long, trichomes weathering, becoming more uniform in age, midvein prominent beneath. Flowers with tomentose pedicels 1–2.5(–4) mm long; calyces 4.5–6 mm long, lobes oblong-lanceolate, oblong-ovate, 3–5 mm long, 1–1.5(–1) mm wide, acute, densely tomentose as young stems outside and at inside tip, moderately sericeous-pilose, glandular inside; corollas violet to purple throughout, white only at very base of tube, or with purple spots on floor of tube, rarely white with yellow spots at floor of tube, 12–18 mm long, tube

dorsi-ventrally compressed, three times wider than high, cylindrical to ampliate, lobes obovate to orbicular-reniform, 3–4.5(-6) mm long and wide, undulate, slightly emarginate, ciliate, tube densely pilose throughout inside with long, tangled trichomes to 2 mm long, lobes densely pilose inside with straight trichomes 0.3–0.8 mm long, corolla sparsely stipitate glandular outside; stamens 4(-5), posterior filaments 6–8 mm long, anterior filaments 4–5 mm long, glabrous to pilose; styles 7–13 mm long, pilose; ovaries densely pilose. Capsules 3–4 mm long, densely pilose above, glandular below.

Leucophyllum ambiguum is characterized by its concolorous, broadly ovate, orbicular, petiolate leaves, by its distinctive dendritic trichomes (fig. 20 a) that usually have long, slender, wavy radii 0.2–0.4 mm long on stems and leaves, by its distinctive violet to purple corollas that typically lack a whitish patch on the tube floor, and by the dense tangled and straight trichomes on the inside surfaces of the corolla tube, throat, and lobes. It also is a disjunct species occurring in the southern extension of the Chihuahuan Desert in arid portions of Hidalgo and Querétaro (fig. 18).

Throughout its range it exhibits some notable variation. Occasional plants have shorter vestiture with trichome radii only 0.1 mm long on both stems and leaves. A population northwest of Metzquititlan, Hidalgo, has corollas with a white patch on the floor of the corolla tube beset with yellow spots (*Rzedowski 32513*, ENCB, MEXU; *F. Gonzalez M. 8486*, MEXU) and in this character approaches *L. ultramonticola* and *L. pruinosum*. Occasional plants have some opposite leaves.

Leucophyllum ambiguum occurs on limestone and calcareous hillsides with *Larrea* and other desert shrubs up to submontane scrub from 1200 to 2500 m.

12. *LEUCOPHYLLUM PRINGLEI* (Greenman) Standley, Contr. U.S. Natl.

Herb. 23:305. 1923. *Faxonanthus pringlei* Greenman in Sargent, Trees & Shrubs 1:23, pl. 12. 1902. TYPE: MEXICO. PUEBLA: limestone hills near Tehuacan, 6000 ft., 22 Aug 1901, C. G. Pringle 8594 (HOLOTYPE: GH! ISOTYPES: A!, ENCB!, MEXU(2 sheets), NY!, PH!, US!).

Erect shrubs (1.5-)3–6 dm tall with several erect stems from a thick woody base, irregularly branched above, old branches persistent; young stems terete, 1–1.5 mm in diameter, hispidulous with erect, multicellular, tapering or distally forked or branched, white trichomes 0.1–0.25(-0.4) mm long, and with sessile glands; older stems marked with raised, persistent leaf bases; largest stems 4–6 mm in diameter; bark gray, vertically fissured; internodes 0.5–1(-2.5) mm long. Leaves alternate, crowded in terminal 2–3 cm of branches, linear-lanceolate to linear-

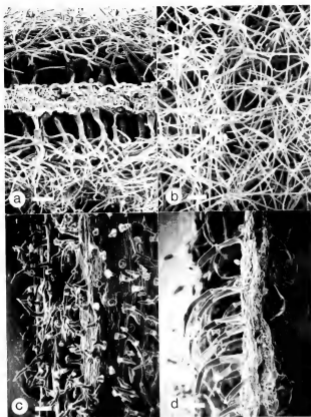


Figure 20. Leaf and stem vestiture of *Leucophyllum ambiguum*, *L. pruinatum*, *L. pringlei* and *Eremogeton grandiflorus*. a. *L. ambiguum*. Leaf cross section showing equal vestiture on both surfaces and basal simple portion of trichomes. Note also long radii (Flyr 587b). b. *L. pruinatum*. Surface view of adaxial leaf vestiture showing long, slender radii (Hensickson and Hess 19117). c. *L. pringlei*. Vestiture of upper stem with weakly branched trichomes. Note large glands. (Compare with fig. 3 d–f). (R. Cruz C. 2098). d. *Eremogeton grandiflorus*. Cross section of leaf with adaxial surface on right, abaxial surface with longer unbranched, curved trichomes on left. Note collapsed trichome cells (Stevens, Donoghue, and Scott 2344). Scale in a = 0.1 mm and holds for b–d.

elliptical, 6–12 mm long, 1.2–2.2 mm wide, ca 0.4 mm thick, acute to obtuse at tip, tapering in lower half to a broad petiole-like base about 1 mm long, 0.5–0.7 mm wide but expanded at very base where jointed with stem, entire, typically glabrous except for a few trichomes as in stem on basal 1–4 mm or with trichomes scattered throughout, viscid, strongly glandular to glandular-punctate, midrib obscure. Flowers with ascending pedicels 3–6 mm long with scattered erect to distally forked trichomes, sometimes with short, stipitate glands above; calyces 6.5–8 mm long, tube ampliate, 1–2.2 mm long, lobes 5, linear-oblongate, subequal, 5.5–7(-10) mm long, 0.5–1.5(-2) mm wide, green, leafy, acute at tip, entire, viscid, with sessile (to stipitate) glands on both sides; corollas light purple to blue, with a white patch marked with golded dots on floor of throat, (20-)22–25 mm long, tube 1–2 mm long, throat broadly campanulate to 12–15 mm wide (pressed), slightly ventricose at floor, lobes orbicular to obovate, medial anterior lobe largest 9–12(-14) mm long and wide, emarginate, 2 lateral anterior lobes slightly smaller, 8–10 mm wide and long, rounded at tip, posterior lobes 8–9 mm long and wide, rounded at tip, tube with slender, unicellular trichomes 1–3 mm long on floor of distal tube and near throat inside, lobes glabrous inside; corolla glabrous outside; stamens 4, included, posterior filaments 9–10 mm long, anterior filaments 6–7 mm long; anthers whitish, glabrous except for tuft of hairs near tip; proximal anthers 3–3.5 mm long, anterior anthers 2–2.5 mm long; ovaries glandular near tip; styles 10–14 mm long, sparsely glandular to stipitate-glandular, expanded, rhomboid, acute at tip. Capsules 5–6.5 mm long, 2.5–3 mm wide; seeds ellipsoidal, 0.5–0.8 mm long, 0.4–0.5 mm wide, angular, muricate in vertical lines.

Leucophyllum pringlei (figs. 19 b, 20 c) is one of the more distinctive species in the genus and is distinguished by its multicellular, uniseriate, tapering or distally-forked, occasionally distally-branched trichomes with multicellular rays, the tack-shaped, sessile glands with 10–15 cells in the heads (figs. 3 d-f, 20 c), its crowded, linear-oblongate, -elliptical, viscid, glanduliferous, leaves and its habit consisting of a series erect stems developing from a woody knot several centimeters in diameter. Corollas are also broadly ampliate and ventricose along the floor. The stigmas are longer, more rhomboid, acute, and usually recurve at the tip when dried.

In Flyr (1970), the taxon constituted the monotypic genus *Faxomanthus*. However, the species fits well within *Leucophyllum* in flower and fruit characters and differs only in its more open corolla throat (a feature also found in the smaller-flowered *L. pruinosum*), larger-headed glands, trichomes with multicellular rays, and more rhomboid, acute style tips. Its branched or forked trichomes (figs. 3 d, e, 20 c) appear derived from a

broader, dendritic trichome type but with smaller multicellular radii. Equally sparse trichomes also occur in *L. laevigatum* var. *laevigatum*. The conspicuous glands are not unique; leaves of all species of *Leucophyllum* have glands with multicellular heads, those of *L. pringlei* are just larger with a greater number of cells. In other species glands are typically obscured by the crowded, nonglandular trichomes.

Phenetically the taxon is quite distinct and it is here recognized as a separate subgenus. Recognition at the generic level is, in the senior author's opinion, not consistent with other generic distinctions in Scrophulariaceae. The two subgenera share a large number of basic characteristics, particularly those associated with flowers and fruits. Differences lie mostly with vestiture and vegetative morphology. The species is also well-isolated geographically from other species in the genus south of Mexican transvolcanic axis. This isolation has undoubtedly contributed to its morphological distinction.

Leucophyllum pringlei is restricted to limestone slopes in south-central Puebla and adjacent Oaxaca from 1600 to 2350 m (fig. 22) and flowers from May through October depending on rainfall.

11. EREMOGETON Standley & L. O. Williams, *Ceiba* 3:172. 1953. *Gbiesbreghtia* A. Gray, Proc. Amer. Acad. Arts. 8:630. 1873 (non A. Richard & Galeotii 1845). Monotypic.

1. EREMOGETON GRANDIFLORUS (A. Gray) Standley & L. O. Williams, *Ceiba* 3:172. 1953. *Gbiesbreghtia grandiflora* A. Gray, Proc. Amer. Acad. Arts. 8:630. 1873. TYPE: MEXICO, CHIAPAS: 1864-70, *Gbiesbreght* 723 (HOLOTYPE: GH!).

Large suffrutescent shrubs to small trees 3-6(-8) m tall; young stems subterete, uniformly villous-sericeous to tomentose with mostly soft, antrorsely curved to wavy, multicellular trichomes 0.2-0.7(-1.0) mm long, older stems (3-)4-6 mm in diameter, prominently marked with raised leaf and pedicel bases; bark furrowed; internodes (1-)6-15 mm long. Leaves alternate to subopposite, oblong-obovate, oblong-ovate, elliptical, ovate, (4-)5-9(-12) cm long, (1.5-)2-5(-6) cm wide, obtuse to acute, apiculate at tip, broadly cuneate at base with margins extending down a 8-15 mm long, 2-4 mm wide, winged petiole, at margins coarsely dentate, serrate to crenate in distal part, teeth obtuse to acute, apiculate, revolute, entire and revolute in lower portion, rarely entire throughout, close vestitured on both surfaces, upper (adaxial) surface with more scattered, soft to slightly rigid (then scabrous) tapering, antrorsely curved, multicellular trichomes 0.2-0.5 mm long, often mixed with stipitate glands, lower (abaxial) surface more densely vestitured with similar, tapering, antrorsely curved,

sometimes longer, more wavy trichomes 0.2–0.6(–1.0) mm long, vestiture more tomentose, longer along prominently raised mid and secondary veins. Flowers solitary in leaf axils, pedicels ascending, 2–3.5 cm long at anthesis, to 4–6 cm long in fruit, vestitured as young stems; calyces 5-lobed, lobes green, leafy, oblong, oblong-oblongate, ascending, 2–3.6 cm long, 4–7 mm wide, separate to within 2–3 mm of base, obtuse to acute at tip, entire, vestitured as lower leaf surface outside, with scattered stipitate glands inside; corollas showy, white, turning cream-white or yellowish, opening in late afternoon, zygomorphic, 6–7.2 cm long, tube abruptly expanded above base, cylindrical (25–)35–40 mm long, 15–20 mm in diameter, (25–30 mm wide pressed), posterior 2 lobes united, 25–30 mm long, together 22–28 mm wide, terminal teeth 11–15 mm long, obtuse to acute, erect, anterior 3 lobes spreading to descending, oblong-ovate, 25–33 mm long, 13–15 mm wide, acute to obtuse, corolla thick, glabrous to stipitate-glandular inside, stipitate-glandular outside where exposed in bud, ciliate with longer, crinkled hairs; fertile stamens 2, filaments 55–60 mm long, 1–1.5 mm thick, whitish, glabrous, adnate to expanded corolla tube base; anthers situated near tip of posterior corolla lobes, anther lobes 2, oblong-linear, slightly divaricate, cream-white, glabrous, longitudinally dehiscent across continuous apex, glabrous; sterile stamens 2 or absent, with filaments 3.3–7 mm long; ovary superior glabrous, grooved along septum, 2-loculed, placentae attached medially along septa; ovules many; style accrescent, 6–7.2 mm long, slightly expanded at obtuse tip, stigmatic along broad terminal band, glabrous to sparsely pilose. Fruit of dark brown ovoid, grooved, apiculate capsules, these dehiscent septocidally to near base, then loculicidally half way to base, subtended by persistent calyx; seeds 50–100 per locule, ellipsoid, 1.7–2.2 mm long, 0.6–0.8 mm wide, dark brown, angulate to flattened by compression, muricate in vertical rows; endosperm oily; embryo small.

Eremogeton (fig. 21) is a very distinct monotypic genus characterized by its uniseriate, multicellular, tapering, unbranched, antrorse trichomes (fig. 20 d), its large, ovate leaves, and its very large flowers with regular, deeply-parted calyces and conspicuous, zygomorphic, thickish corollas, 6–7.2 cm long, with 3 anterior, reflexed to spreading lobes and a 2-toothed, erect, posterior lobe. According to label-data of *W. D. Stevens et al. 2344*, (TEX), the corollas are "white at anthesis, just opening in late afternoon, later cream white." Stamens are typically 2, anterior, however, occasional specimens (including the type) may have two additional abortive, antherless staminodes with short filaments 3–7 mm long (Flyr 1970). The genus also has a conspicuous, probably nectariferous gland on the lower portion of the



Figure 21. Line drawing of *Eremogeton grandiflorus*. Stem with leaves and large flowers; developing fruit with long pedicel at right. (Stevens, Donoghue, and Scott 2344). Scale = 1 cm.

ovary. Capsules are also much larger than in *Leucophyllum* and contain many more seeds.

Eremogeton grandiflorus occurs mostly along limestone bluffs and steep slopes in oak-pine forests of south-central Chiapas, México, and Guatemala from 1200 to 2200 m (fig. 22).

ACKNOWLEDGEMENTS

In January 1970 Lowell David Flyer completed his dissertation in the Department of Botany at The University of Texas at Austin entitled, "A systematic study of the tribe Leucophylleae (Scrophulariaceae)." He recognized 13 species plus two varieties of *Leucophyllum* and the monotypic genera *Faxonanthus* and *Eremogeton*. Unfortunately for the botanical community, Flyer ended his life on 2 November 1971 without publishing his dissertation

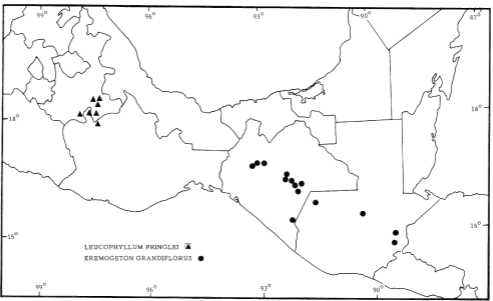


Figure 22. Distribution of *Leucophyllum pringlei* and *Eremogeton grandiflorus* in southern Mexico and Guatemala.

(see obituary by Turner, 1972). In the spring of 1982 Henrickson began a study of the group, using Flyr's dissertation as a starting point, working with the extensive collections at TEX-LL and borrowing or visiting the collections of ASU, ENCB, GH, MEXU, NY, RSA-POM, and US reevaluated the taxonomy and reduced the number of taxa recognized to two genera, *Leucophyllum* (including *Faxonanthus*), with 12 species and 2 varieties, and the monotypic *Eremogeton*. In this treatment the basic systematics of Flyr are followed but descriptions and discussions are largely expanded.

Specimens were visited or borrowed by Flyr from A, BM, CAS, DS, F, GH, K, LA, LL, MICH, MO, MSC, NMC, NY, OXF, PH, SMU, TAES, UC, and US, thanks are extended to curators of these herbaria for loans and courtesies extended. Dr. B. L. Turner, J. Strother, A. M. Powell, R. Irving, J. Rzedowski, P. Echlin, M. C. Johnston, L. H. Shoiners, and others were acknowledged by Flyr (1970) for their help with his dissertation. John Strother, A. S. Tomb, L. Dorr, B. Prigge, D. Michener, J. Mauseth, and K. Nixon as well as B. L. Turner and M. C. Johnston have, in various ways, greatly aided in the preparation of this paper. Robert J. Chinnock of the State Herbarium in Adelaide, South Australia, who is monographing *Eremophila* (Myoporaceae), kindly provided data on characteristics of the Myoporaceae.

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A REVISION OF THE CLASPING-LEAVED *POTAMOGETON* (POTAMOGETONACEAE)

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The genus *Potamogeton* Linnacus has long been considered to be one of the more taxonomically difficult and more ecologically important genera of all the aquatic vascular plants. These difficulties and importances have been summarized earlier (Haynes 1974, 1978) and will not here be discussed. Because of the importance and taxonomic confusion, I have begun a taxonomic revision of the genus.

Potamogeton is a cosmopolitan genus with approximately 100 species of submersed and floating-leaved aquatic plants. The genus has been separated into two subgenera (Raunkiaer 1896) and numerous sections and subsections (Ascherson and Graebner 1907; Hagström 1916). My approach has been to prepare treatments of one or a few subsections at a time, without considering whether the subsection should be recognized, and eventually to combine all these treatments into one volume for the entire genus. At that time the infrageneric classification will be re-evaluated and a treatment presented. This paper concentrates on two quite small subsections, subsection *Perfoliati* Graebner and subsection *Praelongi* Hagström.

Representatives of these two subsections are the only species of the genus with clasping leaves, these leaves all submersed. As a result, Ascherson and Graebner (1907) combined them in subsection *Perfoliati*, although Raunkiaer (1903) had earlier separated them into two groups, these groups without formal rank. Hagström (1916) followed Raunkiaer in separating the groups, naming the *P. praelongus*-group of Raunkiaer subsection *Praelongi*. Fernald (1932) and Ogden (1943) accepted Hagström's taxonomy without comment.

The morphological features, as well as the flavonoid chemistry, are evidence for combining the two subsections into one. However, the stem anatomy is quite different between representatives of the two subsections. Although my inclinations are to combine the two subsections, I do not understand the within and between subsectional variability of the above mentioned characteristics, as well as the other characteristics.

The nomenclature and morphology of the genus, including descriptions, have been published earlier (Haynes 1974, 1978) and will not be restated here.

The treatment that follows is based on extensive field study, growth of plants in similar and varied conditions, cytological examination, chemical examination, and an examination of over 3000 herbarium specimens from the following 26 herbaria: AAU, ALU, B, BM, BR, C, CAN, DA0, F G, GH, LE, K, M, MEL, MO, NSW, NY, P, S, TI, UNA, US, V, W, Z, (abbreviations according to Holmgren et al. 1981). Keys are based upon materials containing fruits; dimensions of leaves are taken from the fully expanded, longest leaves of a specimen; measurements of widths are taken approximately at the widest point of the leaf; and descriptions of fruits are taken strictly from mature structures.

KEY TO THE SUBSECTIONS OF CLASPING-LEAVED *POTAMOGETON*

1. Leaf apex cucullate; fruits with dorsal keel, 4–5.7 mm long *Praelongi*
1. Leaf apex non-cucullate (flattened); fruits without dorsal keels, 1.6–4.2 mm long *Perfoliatis*

POTAMOGETON subsection **PRAELONGI** Hagström, Kongl. Svenska Vetenskapsakad. Handl. 55(5):250. 1916. TYPE: *Potamogeton praelongus* Wulfen. Characteristics of the species.

1. **POTAMOGETON PRAELONGUS** Wulfen in Roemer, Arch. 3:331. 1805. TYPE: AUSTRIA. Labuch, 8 Jun 1763, *Wulfen s.n.* (ISOTYPE: MEL!).
P. flexuosum Wredow, Mecklenb. Fl. 1807.
P. flexicaulis Dethard, in Sterlitzer Anzeig., no. 50. 1809.
P. perfoliatus L. var. *lacustris* Wallman in S. Liljebl., Utkast Sv. Fl. 706. 1816.
P. acuminatum Wahlenb., Fl. Upsal. 116. 1820.
P. salicifolius Wulfg. ex Fries, Summa Veg. Scand. 1:213. 1845.
Spirillus praelongus (Wulfen) Nicuwlund, Amer. Midl. Naturalist 5:17. 1913.

Stems very pale green, simple or branched near apex, terete without nodal glands, to 210 cm long, to 3 mm diam. Leaves usually pale green, rarely olive-green, delicate, mostly alternate, rarely opposite, 11–33-nerved, 8–28 cm long, 1.1–4.6 cm wide; apex cucullate; lacunae absent; stipules white, fibrous, convolute, free from leaf blade, shredding at apex, persistent, 3–8.1 cm long, 3–8 mm wide. Winter buds (turions) absent. Peduncles cylindrical, terminal or axillary, erect to spreading, 9.5–53 cm long, 1–4 mm diam. Spikes cylindrical, 3.4–7.5 cm long, 1–2 cm diam; verticels 7–10, separated by 3–8 mm. Perianth segments 2–3.5 mm long, 1.5–2.5 mm wide; anthers 1.1–2.5 mm long. Fruit olive-green, with dorsal keel, occasionally with lateral keels, widest at or above

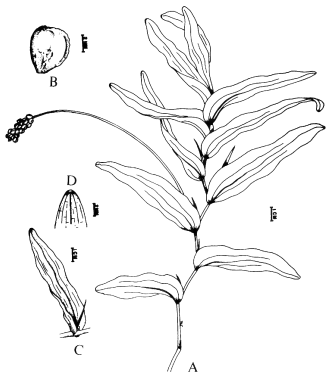


Fig. 1. *Potamogeton praelongus*. A. Habit sketch with axillary inflorescence. B. Fruit. C. Enlargement of node with scirpule. D. Enlargement of leaf apex with cucullate tip.

middle, 4–5.7 mm long, 3.2–4 mm wide; beak erect, marginal, 0.6–1 mm long, 0.6–0.9 mm diam; sides rounded or occasionally with slight central bulge; wall texture mostly wrinkled, rarely smooth. Chromosome number, $2n = 52$.

STEM ANATOMY: The stem anatomy of *Potamogeton praelongus* is characterized by a central stele with seven to nine separate vascular bundles. Ogden (1943) considered this type of stele to be the most primitive and thus labelled it "prototype." The endodermis is composed of U-cells. These

are cells that are thickened on the inner and lateral faces and thin on the outer face. The stem also has interlacunae bundles (vascular bundles at the junctures of walls separating the lacunae), subepidermal bundles (vascular bundles directly underneath the epidermis), and a pseudo-hypodermis of several layers of cells immediately beneath and adjacent to the epidermis.

FLAVONOID CHEMISTRY: The leaf flavonoid chemistry of *Potamogeton praelongus* is the most diverse of any species of the genus reported to date. Roberts and Haynes (submitted) isolated nine flavonoid compounds from the species. These include luteolin aglycone and its glycosides, 7-0-glucoside and 7-0-glucuronide, isoorientin, apigenin aglycone, and its glycosides, 7-0-monoglucoside and 7-0-diglucoside, and chrysoeriol aglycone and its 7-0-glucoside.

DISTRIBUTION: Apparently circumpolar in the Northern Hemisphere. In the Western Hemisphere, from north-central Alaska to southeastern Labrador, south to southern Newfoundland, Maryland, southeastern Colorado, and the Aleutian Islands; also central Mexico and the east-central coast of Greenland. The species, in the Western Hemisphere, reaches its northern limit about latitude 73°N and southern limit about latitude 38°N, disregarding the one Mexican locality. In the Eastern Hemisphere, from northwestern Norway to western Russia, south to west Yugoslavia, west to east-central France and northern Ireland; also Kamchatka Peninsula, southwest to east-central Japan. In the Eastern Hemisphere, the species reaches its northern limit about latitude 68°N and southern limit about latitude 35°N.

Although I have seen no material from the vast majority of Russia, the species undoubtedly occurs there. Juzepczuk (1934) lists the species from all parts of the country.

Potamogeton praelongus, with its zig-zagging stem, semi-clasping leaves, and cucullate leaf tips, is one of the most easily recognizable species of pondweeds. The species has been known to hybridize with *P. perfoliatus* on occasion and to produce a sterile off-spring which can perpetuate itself by vegetative methods. The most commonly collected locality for the hybrid is Varming Lake on the Ribe River near Ribe, Denmark. That lake has now been altered considerably and probably does not exist anymore. With the destruction of the lake, the hybrid apparently was extirpated.

POTAMOGETON subsection **PERFOLIATI** Graebner in Ascherson and Graebner, *Pflanzenr.* 4(11):92. 1907. **TYPE:** *Potamogeton perfoliatus* L.

Plants submersed in fresh or brackish waters, perennial. Stems branched or unbranched, terete, without nodal glands. Leaves all submersed, pellucid, sessile, without lacunae, lanceolate to orbicular, obtuse to acute at

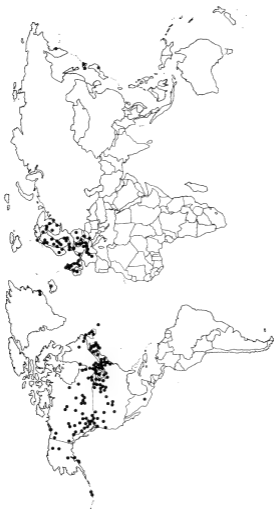


Fig. 2. *Potamogeton praelongus*. Documented distribution.

apex, clasping at base, entire, 3–35-nerved. Stipulates convolute, free from base of blade. Winter buds (turions) absent. Inflorescence emersed, a cylindrical spike with 3–11 whorls of flowers, compact, mostly with 4 flowers at each whorl. Fruit dorsally rounded or keeled, to 4.2 mm long. Chromosome number, $2n = 52$.

KEY TO THE SPECIES

1. Stipules fibrous, persisting as fibers; leaf apex mostly acute; fruits 2.2–4.2 mm long *P. richardsonii*
 1. Stipules delicate, without fibers, mostly decaying early; leaf apex mostly obtuse, rarely acute; fruit 1.6–3 mm long *P. perfoliatus*

2. **POTAMOGETON PERFOLIATUS L.**, Sp. Pl. 1:126. 1753. TYPE: SWEDEN/FINLAND. Lappland. *Linnæus* (LECTOTYPE here designated: Institute de France, Paris, B. Delessert Library; photo of lectotype, BM!).

Potamogeton amplexicaulis Kar. Bull. Soc. Nat. Mosc. 173. 1839.

P. bupleuroides Fernald in Gray, Manual ed. 7. 75. 1908.

P. loeselii Roem. & Schultes, Syst. Veg. 3:508. 1818.

P. perfoliatus L. var. *bupleuroides* (Fernald) Farwell, Amer. Midl. Naturalist 8:264. 1923.

P. perfoliatus L. var. *caudiformis* Aschers. & Graebn., Syn. Mitteleur. Fl. 1:314. 1897.

P. perfoliatus L. var. *cordatilanceolatus* K. Merr. & W. Koch. in Rohl., Deutschland. Fl. ed. 3. 1:852. 1823.

P. perfoliatus L. var. *densifolius* G. Mey., Chloris Han. 523. 1836.

P. perfoliatus L. var. *gracilis* Fr., Novit. Fl. Saec. Alt. 42. 1828.

P. perfoliatus L. var. *loeselii* (Roem. & Schultes) Aschers. & Graebn., Syn. Mitteleur. Fl. 1:314. 1836.

P. perfoliatus L. var. *mandschuriensis* A. Benn., Annuaire Conserv. Jard. Bot. Genève 9:100. 1905.

P. perfoliatus L. var. *prolixus* Hagström, Knögl. Svenska Vetensk. Acad. Handl. 55(5):254. 1916.

P. perfoliatus L. var. *psuedodensus* Aschers. & Graebn., Syn. Mitteleur. Fl. 1:314. 1897.

P. perfoliatus L. var. *rotundifolius* Sonder, Fl. Hamb. 98. 1851.

Spirillus perfoliatus (L.) Nicowl., Amer. Midl. Naturalist 3:17. 1913.

Stem pale green, simple or branched near apex, terete, to 2.5 m long, 0.2–1.9 mm diam. Leaves usually olive-green, delicate, 3–25-nerved, 0.9–7.6(–9.7) cm long, 0.7–4 cm wide; apex mostly round, rarely acute; lateral nerves joining midrib at apex. Stipules translucent, delicate, not shredding at apex, convolute, fugacious, 3.5–6.5 cm long, 1–1.5 mm diam. Peduncles cylindrical, terminal or axillary, erect to rarely recurved, 1–7.3 cm long, 0.5–2.2 mm diam. Spike cylindrical, 0.4–4.8 cm long, 4.5–8 mm diam; verticels 3–9, separated by 1.5–3 mm. Perianth segments 1.3–2.1 mm long, 0.7–1.9 mm wide. Anthers 1–1.2 mm long, 0.2–0.7 mm wide. Fruit light green to brown, without dorsal keel, widest at or above middle, 1.6–3 mm long, 1.3–2.2

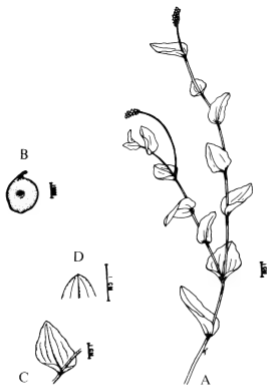


Fig. 3. *Potamogeton perfoliatus*. A. Habit sketch with axillary and terminal inflorescences. B. Fruit. C. Enlargement of node after stipule has decayed. D. Enlargement of leaf apex with flattened (non-cucullate) tip.

mm wide; sides mostly depressed, occasionally rounded; beak central, 0.1–0.9 mm long, 0.1–0.9 mm diam.; wall texture smooth. Chromosome number, $2n = 52$.

STEM ANATOMY: The stem anatomy of *Potamogeton perfoliatus* is characterized by a "trio-type" stele (see discussion of *P. richardsonii* for explanation). The endodermis is composed of O-cells, cells that are thickened on

all—inner, lateral, and outer—faces, giving an appearance of an O. The stems also possess a pseudo-hypodermis, but lack interlacunae bundles and subepidermal bundles (see discussion under *P. praelongus* for an explanation of these tissues).

FLAVONOID CHEMISTRY: The leaf flavonoid chemistry of *Potamogeton perfoliatus* is more complex than *P. richardsonii*. Roberts and Haynes (submitted) isolated seven compounds from the species. These include luteolin aglycone and its glycosides, 7-O-glucoside and 7-O-glucuronide, apigenin aglycone and its 7-O-monoglucoside, and chrysoeriol aglycone and its 7-O-glucoside. Harbourne and Williams (1976) isolated a C-glycoflavone from the species. Roberts and Haynes (submitted) did isolate the C-glycoflavone, isoorientin, from the related species *P. praelongus* and this very possibly is the C-glycoflavone which Harbourne and Williams isolated from *P. perfoliatus*.

DISTRIBUTION: In the Western Hemisphere, from Labrador to Newfoundland and SW to southern Ontario and North Carolina; also Lake Atitlán, Guatemala, east-central coast of Greenland, northeastern Iceland, and the Gulf of Mexico outer coastal plain from western Florida to eastern Louisiana. In the Eastern Hemisphere, widespread from extreme northern Norway to western Kamchatka Peninsula, Russia, south to southern Japan, southern India, and northern Spain; also, southeastern Australia, eastern Sudan, and southeastern Algeria.

Potamogeton perfoliatus, morphologically, is extremely variable, especially in Europe. As a result, the taxon has been divided into two specific and 10 or more subspecific categories. These segregates were based exclusively on vegetative variability. After examining hundreds of specimens, I have been unable to divide the morphology into ranges which warrant taxonomic recognition. This variability is continuous, with no geographical distinctions. I have, therefore, decided not to accept any subspecific categories.

Potamogeton perfoliatus var. *muelleri* Bennett was published based upon several collections by Mr. Mueller from southeastern Australia. I have visited the type locality and have examined the type specimen, as well as several others taken from the type locality. In my opinion, the taxon is not *P. perfoliatus* and I am, therefore, excluding it from further consideration at this time.

3. POTAMOGETON RICHARDSONII (A. Benn.) Rydberg, Bull. Torrey Bot. Club 32:599. 1905. TYPE: U.S.A. Michigan, Robbins s.n. (LECTOTYPE GH).
P. perfoliatus L. var. *lancoletus* J. W. Robbins in A. Gray, Man. ed. 5. 488. 1867, *non* Blytt 1861.
P. perfoliatus L. var. *richardsonii* A. Benn., J. Bot. 27:25. 1889.



Fig. 4. *Potamogeton perfoliatus*. Documented distribution.

P. perfoliatus L. ssp. *richardsonii* Hultén, Fl. Alaska & Yukon 102. 1940.

Spirillus perfoliatus (L.) Nicuwl. var. *richardsonii* (A. Benn.) Nicuwl. Amer. Midl. Naturalist 3:17. 1913.

Stem pale green, simple or occasionally branched near apex, terete, ca 97 cm long, 1–2.8 mm diam. Leaves lanceolate, usually olive-green, delicate, 3–35-nerved, 1.6–13 cm long, 0.5–2.8 cm wide; apex acute to obtuse; lateral nerves joined midrib at apex. Stipules white, fibrous, shredding at apex, mostly persistent as fibers, 1.2–1.7 mm long, 1–3.2 mm diam. Peduncles clavate, terminal or axillary, erect to rarely recurved, 1.5–14.8 cm long, 1–3.9 mm diam. Spike cylindrical, 1.3–3.7 cm long, 5–11 mm diam.; verticels 5–11, separated by 2–5 mm. Perianth segments 1.1–2.5 mm long, 1–2.4 mm wide. Anthers 1.5–1.6 mm long, 0.5–0.6 mm wide. Fruit light green to brown, mostly without dorsal keel, widest at or above middle, 2.2–4.2 mm long, 1.7–2.9 mm wide; beak central, 0.1–1.1 mm long, 0.1–0.9 mm diam; sides rounded, rarely centrally depressed; wall texture smooth. Chromosome number, $2n = 52$.

STEM ANATOMY: The stem anatomy of *Potamogeton richardsonii* is characterized by a central stele in which three of the four median bundles have united to form a "trio" bundle. There are, therefore, only two bundles in the median region of the stele, one of them with two patches of phloem on the inner face. Ogden (1943) designated this stele as the "trio-type" and considered it an advancement over the proto-type but still not the most advanced type. The endodermis is composed of O-cells. These are cells that are thickened on all-inner, lateral, and outer—faces, giving an appearance of an O. The stems also possess a pseudo-hypodermis, but lack interlacunae bundles and subepidermal bundles (see discussion under *P. praelongus* for an explanation of these tissues).

FLAVONOID CHEMISTRY: The leaf flavonoid chemistry of *Potamogeton richardsonii* is less diverse than *P. perfoliatus*. Roberts and Haynes (submitted) isolated five compounds from the species. These include lutcolin aglycone, and its glucosides, 7-O-glucoside and 7-O-glucuronide, and chrysoeriol aglycone and its 7-O-glucoside. Harbourne and Williams (1976) isolated a C-glycoflavone from the species. Roberts and Haynes (submitted) did isolate the C-glycoflavone, isoorientin, from the related species *P. praelongus*, and this very possibly is the C-glycoflavone which Harbourne and Williams isolated from *P. richardsonii*.

DISTRIBUTION: From Aleurian Islands, central Alaska, and Mackenzie Delta to central Quebec, south to New York, Ohio, Colorado, and northern California.

Potamogeton richardsonii has been included with *P. perfoliatus* (Ascherson

and Graebner 1907) and accepted at the specific level by Ogden (1943) and Hagström (1916). The two taxa are quite easily separated over the vast majority of their ranges. In areas of sympatry, however, the two taxa are difficult to separate. This apparent integradation is evidence for recogni-

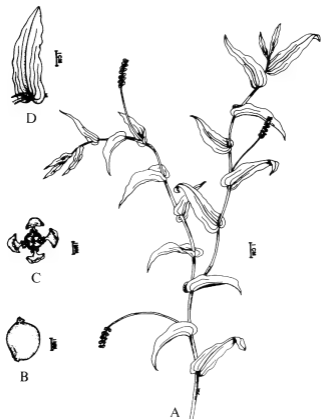


Fig. 5. *Potamogeton richardsonii*. A. Habit sketch with axillary inflorescences. B. Fruit. C. Flower. D. Enlargement of node with persistent stipule.

tion at a subspecific level. These intermediate forms, however, are almost always sterile. If flowers develop, these flowers rarely produce fruit. Should some subspecific category be warranted, one would expect the intermediates produced in an area of sympatry to be fertile, at least fairly commonly.

To test the hypothesis that the two taxa are distinct and should be accepted at the specific rank, individuals of the two taxa were grown in similar conditions (both flowing and non-flowing) in the aquatic biology facility at the University of Alabama. The individuals of the two taxa remained morphologically distinct over the duration of the growth period.

Also, 77 specimens of the complex were examined for 16 morphological characteristics (see Table I). These specimens were taken at random from a group of specimens, each of which possessed all the characteristics measured, including both mature flowers and mature fruits. These specimens were tentatively identified to species, 32 as *P. perfoliatus* and 45 as *P. richardsonii*. The data were analyzed by the NT/SYS statistical package (Rolf, et al. 1977). The specimens were sorted into two groups by the statistical program, the 32 originally determined as *P. perfoliatus* in one group and the 45 originally determined as *P. richardsonii* in the other group.

TABLE I

CHARACTER	P. PERFOLIATUS (N = 32)			P. RICHARDSONII (N = 45)		
	RANGE	X	S.E.	RANGE	X	S.E.
Stem diameter (mm)*	0.2-1.9	0.92	0.78-1.05	1.0-2.8	1.75	1.58-1.88
Leaf width (cm)	0.7-2.6	1.2	1.05-1.35	0.7-2.8	1.24	1.1-1.37
Leaf length (cm)*	0.9-3.8	1.9	1.6-2.2	2.2-10.2	4.4	3.9-4.9
Number veins	3-21	9.9	8.1-11.7	3-35	12.5	10.1-14.9
Peduncle length (cm)*	1.0-7.3	3.6	3.2-4.0	1.5-11.6	5.4	4.5-6.3
Peduncle diameter (mm)*	0.5-2.2	1.4	1.1-1.7	1.0-3.9	2.2	2.0-2.4
Spike length (cm)*	0.4-4.8	1.4	1.0-1.8	1.3-3.7	2.5	2.3-2.7
Spike diameter (mm)*	4.5-8.0	6.4	5.9-6.9	5.0-11.0	8.0	7.2-8.8
Number inflorescence verrucels*	3-9	5.0	4.4-5.6	5-11	8	7.5-8.5
Perianth length (mm)	1.3-2.1	1.52	1.41-1.65	1.1-2.5	1.71	1.61-1.81
Perianth width (mm)	0.7-1.9	1.27	1.17-1.37	1.0-2.4	1.61	1.36-1.86
Fruit length (mm)*	1.6-2.8	2.26	2.15-2.37	2.2-4.2	2.9	2.79-3.01
Fruit width (mm)*	1.3-2.2	1.8	1.7-1.9	1.7-2.9	2.3	2.2-2.4
Fruit beak length (mm)	0.1-0.9	0.45	0.39-0.51	0.1-0.9	0.55	0.50-0.60
Fruit beak width (mm)*	0.1-0.9	0.32	0.27-0.37	0.1-0.9	0.44	0.40-0.48
Number fruits per spike*	3-35	10.8	7.6-14.0	1-65	21.3	16.54-26.1

X—Mean for all measurements of that characteristic.

S.E.—Range of two standard errors above and two standard errors below the mean of that characteristic.

*—Indicates characteristics for which there is no overlap of the two species of the two standard errors above and two standard errors below the mean.



Fig. 6. *Patagonogaster richardsonii*. Documented distribution.

The means and standard error were calculated for each group for each characteristic. Table I lists the range for each characteristic, the mean for that characteristic, and the range of two standard errors above and two standard errors below the mean. Whenever there is no overlap between the standard error ranges of a particular characteristic for the two taxa, then that characteristic is considered to be statistically valid in separating the two taxa. The standard error ranges do not overlap for 11 of the characteristics examined. These characteristics are indicated with an asterisk in Table I.

The growth studies and the statistical analysis, along with the phyto-geography of the species in North America, lead me to the conclusion that the taxa should be accepted at the species level.

The chemical data can be used to help understand the origin of *Potamogeton richardsonii*. Hagström (1916) proposed that *P. richardsonii* evolved by hybridization of *P. praelongus* and *P. perfoliatus*. Ogden (1943) did not accept that theory since either one of the putative parents is or both are absent over much of the range of *P. richardsonii*. Neither luteolin aglycone and its two glycosides nor chrysoeriol aglycone and its glycoside may be used as evidence for or against the hybrid origin theory. However, apigenin and its monoglucoside are quite helpful as both these compounds are shared by the two putative parents, although in trace amounts in *P. perfoliatus*. Neither compound has been detected in *P. richardsonii*, although large quantities of plants have been extracted. The chemical profile of hybrid taxa is normally additive of the two putative parents (Haynes and Williams 1975), although novel compounds may be found in the hybrid (Ordnuff et al. 1973). The chemical data, with apigenin aglycone and its monoglucoside being present in both putative parental species and being absent in the putative hybrid, support Ogden's (1943) theory that *P. richardsonii* arose by means other than hybridization of *P. praelongus* and *P. perfoliatus*.

Hultén (1937) proposed that there were two main refugia in North America—the Rocky Mountains and the continental shelf outside eastern North America—where plants survived during continental glaciation. From these refugia, he stated, the plants probably spread in an easterly and westerly direction, respectively, toward the center of the continent. Some taxa probably survived in one area, while other taxa possibly survived in both areas. Some of the taxa which survived in both refugia migrated until their ranges overlapped; thus, they now have a continuous range across North America. For others, however, migration ceased before the ranges overlapped. Hultén conceded that species surviving in other areas south of the glacial boundary did migrate north and, to some extent, into the once

glaciated lands. However, he suggested that a much smaller proportion of the species now found in the glaciated areas survived in the vast areas south of maximum glaciation than in the two other refugia.

I propose that *Potamogeton perfoliatus* was, prior to the glacial period, a circumpolar species, with a more or less continuous distribution, including North America. Glaciation would have separated this North American population into two smaller allopatric ones, one to the east and one to the west. During glaciation, the two populations differentiated, resulting in each population evolving into a different species. Once the period of glaciation was complete and the distributions overlapped, the reproductive barriers that had been established during glaciation evidently now prevent gene flow from one population to the other. The western population represents *P. richardsonii* and the eastern *P. perfoliatus*. Iltis (1965) indicated that *Gentianopsis procera* and *G. crinita* possibly had a similar history. Apparently species or varieties could have evolved in a matter of 10,000 years. One need only examine a few of the Great Lakes endemics, e.g. *Iris lacustris* (Guire and Voss 1963), *Cirsium pitchei* (Johnson and Iltis 1963), and *Calamovilfa longifolia* var. *magna* (Thieret 1960) for confirmation.

Hagström (1916), when proposing that *P. richardsonii* arose as a hybrid between *P. praelongus* and *P. perfoliatus*, was correct in pointing out that *P. richardsonii* is intermediate in size and the fibrous nature of the stipules between the two putative parents. However, the stem anatomy being completely unlike *P. praelongus*, the flavonoid chemistry being non-additive, and the phytogeography all individually and collectively contradict Hagström's theory.

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TAXONOMY, DISTRIBUTION AND RARITY
STATUS OF *LEAVENWORTHIA*
AND *LESQUERELLA* (BRASSICACEAE)
IN KENTUCKY

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ABSTRACT

A taxonomic treatment and illustrations are provided for the three taxa of *Leavenworthia* and two of *Lesquerella* in Kentucky, and the distribution of each taxon in Kentucky is shown on a dot distribution map. The ecology and rarity status of each taxon at the state and federal level are discussed. *Leavenworthia exigua* var. *laciniata* and *Lesquerella globosa* currently are under review by the Fish and Wildlife Service for listing as endangered and threatened, respectively.

The vascular flora of Kentucky is interesting and diverse, but it has never been comprehensively studied. In her bibliography of Kentucky's botanical literature, Fuller (1979) lists many floristic studies but few taxonomic treatments of individual genera or families. With the ever accelerating destruction of Kentucky's natural vegetation, such treatments become vital, not only as a future document of what is lost but to help save what remains. There is currently a great need for reliable information on the extent and status of all of the state's flora, and this is especially true for the rare taxa. Since all five taxa of *Leavenworthia* and *Lesquerella* are rare in Kentucky (Branson et al. 1981; Chester 1982), and since at the time this study was begun *Leavenworthia exigua* var. *laciniata*, *L. torulosa* and *Lesquerella globosa* were under review by the Fish and Wildlife Service for listing as endangered or threatened [Federal Register 45(242): 82517, 82518, 15 December 1980], we undertook a study of the taxonomy and distribution of these two genera in Kentucky. *Leavenworthia torulosa* since has been removed from the list [Federal Register 48(229):53666, 28 November 1983].

METHODS

This treatment is based on a study of 82 herbarium specimens of *Leavenworthia* and *Lesquerella* collected in Kentucky and located at ALU, APSC, DHL, E, GH, KY, Ky. Agri. Exp. Sta. Herbarium, MICH, MEM, MO, PH, PUL, US, VDB and in several private collections and on extensive field work in Kentucky over the past several growing seasons (herbarium abbreviations follow Holmgren et al. 1981). Determinations of taxa were made using keys in Rollins (1963) for *Leavenworthia* and those in Rollins and Shaw (1973) for *Lesquerella*. Measurements of various plant parts cited in the paper were made using a standard dissecting microscope and are based solely on material from Kentucky. Each symbol on the distribution maps is based on an herbarium specimen.

RESULTS AND DISCUSSION

Leavenworthia

Herbaceous, rosette-forming winter annuals; flowers borne singly in erect peduncles, later flowers (if present) borne in lateral, loose racemes; siliques parallel to septum, gynophore short, funiculus free; seeds in a single row in silique, orbicular and flattened (Fig. 1).

The systematics (Rollins 1963), evolution (e.g., Lloyd 1965, 1967, 1969; Rollins 1963; Solbrig 1972; Solbrig and Rollins 1977) and ecology (e.g., Baskin and Baskin 1971, 1972, 1976) of *Leavenworthia* have been studied in considerable detail. All taxa are winter annuals that in presettlement times were restricted to cedar (limestone or dolomite) glades (Rollins 1963). However, several of the species, including those that occur in Kentucky, also now occur in disturbed situations such as rocky pastures and plowed fields (Rollins 1981).

KEY TO THE SPECIES OF *LEAVENWORTHIA* IN KENTUCKY

1. Siliques markedly torulose; wing of seed very narrow or absent 2. *L. torulosa*
1. Siliques not torulose; wing of the seed well developed. 2
 2. Petals entire, 5–7 mm long; terminal leaflet not markedly larger than the lateral ones; style short and stout, 1.0–2.5 mm long 1. *L. uniflora*
 2. Petals emarginate, 6–10 mm long; terminal leaflet much larger than lateral ones; style slender, 2.0–3.0 mm long 3. *L. exigua* var. *laciniata*

1. *L. UNIFLORA* (Michx.) Britton, Mem. Torrey Bot. Club 5:171. 1894.

Leavenworthia uniflora is the most abundant and widespread species of the genus. In Kentucky, it has been collected in 12 counties (Fig. 2); it grows on limestone or dolomite glades and outcrops in northwest Georgia, northern Alabama, eastern and central Tennessee, southern Ohio,

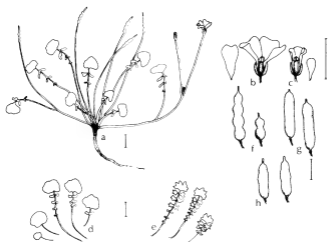


Figure 1. Morphological features of *Leavenworthia*. *L. torulosa*, a. habit, b. flower, c. leaves from basal rosette, f. silique; *L. uniflora*, c. flower, d. leaves, g. silique; *L. exigua* var. *laciniata*, h. silique. Bar equals 1 cm. (Flowers redrawn from Rollins 1963.)

southeastern Indiana and the Ozark Region of southern Missouri and northern Arkansas (Rollins 1963). In Kentucky, *L. uniflora* grows in cedar glades, on disturbed rocky ledges and outcrops and in rocky pastures. Population size varies greatly; often only a few individuals are found at a site, although in favorable situations there may be several thousand plants.

We know of only about a dozen extant populations, but this may be due to lack of thorough botanical collecting in the parts of Kentucky where it grows rather than to its real rarity. In addition, this species is inconspicuous during most of the year, especially during the summer collecting season. Given the large size of several populations and their scattered occurrence over a large area of the state, we do not feel that *L. uniflora* is threatened in Kentucky. It is not considered threatened nationally and is not currently under review. However, *L. uniflora* is listed as endangered in Indiana (Bacone and Hedge 1980) and threatened in Ohio (Roberts and Cooperrider 1982; McCance and Burns 1984).

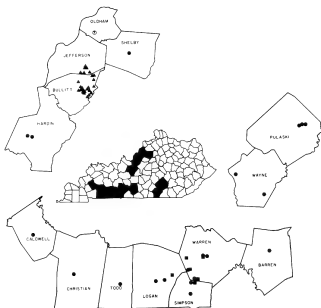


Figure 2. Distribution of *Leavenworthia* in Kentucky. *L. exigua* var. *laciniata* (triangles); *L. torulosa* (squares); *L. uniflora* (circles). Symbols represent exact localities, except for the Oldham County site for *L. uniflora*.

2. *L. TORULOSA* Gray, Bot. Gaz. 5:26. 1880.

Leavenworthia torulosa is primarily a species of the Nashville Basin with outlying populations on the Mississippian Plateau of Kentucky (Fig. 2) and in the Ridge and Valley Physiographic Province of east Tennessee (Rollins 1963). It is found on glades and in disturbed rocky pastures, where it often grows in and around seasonal pools and wet depressions. Although not listed from Alabama by Rollins (1963), there is a specimen of *L. torulosa* in the Mohr Herbarium at the University of Alabama in Tuscaloosa (Baskin and Baskin 1984). The label on the specimen indicates that it was collected by Charles Mohr in 1880 in Madison County. The specimen has not been annotated by Rollins, and thus he apparently was

unaware that the species had been collected in Alabama. Mohr (1901) includes the species in his *Plant Life of Alabama* and refers to its rarity in that state.

Leavenworthia torulosa potentially may be of economic value. Its seeds contain a high level of the fatty acid eicosenoic acid (Miller et al. 1965) that may prove to be of industrial value. Appelquist (1971) states that further studies of *L. torulosa* should be undertaken if a specific industrial need for eicosenoic acid arises.

Baskin and Baskin (1977) have discussed the status of this species in Kentucky and proposed that it was threatened with extinction in the state. In 1980, this species was under review for listing by the Fish and Wildlife Service as threatened [Federal Register 45(242): 82517, 15 December 1980], but it no longer is under consideration [Federal Register 48(229): 53666, 28 November 1983]. *Leavenworthia torulosa* is listed as endangered in Kentucky (Branson et al. 1981) and threatened in Tennessee (Collins et al. 1978; Tenn. Dept. Conserv. 1982) and Alabama (Freeman et al. 1979). Given the paucity of specimens of this taxon collected in Alabama and the apparent lack of any recent collections, we suggest that it should be listed as endangered in that state. It probably is extirpated in Alabama.

3. *L. EXIGUA* Rollins var. *LACINIATA* Rollins, *Contr. Gray Herb.* 192: 75. 1963.

Leavenworthia exigua var. *laciniata* apparently is endemic to Silurian dolomite and limestone outcrops (cedar glades) of Bullitt and Jefferson counties, Kentucky (Fig. 2). It grows in dry sites on glades similar to those of *L. uniflora*, although it never has been found with this species. *Leavenworthia exigua* var. *laciniata* frequently is found on glades that have been disturbed by pasturing or that occur along roadsides, and it has invaded a plowed field adjacent to a glade at one Bullitt County site.

Baskin and Baskin (1981) have studied the ecology and distribution of this species in Kentucky. *Leavenworthia exigua* var. *laciniata* is currently under review for listing by the Fish and Wildlife Service as endangered [Federal Register 45(242): 82517, 15 December 1980]. Because of its limited geographical range and narrow habitat requirements, we believe that it warrants protection at both the state and federal levels. This taxon is listed as endangered in Kentucky (Branson et al. 1981). *Leavenworthia exigua* Rollins var. *exigua* is listed as threatened in Georgia (McCollum and Ettman 1977) and endangered in Tennessee (Collins et al. 1978), and *L. exigua* Rollins var. *lutea* Rollins is listed as endangered in Tennessee (Collins et al. 1978) and Alabama (Freeman et al. 1979). *Leavenworthia exigua* var. *exigua* and *L. exigua* var. *lutea* currently are under review for

listing as threatened by the Fish and Wildlife Service [Federal Register 48(229): 53652, 28 November 1983].

EXCLUDED SPECIES

Leavenworthia aurea Torrey was reported from Kentucky by Short (1840). However, material at PH collected by Short and labeled by him as such is *L. torulosa*. One of the specimens is dated 1840, and the other has no date. In 1840, only two species of *Leavenworthia* (*L. uniflora* and *L. aurea*) had been described. Short knew *L. uniflora*, and he must have assumed that any *Leavenworthia* that was not *L. uniflora* was *L. aurea*. *Leavenworthia aurea* is restricted to calcareous glades and outcrops in southeastern Oklahoma and eastern Texas (Rollins 1963).

A specimen of *Leavenworthia stylosa* Gray in the herbarium of the Field Museum (sheet #790163) bears the label "Kentucky," but it is without name of collector or date. Dr. R. L. Stuckey, of The Ohio State University, kindly analyzed the handwriting and confirmed our suspicion that it is not that of Dr. Short. Since the source of the specimen is in doubt and the collector is unknown, this species should not be included in the Kentucky flora until more convincing evidence is found that it does occur in the state.

LESQUERELLA

Herbaceous, stellate-pubescent annuals or perennials; flowers orange-yellow (in ours), borne in dense, nearly flat-topped racemes (elongating as fruit matures); siliques globose or somewhat compressed, wall turgid or thin and papery, funiculus attached to septum towards the base, septum entire with prominent central nerve above; seeds globose (Fig. 3).

This genus of about 70 species recently was monographed by Rollins and Shaw (1973). It has been the subject of some interesting studies of inter-specific hybridization (Rollins 1957; Rollins and Solbrig 1973). Seeds of a number of species of *Lesquerella* have been investigated as a source of industrial oils (Hinman 1984). Both species of *Lesquerella* that occur in Kentucky have been investigated for their oil content (Barclay et al. 1962; Mikolajczak et al. 1962). Very little information is available in the literature on the species' ecology.

KEY TO THE SPECIES OF LESQUERELLA IN KENTUCKY

1. Plants of alluvial situations; most leaves auriculate; siliques 4–7 mm long, strongly compressed 1. *L. lescarii*
1. Plants of dry, rocky or gravelly situations; leaves never auriculate; siliques 2–2.8 mm long, globose 2. *L. globosa*



Figure 3. Morphological features of *Lesquerella*. *L. lescarii*, a. habit, c. siliqua, e. trichomes; *L. globosa*, b. siliqua, d. trichomes. Bar equals 1 cm, except for trichomes where it equals 0.1 mm.

1. *L. LESCURII* (Gray) Wats., Proc. Amer. Acad. Arts 23:250. 1888.

Lesquerella lescarii recently was collected in Kentucky for the first time, from Trigg County (Fig. 4) just north of the Tennessee state line, by Dr. E. W. Chester of Austin Peay State University in Tennessee (Chester 1982). According to Rollins (1981), it is a species with "weedy tendencies" that grows in old fields, river bottoms and roadsides. In Kentucky, it is restricted to disturbed bottomlands along the Cumberland River. The impoundment of the Cumberland River by Kentucky Dam probably destroyed much of the suitable habitat for this species in Kentucky.

This species was shown to be more abundant in Tennessee than previously thought and thus is no longer under consideration for protection by federal authorities [Federal Register 45(242): 82553, 15 December 1980]. *Lesquerella lescarii* was listed as threatened in Tennessee by Collins et al. (1978), but it no longer is considered to be rare in Tennessee (Tenn. Dept. Conserv. 1982). Apparently, the species has a very narrow geographical distribution in Kentucky and thus is a rare plant in that state.

2. *L. GLOBOSA* (Desv.) Wats., Proc. Amer. Acad. Arts 23:252. 1888.

Lesquerella globosa is a taxonomically isolated member of the genus confined to Kentucky (Fig. 4) and Tennessee, except for its occurrence at one outlying site in southwestern Indiana (Rollins and Shaw 1973). It was collected once in Indiana by Deam et al. (1941), but Deam thought that it may have been introduced into that state (Rollins and Shaw 1973). According to Rollins and Shaw (1973), *L. globosa* is a perennial; Payson (1921) says that it is biennial or perennial. Essentially nothing is known about the ecological life cycle of this species, and its autecology is in need of study. We have collected it in a variety of situations, from gravelly roadsides and rights-of-way to (calcareous) shaley, exposed slopes and rocky ledges.

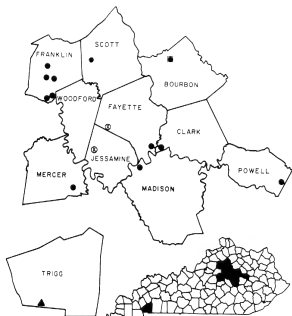


Figure 4. Distribution of *Lesquerella* in Kentucky. *L. globosa* (circles); *L. lescarii* (triangle). Symbols represent exact localities, except for the sites in western Jessamine and southwestern Fayette counties where they are approximate.

Rollins and Shaw (1973) give the distribution of *L. globosa* in Kentucky as Franklin, Mercer and Powell counties, and they cite only one specimen from each county. Interestingly, *L. globosa* has been reported from Ohio (Jones 1940) and Kansas (Rydberg 1932), but apparently there are no specimens from either of these two states.

Lesquerella globosa currently is under review by the Fish and Wildlife Service for listing as threatened [Federal Register 45(242):82518, 15 December 1980]. The species is listed as endangered in Indiana (Bacone and Hedge 1980) and as threatened in Tennessee (Collins et al. 1978; Tenn. Dept. Conserv. 1982) and Kentucky (Branson et al. 1981). Although several extant populations in Kentucky are known, the continued existence of this species is precarious. Most of the sites are immediately adjacent to roads, which, if widened, could destroy them. According to Rollins (1952), *L. globosa* is the only species of *Laetevortibia* or *Lesquerella* in Kentucky that does not have weedy tendencies. However, in Kentucky, *L. globosa* has been found along gravelly roadsides and on recent roadcuts.

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DIOECY IN NORTH AMERICAN CACTACEAE: A REVIEW

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ABSTRACT

Of the six species of Cactaceae described as dioecious, only *Opuntia stempetala* Engelm., *O. grandis* Pfeiffer and *O. glaucusans* Salm-Dyck are dioecious. *Mammillaria davisii* K. Brandegee and *M. neopalmeri* Craig are gynodioecious or possibly trioecious, differing from one population to another. *Selenicereus innesii* Kimnach is gynodioecious or probably hermaphroditic with sterile, abortive flowers that appear pistillate. Inadequate data and careless word usages have obscured the true sexual condition of the latter three species.

The sexual condition of the Cactaceae is generally regarded as being hermaphroditic, or monoclinal (Core 1955; Porter 1959): that is, all plants bearing perfect flowers (Swartz 1971). That there are exceptions is indicated by the Britton and Rose (1937) description of the family: "Flowers usually perfect . . ." Likewise, Bravo-Hollis (1978) in her description of the order Cactales hints that exceptions exist: "Flores . . . casi siempre hermafroditas . . ." Benson (1969a, 1969b, 1969c, 1982), in his description of the family avoids the issue.

To pursue the statement of Britton and Rose (1937), one must scan their 1235 species descriptions, for no mention of imperfect flowers is made at the generic level. One finds that three Mexican species of *Opuntia*, series *Stenopetalae*, and one primarily Mexican species of *Mammillaria* (as *Neomammillaria*) are considered dioecious.

Recently a new species from St. Vincent Island, West Indies, *Selenicereus innesii* Kimnach, was described as "the only confirmed example of complete dioecy (sic) in the Cactaceae" (Kinnach 1982).

TERMINOLOGY

Before examining these claims of dioecy (= dioecism, cf. Bawa & Opler 1975) in the Cactaceae one must first establish an understanding of the terminology. The usual sexual condition in cacti is *hermaphroditic* or *monoclinal*. This means that all plants of a given taxon have perfect (bi-sexual) flowers (Usher 1966; Swartz 1971, Radford et al. 1974). In contrast to hermaphroditic is *monoecious*: plants with flowers not perfect, the

staminate and pistillate flowers on the same individual. *Dioecious* plants also have all flowers imperfect (unisexual) but with the staminate and pistillate flowers on separate individuals (Radford et al. 1974). *Gynodioecious* seems to be transitional between hermaphroditic and dioecious (Ross 1970) with some plants bearing perfect flowers and others pistillate ones. The uncommon term, *trioecious*, refers to a species with some plants staminate, some pistillate, and some perfect (Jackson 1928, p. 392; Usher 1966; Swartz 1971; Radford et al. 1974, p. 144):

Although some authors describe individual flowers (rather than whole plants) as dioecious (Britton & Rose 1937; Kimnach 1982) or monoecious (Standley 1920–1926), in modern usage these words correctly may be used only to describe the arrangement of reproductive parts on whole plants (Lawrence 1951). Hence one may call a single flower staminate, pistillate or perfect, but before one may use the words defined in the preceding paragraph, one must know the sexual condition of other individual plants of the species (Lawrence 1951).

DISCUSSION

The pistillate flowers of *Selenicereus innesii* are described as lacking stamens and staminal nectaries, and as often having a reduced number of ovules (Kinnach 1982). The stamen-bearing flowers have nectaries, more numerous ovules, and a "style ca 4–5 cm long, ca 1 mm thick, the apical portion magenta, white below, the stigma lobes 7–8, lobate, obtuse, slightly expanding, 1–1.5 mm long and to 1 mm wide near apex." (Kinnach 1982). Kinnach refers to these as "perfect flowers."

It is clear from the description and illustrations (Kinnach 1982) that *S. innesii* is gynodioecious with pistillate and perfect flowers but no staminate ones. Therefore, this cannot be considered a species with "complete dioecy."

Of interest is the description of the ovule chamber in the flowers of the pistillate plant: "much of the cavity being occupied by one or more rudimentary styles terminating in stigmatic papillae." This, combined with the fact that the fruits and seeds are unknown, suggests that the structurally pistillate flowers may actually be malformed to the point of being totally sterile. If this proves to be the case and only the perfect flowers are functional, the species is neither dioecious nor gynodioecious but functionally hermaphroditic.

Mammillaria dioica K. Brandege is one of the four species considered by Britton and Rose (1937) as dioecious. However, they say it is "incompletely dioecious." When the species was originally described,

Brandegee (1897) stated that "Both the type and the variety (*insularis*) are nearly dioecious, many plants male, with imperfect, less-divided style-branches, which rarely bear fruit, and the few which occasionally appear (are) very slender and few-seeded; many female, with entirely abortive anthers and very small flowers, which usually produce a row of thick oval or clavate, coral berries; others hermaphrodite or imperfectly dioecious in all degrees." Lindsay (1967) commented that the *M. dioica* segregate, *M. engelensis* Craig, also has "occasional pseudo-dioecious flowers." Of *M. dioica*, Benson (1969b) states "plant with a strong tendency to be dioecious, i.e., for the flowers of some plants to have small, sterile anthers and large stigmas and those of other plants the opposite." In their discussion of *M. dioica*, Lindsay and Dawson (1952) state that dioecy represents "an exceptional rather than a usual character of the plant. The dioecious condition is not frequently observed, and moreover, is not confined to *M. dioica* but occurs occasionally in other species such as *M. neopalmeri*." Brandegee (1897) discussed *M. neopalmeri* (as *M. dioica* var. *insularis* K. Brandegee) with *M. dioica*, stating that flower parts are the same in both taxa (see above quotation from Brandegee).

A population of *M. dioica* was examined by Ganders and Kennedy (1978). They found some plants with perfect flowers and others with pistillate flowers. Both set fruit with apparently normal seed. No "male" flowers were seen. The pistillate flowers bore "stamens with indehiscent anthers that contain no pollen" (Ganders & Kennedy 1978). In a microscopic examination of the flowers of *M. dioica* and its segregates, *M. estebanensis* Lindsay, and *M. multidigitata* Lindsay, Bemis et al. (1972) determined that the functionally pistillate, "male sterile," flowers have indehiscent anthers with malformed pollen. Ganders and Kennedy correctly state that a (functionally) gynodioecious condition is indicated. However, they point out that they (Ganders and Kennedy) studied only one inland population, and that coastal plants observed by Brandegee (1897) may have been misinterpreted or may actually have had a different sexual condition. If the plants are as described by Brandegee (1897) and as indicated by Lindsay and Dawson (1952), the term trioecious would most accurately describe *M. dioica* and *M. neopalmeri*.

The description of *Opuntia* series *Stenopetalae* (Britton & Rose 1937) states "This is an anomalous group in *Opuntia* since the flowers are dioecious and the petals are linear and more or less erect." *Opuntia stenopetala* Engelm. is described as having "male flowers with an abortive, pointed style, but female flowers with 8 or 9 yellow stigma lobes on style . . ." *Opuntia grandis* Pfeiffer and *O. glaucescens* Salm-Dyck, the other two species of the series, are not described in comparable detail; no further mention is

made of dioecy in *Opuntia* in Britton and Rose (1937).

Bravo-Hollis (1978) supports the observations of Britton and Rose (1937) in her description of the genus *Opuntia*: "Flores generalmente hermafroditas . . ." Her key separates subgenus *Stenopuntia* from subgenus *Opuntia* on the basis of plants "unisexual" versus hermaphroditic, respectively. The "unisexual" character is repeated in the descriptions of the subgenus *Stenopuntia*, of *Opuntia stenopetala* and of var. *stenopetala*. The latter description is the most detailed: "estilo abortado en las flores masculinas, en las femeninas es muy grueso en la parte media; lóbulos del estigma 8 a 9, amarillos . . ." A population of this variety from el Cardonal, Hidalgo, Mexico, is described thus: "En las flores masculinas el gineceo está parcialmente atrofiado y el estilo es claviforme, abajo rosa y arriba amarillento con los lóbulos del estigma atrofiados pues terminan en una punta aguda, rígida; el ovario también atrofiado" (Bravo-Hollis 1978). The pistillate flowers are not described. *Opuntia stenopetala* var. *inermis* Bravo has similar flowers and *O. glaucescens* is "generalmente dioica" (Bravo-Hollis 1978). Although Bravo-Hollis' description of *O. grandis* does not mention dioecy, the species is in the subgenus characterized as "unisexual."

I examined the flowers of *O. stenopetala* on herbarium specimens at ASU. Seven of the eight sheets from different localities had only staminate flowers, a disproportionate number resulting from collection for meiotic chromosome studies (Pinkava, pers. comm.). Present with the stamens was a pointed style which lacked a stigma (Fig. 1).¹ Ovules were apparently lacking in the reduced ovule chamber in the staminate flowers of all but one specimen. The eighth sheet had flowers with style, stigma, and stamens (Fig. 2), but when the mature stamens were examined at 400x magnification, they were found to be indehiscent and completely lacking pollen. Thus, as in *Mammillaria dioica*, the flowers of the specimen appear perfect but are functionally pistillate. Because this small sample supports the previously published descriptions of the species, *O. stenopetala* is to be considered functionally dioecious. *Opuntia grandis* and *O. glaucescens* were not available for me to study. However, we might cautiously assume that they are also dioecious because according to both Bravo-Hollis (1978) and Britton and Rose (1937) the three species constitute a series or subgenus characterized by unisexual flowers.

CONCLUSIONS

Only six species of Cactaceae have been described as dioecious. Of these only *Opuntia stenopetala* is almost certainly dioecious. *Opuntia grandis* and *O.*

¹For illustrated longitudinal sections of the flowers of *M. dioica* and *S. inermis*, see Ganders & Kennedy (1978) and Kinnach (1982), respectively.

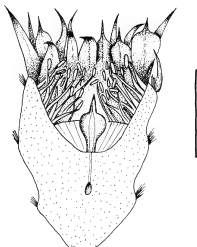


Figure 1. Staminate flower of *Opuntia stenopetala* in longitudinal section. Scale line equal to 1 cm.

glaucescens are probably dioecious also. *Mammillaria dioica* and *M. neopalmeri* are gynodioecious or possibly trioecious, apparently differing from one population to the next. *Selenicereus innesii* is gynodioecious or possibly hermaphroditic with sterile, abortive flowers that appear pistillate.

The sexual conditions of these cacti have been misunderstood for two reasons. First, inadequate data for the populations make it difficult to accurately assess the sexual condition of the species. Second, careless usage of the word dioecious has usually obscured the true sexual condition even where populations or species were studied adequately.

According to Brandegee (1897), other species, presumably of *Mammillaria*, are "completely unisexual." Doubtless there are species, in addition to those discussed here, in which the arrangements of reproductive parts need to be carefully observed and accurately reported.

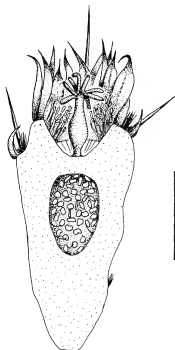


Figure 2. Functionally pistillate flower of *Opuntia stenopetala* in longitudinal section; the stamens produce no pollen. Scale line equal to 1 cm.

ACKNOWLEDGEMENTS

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AMPHIBROMUS SCABRIVALVIS (GRAMINEAE) IN LOUISIANA

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The South American grass *Amphibromus scabrivalvis* (Trin.) Swallen was reported in 1967 (Flinchum & Baker 1967) as an introduced weed in Louisiana strawberry fields (Tangipahoa Parish). Since then, the name of the species has appeared in some pertinent floristic accounts (Allen 1980; Kartesz & Kartesz 1980; Thieret 1972) but not in others that should have included it (Gould & Shaw 1983; Shetler & Skog 1978; Soil Conservation Service 1982). The purpose of our paper is to call attention to the continued occurrence of this grass in the United States and to present descriptive data on the species.

AMPHIBROMUS IN LOUISIANA

The date of arrival and the method of introduction of *A. scabrivalvis* into Louisiana are uncertain, although the species is said to have been discovered in Tangipahoa Parish "in the late 1950's" (Flinchum & Baker 1967). One strawberry grower told us that he first noted *Amphibromus* the year after he had set out strawberry plants imported from Argentina. Whatever the source, the new weed was obviously "established and actively growing," increasing "the cost of production [of strawberries] . . . because of the extra labor and time needed to control it" (Flinchum 1966). In 1984, about a quarter of a century later, attempts are still being made to eliminate the grass, which apparently has not spread far from the original point of introduction.

In Louisiana, *A. scabrivalvis* is well adapted to the cultural practices used in the production of strawberries, which are grown there as annuals and are generally mulched with black plastic. When the soil is prepared in fall (late October or early November) to receive the strawberry transplants, the grass makes its appearance. The infestation may be from perennating buds left in the soil or from caryopses produced during the preceding season. The plant is more or less dormant during winter, but vigorous growth and tillering are resumed as soon as spring weather becomes favorable. Terminal panicles appear in April-June. Maturation of *Amphibromus* caryopses occurs just before the strawberry season is completed. After harvest, a non-selective,

top-kill herbicide (e.g., Paraquat) is sprayed over the fields to eliminate strawberry plants and weeds (the grass, if not sprayed, may continue vegetative growth during the summer). A second crop (e.g., of peppers) is then set into the soil through existing holes in the plastic mulch.

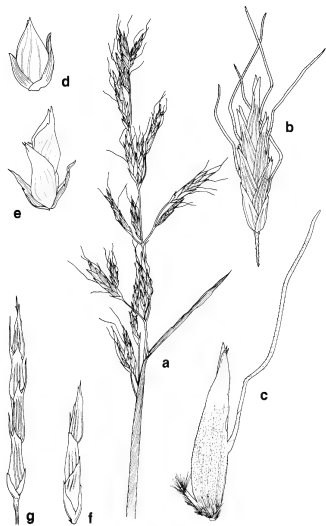
CLEISTOGAMY

According to Campbell et al. (1983), cleistogamy has been reported in 83 genera of grasses—about 19% of the total number of genera in the family. *Amphibromus* is one of these (Burkart 1969; Nicora 1978; Rosengurtt & Arrillaga de Maffei 1961; Rosengurtt et al. 1970; Stopp 1958; Torres 1970). In *A. scabrivalvis*, cleistogamous spikelets (Fig. 1d, e, f, g) are produced within the leaf sheaths at all nodes of the stem (the number of nodes may be as many as 10). Up to three or four of these nodes may, as often as not, be underground. The spikelets ("cleistogenes"; see Chase 1918) at the lowermost one or two nodes (Fig. 1d, e) are strikingly different from those of the terminal panicle (Fig. 1a, b, c), so different, indeed, that if their source were not known they would hardly be considered to belong to *A. scabrivalvis* at all. Floret number is one to three (spikelets of the terminal panicle produce three to nine); the apex of the lemma is but slightly notched, erose, or mucronulate (lemmas of terminal spikelets are deeply 2-lobed to or slightly below the middle and bear a long, dorsal awn); and the caryopses are 3–4.5 mm long and 1.5–2 mm wide (caryopses of terminal spikelets are 2–3 mm long and 1.2–1.3 mm wide).

At successively higher nodes the cleistogamous spikelets (Fig. 1f, g) become progressively more like those of the terminal panicle: floret number increases, lemma lobing is initiated and becomes deeper, awns appear and grow longer (although not more than about half the length of the awns of terminal spikelets), and caryopsis size decreases.

That *A. scabrivalvis* commonly produces its most reduced cleistogamous spikelets underground is a phenomenon matched, we believe, by few other grasses. Indeed, Campbell et al. (1983) listed only four genera—*Amphicarpum*, *Cbloris*, *Eremitis*, and *Paspalum*—that have subterranean spikelets. The spikelets in these are "borne on specialized rhizomes" rather than at the base of the culms as in *A. scabrivalvis*. Such burial, resulting in the complete loss of dispersal from the parent plant, would seem to be an

Figure 1. *Amphibromus scabrivalvis*. a, panicle; b, chasmogamous spikelet from panicle; c, floret from chasmogamous spikelet; d, e, cleistogamous spikelets from lowest leaf sheath (underground); f, g, cleistogamous spikelets from 5th and 6th leaf sheaths. The vertical lines = 5 mm.



example of atelochory, "the limitation of dispersal to the already occupied, obviously suitable spot" (van der Pijl 1972). The advantage of such an arrangement to *Amphibromus* is obscure.

Campbell et al. (1983) distinguished four types of cleistogamy in grasses. *Amphibromus scabrivalvis* does not fit convincingly into any of these, combining, as it does, features of types I and II. These are described as follows: "Type I. Sheath fertilization. Inflorescences or spikelets remain within the leaf sheaths of the middle or uppermost part of the stem" and "Type II. Unlike Type I . . . Type II occurs only within the lowermost sheaths and is usually associated with major inflorescence and spikelet modifications, with fruit dimorphism, and sometimes with specialized dispersal mechanisms." Certainly the lowermost cleistogamous spikelets of *A. scabrivalvis* can easily be referred to Type II, but the presence of cleistogamous spikelets in sheaths *all along* the stem would appear to be a connecting link to Type I.

ENLARGED BASAL INTERNODES

The first, second, third, and sometimes the fourth internodes of *A. scabrivalvis* may become swollen (Fig. 2). These enlarged internodes are generally underground but can occasionally appear above the soil surface. They are hollow (as are the more distal, normal internodes) and have scattered vascular bundles. Similar structures can be seen in other grasses, e.g., *Arrhenatherum elatius* var. *bulbosum*, some species of *Melica*, and *Pbleum pratense*. Such structures have been described as "tuberous" or "bulblike," but we prefer to call them corms, which seems to be more in harmony with their morphology.

TAXONOMY

The genus *Amphibromus*, which belongs to the tribe Aveneae (Macfarlane & Watson 1982), was last studied in its entirety by Swallen (1931), who recognized five species—one of Australia, one of Tasmania, one of New Zealand, and two of South America. He ascribed *A. scabrivalvis* to "open grassland" in Peru, Bolivia, Uruguay, and Chile; the species also occurs in Argentina (Cabrera 1953) in "suelos inundables, zanjias, etc."

The Louisiana plants are *A. scabrivalvis* var. *scabrivalvis*, not var. *indigestus* Nicora (Nicora 1973).

The following description of *A. scabrivalvis*, based upon Louisiana specimens, largely follows the format drawn up by Brandenburg & Estes (pers. comm.) for the Poaceae in the *Vascular Flora of the Southeastern United States*.

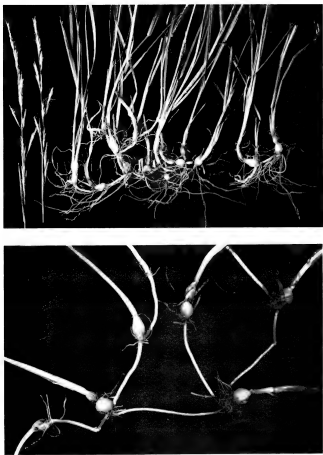


Figure 2. *Amphibromus scabrivalvis*. Plants (upper), X $\frac{1}{2}$, and rhizome (lower), X $\frac{1}{2}$, showing enlarged basal internodes (from Flinchum 1966).

Rhizomatous perennial. **CULMS** erect to decumbent, mostly unbranched, terete, 1.5–6.5 dm tall, glabrous or, just below the inflorescence, slightly scabrous, hollow at internodes, the lowest 1–3(4) internodes often swollen, the leaves mostly cauline. **SHEATHS** open or, at base, closed, terete, mostly longer than internodes, glabrous, the margins scarious, auricles none. **LIGULES** scarious, 5–16 mm tall, glabrous. **COLLARS** yellow, somewhat indurate, glabrous. **BLADES** bluish-green, rolled in bud, linear, 5–25(40) cm long, 3–5 mm wide (uppermost blades reduced to as little as 1 cm long and 1.5 mm wide), chartaceous, scabrous above, especially proximally, glabrous or slightly scabrous below, the midrib not or but slightly more prominent than other veins; apex acute; margins smooth to scabrous; blade anatomy pooid; horizontally elongated silica bodies present over veins abaxially.

Inflorescence a terminal panicle (intravaginal, cleistogamous spikelets also present; see below), often basally included in uppermost sheath, ovate to narrowly ovate, 7–27 cm long, the branches flexuous, ascending to horizontally spreading, 2–8 cm long, 1 per node (sometimes appearing as 2 or 3, with 1 of them bearing spikelets nearly to its base).

Spikelets laterally compressed, disarticulating above the glumes and between the florets, each floret falling attached to the adjacent rachilla internode; reduction distal.

Chasmogamous spikelets (those of the terminal panicle) narrowly ovate, 12–25 mm long (excluding awns), 2–2.5 mm wide, 3–9 floreted, pedicels lacking or up to 10 mm long, scabrous; rachilla sometimes exposed in intact spikelets, prolonged to 1 mm beyond uppermost floret, the internodes 2.5–3 mm long, upwardly pilose on abaxial side, the trichomes longest (ca 1 mm) at internode apices. **GLUMES** $\frac{1}{2}$ – $\frac{2}{3}$ as long as the lemmas above them, narrowly ovate, scarious (green only along nerves, if at all); first glume 4.7–6.5 mm long, 1–3 nerved, second glume 5–8 mm long, 3–5 nerved, nerves of both glumes scabrous, outermost 2 nerves much the shortest, sometimes obscure; internerves glabrous; apex acute, sometimes slightly notched or erose, nerveless; margins scabrous. **LEMMAS** awned, pale green to stramineous, ovate to narrowly ovate, 5–11 mm long, chartaceous, 7–9 nerved, the nerves and internerves scabrous, with a small tuft of trichomes to 1 mm long on each side of callus; apex deeply 2-lobed to or slightly below the middle, the lobes scarious and often erose or slightly notched distally; margins scabrous; awn arising at or just below middle of lemma (0.5–1 mm below base of cleft), 8–17 mm long, geniculate at or somewhat below the middle, more or less twisted below the bend, scabrous; callus glabrous proximally, white pilose distally, the trichomes to 1 mm long. **PALEAS** shorter than lemmas, bowed out basally,

4–6 mm long, chartaceous, 2 keeled, 2 nerved, the nerves scabrous, reaching the apex; apex scarious, often notched; margins scabrous to ciliate distally. **LODICULES** 2, scarious, 1–1.5 mm long, not vasculated. **STAMENS** 3, anthers 0.7–2 mm long, yellow. **CARYOPSES** narrowly ellipsoid to narrowly ovoid, yellow brown, 2–3 mm long, 1.2–1.3 mm wide, pubescent at apex, longitudinally and shallowly grooved, somewhat laterally compressed.

Cleistogamous spikelets (the most reduced ones, i.e., those in the lowermost sheath) ovate to broadly ovate, 6–10 mm long, 2.5–4.5 mm wide, 1–2(3) floreted, pedicels lacking; rachilla not exposed, prolonged to 2.5 mm beyond uppermost floret, the internodes 2.5 mm long, upwardly pilose on abaxial side, the trichomes longest (ca 0.5 mm) at internode apices. **GLUMES** $\frac{1}{2}$ – $\frac{3}{4}$ as long as the lemmas above them, nearly setaceous to narrowly ovate, scarious; first glume 4–4.5 mm long, 1 nerved, second glume 4.7–5.5 mm long, 3 nerved, nerves of both glumes scabrous, sometimes obscure; internerves glabrous; apex acute, sometimes notched or erose, nerveless; margins scabrous, sometimes denticulate. **LEMMAS** awnless or mucronulate, stramineous, ovate to broadly ovate, 6–8.5 mm long, chartaceous, 7–13 nerved, the nerves scabrous to nearly smooth, obscure to obvious, the internerves scabrous or hispidulous, with a small tuft of trichomes to 0.5 mm long on each side of callus; apex erose, slightly notched, or mucronulate; margins scabrous distally; callus glabrous proximally, white pilose distally, the trichomes to 0.5 mm long. **PALEAS** shorter than lemmas, bowed out basally, 5–6 mm long, chartaceous centrally, with a wide scarious margin and apex, 2 keeled, 2 nerved, the nerves scabrous, reaching the apex; apex often notched; margins scabrous to ciliate distally. **LODICULES** scarious, 1 mm long, not vasculated. **STAMENS** at least 1, anthers 0.7 mm long, yellow. **CARYOPSES** ellipsoid, yellow brown, 3–4.5 mm long, 1.5–2 mm wide, pubescent at apex, longitudinally and shallowly grooved, somewhat laterally compressed.

Specimens examined: LOUISIANA, Tangipahoa Parish: strawberry fields 2–2.5 mi N of Independence, 18 May 1960, C. A. Brown *s.n.* (US); 8 May 1967, E. R. Watson 562 (LSU); 24 Apr 1971, J. W. Thieret 32968 (DUKE – 2 sheets, LAE, LSU, NCU – 2 sheets, SMU, VDB – 2 sheets); 9 May 1984, M. L. Calaway 84-6 (GH, KNK, NCU, NY, US).

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OBSERVATIONS ON THE DISTRIBUTION AND
ECOLOGY OF *SIDA*
HERMAPHRODITA (L.) RUSBY (MALVACEAE)

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ABSTRACT

Sida hermaphrodita (L.) Rusby (Malvaceae) is a perennial herb of riverine habitats in the northeastern and midwestern United States that presently is under consideration for listing as a federally endangered or threatened species. Although the species is rare in most sections of its range, it is locally common in a limited area along the Kanawha and Ohio rivers in West Virginia and Ohio. In contrast to previous reports, evidence is presented that *Sida hermaphrodita* is indigenous to the Great Lakes drainage. Its distribution and abundance is not limited either by soil type or by low seed viability or germination potential. Gametophytic and sporophytic chromosome numbers are 14 and 28, respectively. Although *Sida hermaphrodita* is not immediately in danger of extinction, its habitat continues to be severely altered by man, and no populations of this species presently are protected from destruction.

INTRODUCTION

Sida hermaphrodita (L.) Rusby (Malvaceae) (Virginia mallow, River mallow) is a polycarpic perennial herb of open, moist, sunny to partly shaded riverine habitats. The species is the only member of *Pseudonapaea* A. Gray, a section without close affinity to any other section in the genus (Clement 1957; Fryxell 1985). The shoots emerge from the soil in April and early May from buds at the base of the previous year's stems and from the ends of numerous radiating rhizomes. Many large populations possibly

are clonal. Flowering begins in early August and continues until a hard frost occurs. Seeds are dispersed throughout the winter, and they germinate in early spring. It is not known how old the plants are when they first flower in their natural habitat, but well-watered plants grown in a transplant garden can reproduce the same year the seeds germinate.

Although geographically widespread (Fig. 1), *Sida hermaphrodita* is rare in most parts of its total range. Thomas (1979) studied populations of this species in the Potomac and Susquehanna drainages. He documented that the species had been extirpated from two-thirds of the sites where it had occurred one hundred years prior to his study. On the basis of these results, Thomas recommended that *S. hermaphrodita* be considered for federal listing as an endangered or threatened species. Thomas (1980) also suggested that the species was declining because of occasional flooding of its habitat, natural plant succession, soil compression in (human) populated areas, and low seed germination.

Sida hermaphrodita recently has been assigned to Category 2 status of the U.S. Fish and Wildlife Service (Arnett 1983), indicating that it possibly should be federally listed but that substantial supporting evidence is lacking. The present study attempts to determine the geographical distribution of *S. hermaphrodita* and to ascertain if either soil type or low seed germination potential and/or viability is responsible for the rarity of the species.

A considerable amount of research on *Sida hermaphrodita* by Russian botanists previously has not been cited in the western literature. The species has been studied since 1930 in the southern Ukraine for its economic potential as a soil stabilizer, fodder crop, honey plant, and fiber plant for the pulp and paper industry (Medvedev 1940; Dmitrashko et al. 1971). Seed anatomy (Savchenko & Dmitrashko 1973) and seed germination (Dmitrashko 1970, 1972, 1973) have been studied in an attempt to increase germination percentage. These latter studies indicate that without pretreatment, 10 to 15% of freshly gathered seeds germinate. After 6 to 8 months of storage in a laboratory, germination percentage was 60%, but after 13 years storage it was less than 10%. Germination percentages have been increased to various degrees by different treatments, including scarification, soaking in hot water, sulfuric acid, and irradiation with cobalt-60. Spooner wrote Dmitrashko for further details of this research and requested seeds to compare germination results with those reported in this paper. However, Dmitrashko is now retired, and all research on *S. hermaphrodita* at his institution has been discontinued (in litt. 1982, V. Koval, Dean of Biol. Sci., Odessa State Univ.).

MATERIALS AND METHODS

Field work was planned using locational data from the following sources: specimens cited in Clement (1957), Iltis (1963), Cusick & Silberhorn (1977), Broome et al. (1979), Thomas (1979), Wiegman (1979), Cranfill & Medley (1981); herbarium specimens from the institutions cited in the acknowledgements; and from Ohio field survey records maintained in the data base of the Division of Natural Areas and Preserves, Ohio Department of Natural Resources, Columbus, Ohio.

Bulk soil samples from selected populations were analyzed in the Ohio Soil Characterization laboratory of the Agronomy Department, The Ohio State University. Samples were ground to pass a 2 mm sieve, and all analyses were performed on the <2.0 mm fraction. Analyses included pH, particle-size distribution (texture), and organic carbon. Values of pH were determined using a suspension 1:1 v/v soil/distilled water ratio. The pipette method of Kilmer and Alexander (1949), as modified according to Method 3A1 of the Soil Conservation Service (1972), was used to determine particle-size distribution. Percent organic carbon was determined by the combustion method of Allison et al. (1965) outlined in Method 6A2b of the Soil Conservation Service (1972).

Germination/viability tests were conducted during February 1984 on seeds of *S. hermaphrodita* collected from 10 natural populations in Adams (two populations), Scioto, Lawrence (two populations), Gallia, and Williams counties, Ohio and from Allegany (two populations) and Cecil counties, Maryland in late summer or autumn of 1982. Seeds were scarified (*i.e.*, a hole was cut through the seed coat) and then incubated on moist filter paper in temperature- and light-controlled incubators at alternating temperatures of 35° (day)/20°C (night) at a 14 hour daily photoperiod (20 μ E/m²/sec, 400–700nm, of cool white fluorescent light) for 15 days. Three replications of 50 seeds each were used for each population.

The meiotic chromosome count was obtained utilizing techniques outlined in Keil and Stuessy (1975). The mitotic count was made from root tips of freshly germinated seeds. Root tips were pretreated in 0.05 M colchicine for 6 hr at 25°C, fixed in a 3:1 v/v solution of absolute ethanol/glacial acetic acid, hydrolyzed in 0.1 N HCl for 15 min at 50°C, and then squashed in acetocarmine. Voucher specimens for the chromosome counts are deposited at OS and US.

RESULTS AND DISCUSSION

The historical geographical distribution of *Sida hermaphrodita* is shown in Fig. 1. This map is based on the sources cited above plus new records

obtained during this study. Significant early collections not included in the publications of Clement (1957), Iltis (1963), and Thomas (1979), as well as a representative selection of recent new collections, are listed in the appendix to this article.

The most extensive and vigorous populations of *Sida hermaphrodita* are located along the Kanawha River from Charleston, West Virginia to its confluence with the Ohio River at Point Pleasant, and then downstream along both sides of the Ohio River to the vicinity of Huntington, West Virginia. Numerous populations of *S. hermaphrodita* are scattered along this corridor. The majority of plants grow in sunny, moist, disturbed situations along roadsides and railroad rights-of-way. They occasionally grow in the cinders of railroad embankments. Other populations grow in partially-shaded areas at the edges of woods near streams and rivers. All of these sites are located on riverine terraces or floodplains.

Sida hermaphrodita is rare and local in all other sections of its range. In the Ohio River Valley widely scattered populations occur as far west as Clermont Co., Ohio and Campbell Co., Kentucky. In West Virginia, the species occurs sporadically along the Kanawha and New rivers from Charleston south to Summers County. Though not common, small but vigorous stands of *S. hermaphrodita* occur in these valleys.

Thomas (1979) has documented the historical distribution and continuing decline of *S. hermaphrodita* in the Potomac and Susquehanna drainages in Maryland, Pennsylvania, Virginia, and the District of Columbia. Recent field work by Cusick and Spooner has confirmed the rarity of the species in this area.

In Tennessee, the species has not been rediscovered since Gattinger's collections of 1883-1885. Iltis (1963) maps one of Gattinger's specimens as an adventive population, though he does not explain his reason for such an opinion. We consider *S. hermaphrodita* indigenous to that state. *Sida hermaphrodita* presently is presumed extirpated from Tennessee (in litt, P. Somers, Tennessee Heritage Program).

The presence of Virginia mallow in Virginia only recently has been substantiated by specimens (Harvill et al. 1981). Apparently it is very rare in that state. More field work is needed to determine the status of *S. hermaphrodita* in Virginia.

The occurrences of *Sida hermaphrodita* in Massachusetts, New Jersey, and New York are problematical. The few specimens from these states lack habitat data, and they may have been collected from adventive populations or cultivated plants. Whether or not the species is indigenous in these states is debatable.

Disjunct populations of *Sida hermaphrodita* are known from a limited

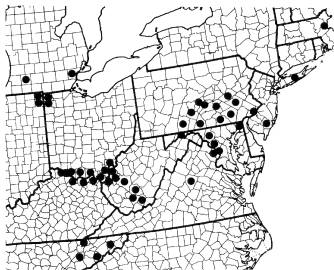


Figure 1. Historical geographical distribution of *Sida hermaphrodita*.

area of northwest Ohio, southcentral Michigan, and northeast Indiana. These are the only known localities of the species in the Great Lakes drainage. The species generally has been considered non-indigenous to this region (Deam 1940; Iltis 1963; Thomas 1979). However, in our opinion *S. hermaphrodita* is native in this part of its range.

Bradner (1892) reported *S. hermaphrodita* from Steuben Co., Indiana. Deam (1940), however, excluded the species from the Indiana flora, considering it a possible adventive from cultivation. In his catalog of the Steuben County flora, Bradner marks those species that are adventive or naturalized. *Sida hermaphrodita* is not so marked, and thus Bradner considered it indigenous. Unfortunately, there is no specimen to substantiate Bradner's report. The species recently was discovered by Cusick in adjacent Dekalb County growing on the bank of a small stream near its confluence with the St. Joseph River.

In northwest Ohio, two extensive populations of *S. hermaphrodita* are extant in Williams County. They occur on (apparently) undisturbed soils along a small tributary of the St. Joseph River. There also are two

nineteenth century collections from Defiance and Williams counties. No habitat data are included on the labels of these specimens, but the Williams County collection is from the drainage of the St. Joseph River.

Sida hermaphrodita was reported from along railroad tracks in Kalamazoo County, Michigan (Tuthill 1876). There are two Farwell specimens of this species collected in Wayne County in 1924 and 1931. One is from a railway right-of-way, and the other is labelled "low, moist ground." The species presently is not known to be extant in Michigan.

Ittis (1963) cites these reports of *S. hermaphrodita* from Michigan and Ohio, but he dismisses them as being based on escapes from old gardens. Ittis apparently was unaware of the Indiana records of this species. There are numerous occurrences of *S. hermaphrodita* along railroads in sections of the range where the species unquestionably is native. We feel that previous authors have been overly impressed by the disjunct distribution pattern of Virginia mallow. Unusual disjunctions in range are well documented for many vascular plants. Points in favor of an indigenous status for *S. hermaphrodita* in the Great Lakes drainage include the age of the records, their clustered geographical distribution, and the persistence of the species in the region. Today, *Sida hermaphrodita* is extremely rare in the Great Lakes drainage. Its riverine habitat in this region nearly has been annihilated by stream channelization and modern agricultural practices.

Soils have been implied to be a limiting factor in the distribution of *S. hermaphrodita* (Thomas 1979). However, our research suggests otherwise. Most stands of this species are found on disturbed and fill soils of roadsides and railroad rights-of-way. Other populations grow on naturally disturbed floodplain or terrace soils. Soil types from two such natural sites are Sloan (Williams Co., Ohio) and Wheeling (Adams Co., Ohio). Sloan soils are fine-loamy, mixed, mesic Fluvaquentic Haplaquolls and are distributed widely in Indiana, Michigan, New York, and Pennsylvania. Wheeling soils are fine-loamy, mixed, mesic Ultic Hapludalfs that are common in Indiana, Kentucky, Illinois, and Virginia (National Cooperative Soil Survey 1979). The combined acreage of these two soils is over 280,000 acres. Surface horizons from both "natural" and mechanically altered soils in which plants of *S. hermaphrodita* grow were analyzed (Table 1). These soils have a wide variety of textures (silt loam, sandy clay loam, and clay loam), the pH varies from 5.4 to 7.5, and organic matter content is medium to high. Thus, we conclude that physical-chemical properties of the soils are not a factor limiting the geographical distribution of *S. hermaphrodita*.

Thomas (1980) obtained very low germination percentages ($\bar{x} = 6.6\%$) of *Sida hermaphrodita* seeds collected from natural populations in Maryland,

Table 1. pH, texture and organic carbon content of soil collected from selected populations of *Sida hermaphrodita*.

LOCALITY	pH	ORGANIC				TEXTURE
		CARBON	% SAND	% SILT	% CLAY	
Williams Co., OH	7.4	3.78	43.2	37.3	19.5	loam
Adams Co., OH	6.3	4.48	41.6	42.6	15.8	loam
Scioto Co., OH	6.9	3.76	26.8	51.1	22.1	silt loam
Lawrence Co., OH	5.4	4.40	15.3	59.2	25.5	silt loam
Lawrence Co., OH	6.6	2.87	23.8	47.9	28.3	clay loam
Lawrence Co., OH	6.9	4.58	37.5	37.7	24.8	loam
Gallia Co., OH	5.8	2.98	27.7	49.5	22.8	loam
Gallia Co., OH	7.5	2.07	17.4	53.8	28.8	silty clay loam
Mason Co., WV	7.2	10.80	57.4	22.4	20.2	sandy clay loam
Putnam Co., WV	7.2	5.69	34.4	48.6	17.0	loam

Pennsylvania, and Virginia. However, he did not scarify the seeds. On the basis of these results, Thomas suggested that the low germination percentage of the seeds may be a factor contributing to the rarity of this species. However, in our germination tests, utilizing scarified seeds, 81 to 99% of the seeds collected from the 10 populations of *S. hermaphrodita* in Maryland and Ohio germinated. The average germination for all 10 populations was 92%. Hard seeds are common in a number of species in the Malvaceae (Rolston 1978), including *Sida spinosa* L. (Baskin & Baskin 1984). Egley and Paul (1981, 1982) have shown that water impermeability in *Sida spinosa* seeds is due, in part, to a compact layer of integumentary palisade cells. A similar layer of cells occurs in seeds of *Sida hermaphrodita* (Savchenko & Dmitrashko 1973). The low germination percentages obtained by Thomas (1980) apparently are due to his failure to scarify the seeds.

A large plant of *Sida hermaphrodita* can produce several thousand seeds, most of which are viable and potentially can germinate. And, in fact, many seeds of this species do germinate in the natural habitat. On 13 May 1984, J. Baskin observed several hundred seedlings (with cotyledons only or with cotyledons plus 1, 2, or 3 leaves) within ca 25 m² in each of two natural populations in Adams and Scioto counties, Ohio. Thus, the rarity of *S. hermaphrodita* is not due to low seed viability or to low germination potential.

Habitat destruction undoubtedly is the dominant limiting factor in the natural distribution of *Sida hermaphrodita*. Undisturbed riverine woodlands and stream terraces are of exceptional rarity. These were among the earliest

natural systems to be altered by man, since rivers were the avenues of transportation, and alluvial soils were fertile and easily cultivated. Many of the writers cited above considered populations of *S. hermaphrodita* non-indigenous because of their occurrence in disturbed situations. However, the natural habitat of Virginia mallow was among the earliest to be disturbed by humans. This study suggests that high seed germination potential and ability to grow in disturbed habitats have contributed to the survival of Virginia mallow.

Sida hermaphrodita is in little danger of extirpation nationally. Indeed, extensive and vigorous populations are not rare in the center of its geographic range. But the species is decidedly rare in the more isolated sections of its range, such as the Potomac and Great Lakes drainages. Also, its natural habitat is under continual alteration by man. At present, there are no populations of *Sida hermaphrodita* protected from destruction in any part of its geographic range. There is a special need for preservation of the species in riverine habitats in the Great lakes drainage. We think it desirable that natural populations of Virginia mallow be preserved from further destruction in all parts of its range.

The first chromosome count of *Sida hermaphrodita* ($2n = 28$) was reported by Spooner & Hall (1983) from a plant collected in Fairfax Co., VA, Spooner, Thomas & Abercrombie 2166 (OS). A meiotic count ($n = 14$) has been obtained from a plant collected in Mason Co., WV, Spooner 2161 (OS). Irtis and Kawano (1964) demonstrated that Skovsted's (1935) report of $2n = 28$ for *Napaea dioica* L. was probably based on a misidentified plant of *S. hermaphrodita*. However, Skovsted made no voucher. Base numbers of $n = 7$ and 8 are common in *Sida* and have proved useful in assessing relationships in this large genus (Bates & Blanchard 1970; Bates 1976; Fryxell 1985).

CONCLUSIONS

Sida hermaphrodita is a widely distributed species that is common only in a small part of its total range, namely portions of the Kanawha and Ohio River valleys. Elsewhere, it is rare and local. Populations grow in both mechanically and naturally disturbed soils in a variety of riverine habitats. Its distribution is limited neither by rarity of soil type nor by low seed germination potential. The species appears to be in no immediate danger of extirpation at the national level, and thus it should be withdrawn from consideration for federal listing as endangered or threatened. However, only a few populations are known from natural riverine habitats, and no stands of *S. hermaphrodita* are protected from future destruction.

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APPENDIX

Selected additional records for *Sida hermaphrodita* obtained during this study or not mentioned in earlier publications (see text). Locality data have been condensed; full information is available from the authors. AWC = Allison W. Cusick; DMS = David M. Spooner.

DISTRICT OF COLUMBIA: 18th St near river, 16 Jun 1887, *E. Borges s.n.* (MARY).

INDIANA: DEKALB CO.: Nancy Davis Ditch, Sect 13, Concord Twp, 6 Aug 1984, AWC 23766 (E MICH, NY, OS, US). STEUBEN CO.: see Bradner (1892).

KENTUCKY: CAMPBELL CO.: bank of Ohio River, 1 mi S of Oncoota, 31 Jul 1984, AWC 23752 (E NCU, VDB). GREENUP CO.: bank of Ohio River, US Rt 23, 2 1/2 mi S of Siloam, 13 Aug 1984, AWC & DMS 23821, (MICH, NY, OS, NCU, US). MASON CO.: gravel pit area along Ohio River E of Maysville, 5 Aug 1978, *J. Thieret 50628* (EKY, MUHW).

MARYLAND: ALLEGANY CO.: N side of Potomac River E of Lake, 13 Aug 1982, *DMS. Thomas & Abernethie 2167* (OS). CECIL CO.: RR right-of-way, Conowingo Lake (Susquehanna River) just S of PA state line, 5 Oct 1979, *Hill & Broome 8853* (MARY); Susquehanna River, 0.15 mi S of PA state line, *DMS 2164*, 12 Aug 1982 (OS). FREDERICK CO.: Licksville, 17 Aug 1950, *G. M. Freeman s.n.* (NA).

OHIO: ADAMS CO.: bank of Ohio River upstream from Stout, *DMS. A. Spooner, C. Baskin, & J. Baskin 2360*, 1 Oct 1983 (OS, US). CLERMONT CO.: Ohio River floodplain, US Rt 52 at Pond Run Rd, 3 Oct 1978, *AWC 18919* (OS). GALIA CO.: mouth of Big Creek, Sect 8, Guyan Twp, 13 Oct 1979, *DMS 215* (OS); floodplain of Ohio River, SW of Chickamauga Creek, Gallipolis, *DMS 2158*, 11 Aug 1982 (MICH, NY, OS, US). LAWRENCE CO.: Ohio River bank, S of Proctorville, 17 Sep 1979, *DMS 189* (MU); Sect 17, Rome Twp, *DMS 2159*, 11 Aug 1982 (NY, OS, US). MEigs CO.: weedy thickets along Ohio River 0.5 mi S of Middleport, 15 Jul 1974, *AWC 13509* (KE). SCOTTS CO.: Moores Lane, Washington Twp, 25 Sep 1981, *DMS & M. Silagy 1026* (OS). WILLIAMS CO.: Sect. 31, Superior Twp., 18 Aug 1981, *AWC 21116* (OS); Sect 5 & 6, Center Twp, 18 Aug 1981, *AWC 21117* (OS).

PENNSYLVANIA: BERKS CO.: Oley Furnace, Oley Twp, 27 July 1969, *W. C. Brumbach 6880* (BH). MIFFLIN CO.: ca 4 mi E of Lewistown, 12 Aug 1921, *E. M. Gress s.n.* (OKL).

VIRGINIA: ALBEMARLE CO.: James River at Warren Ferry, 25 Jun 1977, *C. Stevens s.n.* (herbarium of C. E. Stevens). FAIRFAX CO.: bank of Potomac River N of Dead Run, *T. Bradley 6926*, 16 Sep 1974 (GMUF); same location, 12 Aug 1982, *DMS, Thomas & Abercrombie 2166* (OS, US) (chromosome voucher).

WEST VIRGINIA: CABELL CO.: along Hwy 2, 7 mi E of Lesage, 30 Sep 1975, *D. Ervyns 1189* (MUHW); floodwall of Ohio River near Guyandotte, 11 Aug 1982, *DMS 2160* (NY, OS). FAYETTE CO.: New River, 2.5 mi below McCreery, 11 Aug 1941, *J. Tosh 1158* (WVA). KANAWHA CO.: Rush Creek, Kanawha State Forest, 15 Aug 1966, *M. Dennis s.n.* (WVA); N side of Kanawha River at Rt I-64 bridge, Charleston, 15 Aug 1984, *DMS & AWC 2383* (E MICH, OS, NCU, WVA, US). MASON CO.: St Rt 2, N of Gallipolis Ferry, 17 Aug 1970, *AWC 11246* (OS); just N of Cabell Co. line on St Rt 2, 11 Aug 1982, *DMS 2161* (OS, US) (chromosome voucher); along RR, St Rt 62, 2 mi SE of jct of St Rt 2, 11 Aug 1984, *DMS & AWC 2368* (MICH, OS, NCU, WVA, US). PUTNAM CO.: roadside, jct of I-64 & US Rt 35, Southside, 26 Sep 1975, *D. Kirk 25* (WVA); RR embankments, 1.25 mi S of Robertsburg, 11 Aug 1984, *AWC & DMS 23793*. (E MICH, OS, NCU, WVA, US). RALEIGH CO.: W side of New River, ½ mi E of Terry P.O., 12 Aug 1984, *AWC & DMS 23809* (MICH, OS, NCU, WVA, US); W side of New River at Sandstone Falls N of Hinton, 12 Aug 1984, *DMS & AWC 2381* (E MICH, OS, NCU, WVA, US). SUMMERS CO.: New River, Hinton, 13 Aug 1963, *E. McNeil s.n.* (WVA).

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ADDITIONS AND NOTEWORTHY VASCULAR PLANTS FROM ARKANSAS, WITH SOME ECOLOGICAL NOTES

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ABSTRACT

Six vascular plant taxa are reported as new to the Arkansas flora (*Cirsium muticum*, *Liparis loeselii*, *Pedicularis lanceolata*, *Rhynchospora capillacea*, *Solidago patula* var. *strictula*, *Solidago riddellii*) and two noteworthy collections (*Buchnera floridana*, *Scleria verticillata*) are presented with brief ecological notes.

This paper presents eight new or otherwise noteworthy records of vascular plants collected during 1984 field studies. These collections provide evidence that much remains to be learned about the Arkansas flora. Many counties have not been systematically searched by collectors and offer potential for significant discoveries. Nomenclature follows Kartesz & Kartesz (1980) except for *Buchnera floridana* and *Cypripedium kentuckiense*.

BUCHNERA FLORIDANA Gandog. (Scrophulariaceae). Ashley Co.: NW ¼ of section 1, T18S, R8W, Crossett North 7.5' Quad, Crossett Prairie, 2 Sep 1984, Orzell 1420 & L. Peacock (APCR, UARK, VDB). Abundant in a 10 acre remnant coastal plain prairie. Previously reported for Arkansas by Buchholz & Palmer (1926) and Demaree (1941, 1943) but considered unsubstantiated by Smith (1978). Similar to *Buchnera americana*, but distinguished by the obscurely 3-veined, lanceolate to oblanceolate leaves, shorter corolla tube (6–10 mm) and corolla lobes (2–5 mm) (Godfrey & Wooten 1981, Radford et al. 1968, Pennell 1935, Correll & Johnston 1970). Vouchers were verified by Dr. Robert Kral at Vanderbilt University.

CIRSIIUM MUTICUM Michx. (Asteraceae). Garland Co.: SW ¼, SW ¼, NW ¼ of section 16, T3S, R22W, Percy 7.5' Quad, along Meyers Creek, Ouachita National Forest, 5 Sep 1984, Orzell 1424 (UARK), 20 Sep 1984, Orzell 1427, G. Tucker & L. Peacock (MO). Rare, in a wooded acid seep on

saturated muck underlain by gravelly substrate, shaded by *Acer rubrum* L., *Carpinus caroliniana* Walt., and *Magnolia tripetala* L. Associates were *Cypripedium kentuckiense* C. E. Reed, *Juncus coriaceous* Mackenzie, *Liparis loeselii* (L.) L. C. Rich., *Onoclea sensibilis* L., *Pedicularis canadensis* L., *Rudbeckia fulgida* Ait. var. *umbrosa* (C. L. Boynt. & Beadle) Cronq., *Senecio aureus* L., *Smilax bona-nox* L., and *Thelypteris palustris* Schott.

Although *Cirsium muticum* is rather wide ranging (Cronquist 1980, Correll & Correll 1975, Godfrey & Wooten 1981) it is local and sporadic in the southern extension of its range, particularly in Louisiana, Texas, Oklahoma, Missouri and Tennessee. The Arkansas record is the first from the state and from the Ouachita Province (Fenneman 1938) for this northern plant. Nearest collections are isolated occurrences in east Texas, where it is very rare (Correll & Correll 1975), a single collection from southeastern Oklahoma (Taylor & Taylor 1978), scattered records in southeastern Missouri (Steyermark 1963, Orzell 1984), reported from Louisiana (R. Dale Thomas, pers. comm.), and recent collections by E. Bridges in the Western Highland Rim of west-central Tennessee. The infrequent occurrence of *C. muticum* in the southern extent of the range seems to be correlated to its fidelity to rather undisturbed seepage wetlands.

LIPARIS LOESELII (L.) L. C. Rich. (Orchidaceae). Garland Co.: SW $\frac{1}{4}$, SW $\frac{1}{4}$, NW $\frac{1}{4}$ of section 16, T3S, R22W, Percy 7.5' Quad, along Meyers Creek, Ouachita National Forest, 26 Jul 1984, Orzell 1391 (NYS, VDB), 20 Sep 1984, Orzell 1428, G. Tucker & L. Peacock (MO, UARK). Scattered in wooded acid seeps usually covered with the moss, *Thuidium delicatulum* (Hedw.) B.S.G. over a seepy gravel substrate. Associates include *Acer rubrum* L., *Athyrium filix-femina* (L.) Roth var. *asplenioides* (Michx.) Farw., *Carex bromoides* Willd., *Cirsium muticum* Michx., *Euonymus americanus* L., *Lindera benzoin* (L.) Blume, *Magnolia tripetala* L., *Platanthera clavellata* (Michx.) Luer, *Ranunculus recurvatus* Poir., and *Senecio aureus* L.

This is the first record of *Liparis loeselii* from Arkansas, disjunct approximately 200 miles from populations isolated in the Ozark Plateaus of southeastern Missouri (Orzell 1983, 1984). The Garland County station in the Ouachita Province of Arkansas represents a significantly disjunct population for this northeastern species, and is the southernmost known occurrence of *L. loeselii*. Specimens were verified by Dr. Charles Sheviak at the New York State Museum.

PEDICULARIS LANCEOLATA Michx. (Scrophulariaceae). Fulton Co.: NW $\frac{1}{4}$, SE $\frac{1}{4}$, NE $\frac{1}{4}$ of section 7, T20N, R8W, Salem 15' Quad, 13 July 1984, Orzell 1373 (APCR), 2 Oct 1984, Orzell 1437 (APCR, MO, UARK, VDB). Occasional on quaking sphagnum peat, saturated by cold minerotrophic seepage with *Carex lurida* Wahlenb., *Dichanthelium*

scoparium (Lam.) Gould, *Eupatorium perfoliatum* L., *Linum striatum* Walt., *Oxypolis rigidior* (L.) Raf., *Parnassia grandifolia* DC., *Rhynchospora capitellata* (Michx.) Vahl, *Rudbeckia fulgida* Ait. var. *umbrosa* (C. L. Boynt. & Beadle) Cronq., and *Senecio aureus* L.

Pedicularis lanceolata is primarily a northeastern calcicole with isolated localities in the Ozark Plateaus of southeastern Missouri. The Fulton County collection is the first in Arkansas and a range extension into the state from adjacent southeastern Missouri.

RHYNCHOSPORA CAPILLACEA Torr. (Cyperaceae). Baxter Co.: Sections 13, 14, & 15, T18N, R12W, Norfolk Dam South 7.5' Quad, along streamside of Otter Creek, 10 Jul 1984, Orzell 1353 (APCR, MO, UARK, VDB). Seepage margins of streamside along calcareous seep-fed streams, with *Calamintha arkansana* (Nutt.) Shinnars, *Helenium* sp., *Lysimachia quadriflora* Sims, and *Rudbeckia fulgida* Ait. var. *umbrosa* (C. L. Boynt. & Beadle) Cronq., and on damp weathered dolomite bedrock with *Equisetum byemale* L., *Juncus* spp. and *Vernonia* sp. The senior author also has observed *Rhynchospora capillacea* in Arkansas from streamside seep-fens on the Salem Plateau in Sharp, Stone, and Marion counties, and from a sedge-shrub fen in Marion County.

Rhynchospora capillacea is an obligate calcicole in the Ozark Plateaus of southeastern Missouri where it occurs in calcareous seep fens and on moist calcareous (dolomite) outcrops. The Arkansas collections represent the first in the state and extension of the known range southward from Missouri. Vouchers were verified by Dr. Robert Kral at Vanderbilt University.

SCLERIA VERTICILLATA Muhl. ex Willd. (Cyperaceae). Sharp Co.: Section 7, T18N, R4-5W, Sirka 7.5' Quad, along Rock Creek, Harold Alexander Wildlife Management Area, 23 Oct 1984, Orzell 1557 & E. Bridges (APCR, MO, UARK). Dolomite bedrock along streamside seep fens with other calcicoles, such as *Lysimachia quadriflora* Sims, *Parnassia grandifolia* DC., *Pycnanthemum virginianum* (L.) Durand & Jackson, *Rhynchospora capillacea* Torr., and *Solidago riddellii* Frank.

In the midwest, where its distribution is local and sporadic, *Scleria verticillata* requires a constant supply of cold, calcareous, minerotrophic water and a mildly disturbed substrate (Smith 1983). Both ecological requirements are met along Rock Creek, which is permanently fed by cold springs moderating the microclimate, and where scouring flash floods produce a suitable disturbed substrate.

Nearest records are from the Ozark Plateaus of southeastern Missouri (Steyermark 1963), where *Scleria verticillata* is a rare disjunct restricted to fens (Orzell 1984). There is a historical collection from northwestern Arkansas, Benton County, *Plank s.n.*, undated specimen at MO (Smith 1978, Fairey 1967).

Rediscovery of *Scleria verticillata* in Arkansas from a calcareous seep-fed stream is further evidence that such streams provide a refugium for disjunct taxa in the Ozark Plateaus.

SOLIDAGO PATULA Muhl. var. *STRICTULA* Torr. & Gray (Asteraceae). Union Co.: Corner of sections 17, 19, & 20, T16S, R14W, Calion 7.5' Quad, 2 Sep 1984, Orzell 1415, C. Amazon & L. Peacock (APCR, UARK). Uncommon in artificially open acid seepage slope under powerline with *Alnus serrulata* (Ait.) Willd., *Aster umbellatus* P. Mill., scattered *Myrica cerifera* L., *Panicum* sp., and *Xyris torta* Sm.

Solidago patula var. *strictula* is reported as occurring mostly on the coastal plain from Virginia to Florida and west to Texas (Cronquist 1980, Wilhelm 1984). Although widely distributed, the variety is considered infrequent in the Carolinas (Radford et al. 1968), and Louisiana (R. Dale Thomas, pers. comm.). It is rather frequent in southeastern Texas but has only been collected twice in southeastern Oklahoma (*Solidago salicina* Ell. in Taylor & Taylor 1978, 1984). The Union County collection is the first from Arkansas and a range extension from adjacent northern Louisiana parishes.

SOLIDAGO RIDDELLII Frank (Asteraceae). Sharp Co.: Section 7, T18N, R4-5W, Sitka 7.5' Quad, along Rock Creek, Harold Alexander Wildlife Management Area, 23 Oct 1984, Orzell 1555 & E. Bridges (APCR, MO, UARK, VDB). Abundant along a narrow streamside of Rock Creek, a calcareous spring-fed stream, and in calcareous seep fens surrounding springs. Associates include *Lysimachia quadriflora* Sims, *Parnassia grandifolia* DC., *Pycnanthemum virginianum* (L.) Durand & Jackson, *Rhynchospora capillacea* Torr., and *Scleria verticillata* Muhl. ex Willd.

Solidago riddellii is a rare disjunct, restricted to fens in the Ozark Plateaus of southeastern Missouri (Orzell 1984). Populations of *S. riddellii* in southeastern Missouri and the Sharp County location in northeastern Arkansas are several hundred miles disjunct from the main range in the north-central states from Ohio to Minnesota. The Arkansas station is the southernmost record.

SUMMARY

Buchnera floridana, although previously reported from Arkansas, had not been generally recognized as occurring in the state and is here documented from the Arkansas coastal plain. Three Arkansas state records (*Pedicularis lanceolata*, *Rhynchospora capillacea*, *Solidago riddellii*) with fidelity to fens are generally northern in distribution. All have a disjunct population center in the Ozark Plateaus of southeastern Missouri which is now known to extend into adjacent northeastern Arkansas. *Liparis loeselii*, with a northeastern

distribution, represents a significant disjunct new to Arkansas and to the Ouachita Province, by far the southernmost locality for this orchid. Three additional Arkansas state record plants (*Cirsium muticum*, *Scleria verticillata*, *Solidago patula* var. *strictula*) although wide ranging are restricted to seepage wetlands with local and sporadic distribution particularly in Arkansas and several surrounding states.

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THE VASCULAR FLORA OF CENTRAL FLORIDA: TAXONOMIC AND NOMENCLATRURAL CHANGES, ADDITIONAL TAXA¹

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ABSTRACT

Fifty-one taxa new to the vascular flora of central Florida, 30 of which are exotics, and 65 nomenclatrural or taxonomic changes are reported.

When a flora is published, it is only a statement of present knowledge and not a finite product; there are invariably changes, some even before the ink is dry. An excellent example is the report of over 30 additions by Anderson (1984) to the vascular flora of the Florida panhandle (Clewell, in press). The publication of a flora usually has a stimulatory effect resulting in the urge to discover taxa overlooked by the author(s) and to refine certain treatments. This is, or should be, one of the intentions of the author(s) of a flora. The recently published vascular flora of central Florida (Wunderlin 1982) has had this desired effect, and some of the results are presented here. We hope this paper will further stimulate others to bring forth their findings.

The following includes 51 taxa reported as new to the region. Of these, 30 are exotic species, the introduction of which carries strong implications concerning possibly detrimental changes in the native flora of Florida. Specimens examined or representative specimens and the herbaria in which they repose are cited. Also reported are 65 nomenclatrural or taxonomic changes deemed necessary because of recent taxonomic findings. The families are arranged according to the Englerian sequence.

PTERIDACEAE

PTERIS MULTIFIDA Poir. This Old World species is cultivated and occasionally naturalized. Citrus Co.: *Diddell s.n.* (FLAS); *E. St. John s.n.* (FLAS); *R. St. John s.n.* (FLAS).

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TRISMERIA TRIPOLIATA (L.) Diels. This tropical species native to south Florida is probably a chance introduction into Hernando County. Hernando Co.: *Mason s.n.* (FLAS). Palm Beach Co.: *Farnsworth s.n.* (FLAS).

BLECHNACEAE

STENOCHLAENA TENUIFOLIA Moore. A native of Asia and occasionally cultivated, this species was found as an escape at one site in central Florida in the 1930's where it still occurs. It was reported by Lakela and Long (1976) but overlooked by Wunderlin (1982). It was again found in 1984 at a second site. Hillsborough Co.: *E. St. John s.n.* (FLAS); *Wunderlin & Buchner 9824* (USF).

ASPIDACEAE

THELYPTERIS RETICULATA (L.) Proctor. This is the northernmost station for this tropical species in Florida. Lee Co.: *Craighead s.n.* (FTG).

ZANICHELLIACEAE

ZANICHELLIA PALLISTRIS L. The inclusion of this species adds the family Zanichelliaceae to the flora. Citrus Co.: *Hartman 51* (FLAS); *Swindale 1156* (FLAS).

CYMODOCEACEAE

SYRINGODIUM FILIFORME Kuetz. = *Cymodocea filiformis* (Kuetz.) Correll. Leaf form and inflorescence differences provide supporting evidence that *Syringodium* should be treated as distinct from *Cymodocea*. Our species is retained in the former genus by den Hartog (1970).

POACEAE

ERIOCHLOA MICHAUXII (Poir.) Hitchc. var. *simpsonii* Hitchc. This rare, distinctive variety is endemic to Collier and Lee counties. Lee Co.: *Brambach 5583* (USF); *Brambach 5788* (FLAS).

LEERSIA VIRGINICA Willd. This species is somewhat frequent in north Florida and so was expected in our area. Marion Co.: *Hall 1354* (FLAS). Osceola Co.: *Shaw & Poppleton 1522* (USF). Sumter Co.: *Wunderlin et al. 6590* (USF).

LEPTOCHLOA FILIFORMIS (Lam.) Beauv. This South American species occurs in our area as a weed in a sugar cane field. Palm Beach Co.: *Dosky s.n.* (FLAS).

LUZIOLOA FLUITANS (Michx.) Terrell & H. Robins. = *Hydrochloa carolinensis* Beauv. *Hydrochloa* is reduced to synonymy under the older name *Luziola*; the oldest valid epithet is *fluitans* of Michaux (Terrell & Robinson 1974).

PASPALUM NICORAE Parodi. This introduction from South America is found locally in pastures and along roadsides in our area. Hendry Co.: *Hall 618* (FLAS, USF). Orange Co.: *Gruis s.n.* (FLAS).

PHARUS LAPPULACELUS Aubl. Study by E. Judziewicz (pers. comm.) reveals that this is the correct name for the Florida material and must replace *P. parvifolius* Nash which has been misapplied.

Acceptance of *Piptochaetium* as a segregate of *Stipa* (M. Barkworth, pers. comm.), necessitates the following two changes.

PIPTOCHAETIUM AVENACEUM (L.) Parodi = *Stipa avenacea* L.

PIPTOCHAETIUM AVENACIODES (Nash) Valencias & Costas = *Stipa avenacioides* Nash.

ROTTBOELLIA EXALTATA L. f. An introduction from tropical Asia, this troublesome weedy grass is becoming increasingly frequent in Florida. Palm Beach Co.: *Johnson s.n.*

(FLAS). *Marrin Co.*: *Orenigo s.n.* (FLAS); *Breyer s.n.* (FLAS). *Hillsborough Co.*: *Wanderlin 9426* (USF).

SETARIA ITALICA (L.) Beauv. This native of Eurasia is cultivated and sparingly naturalized in Florida. *Sarasota Co.*: *Sbwey 2586* (USF).

CYPERACEAE

CAREX STIPATA Muhl. This common species of eastern North America is now known to extend into the northwestern part of central Florida. *Citrus Co.*: *Barlett s.n.* (USF).

Dichromena is not readily separated from *Rhynchospora* and is best treated as a section of the latter (Thomas 1984); the following two nomenclatural changes are necessary.

RHYNCHOSPORA COLORATA (L.) Pfeiffer = *Dichromena colorata* (L.) Hitchc.

RHYNCHOSPORA LATIFOLIA (Baldw.) Thomas = *Dichromena latifolia* Baldw.

RHYNCHOSPORA ELIOTTII A. Dietr. This northern species has been found well into central Florida. *Polk Co.*: *Wheeler s.n.* (FLAS).

RHYNCHOSPORA FLORIDENSIS (Britt. ex Small) Pfeiffer. Thomas (1984) cites the following specimen of this Caribbean and south Florida species. *Polk Co.*: *Jennings s.n.* (CM, n.v.).

ARECACEAE

LIVISTONA CHINENSIS R. Br. This Old World palm is commonly cultivated in Florida and sparingly naturalized. *Manatee Co.*: *Sbwey 2589* (USF).

BROMELIACEAE

DYCKIA BREVIFOLIA Bak. A native of Brazil, this species is occasionally cultivated in central Florida and is locally escaped. Two patches of plants and scattered seedlings were found in a dry disturbed area that was formerly sand pine scrub. *Pinellas Co.*: *Baker 2602A* (USF).

COMMELINACEAE

COMMELINA CAROLINIANA Walt. Although reported from Florida by Small (1933), Radford et al. (1968), and Ward (1968), its rareness and resemblance to *C. eriza* obscured its identity until study by R. Faden (pers. comm.) confirmed its presence in central Florida. *Lee Co.*: *Hoffman 12* (FLAS). *Manatee Co.*: *Genelle & Fleming 2207* (USF); *Garber s.n.* (US). *Palm Beach Co.*: *Felix s.n.* (FLAS, US).

COMMELINA NIGRITIANA Benth. var. *GAMBIAE* (C. B. Clark) Brenan. Robert Faden (pers. comm.) has determined that our plants are best referred to var. *gambiae*.

Plants from Highlands County previously assigned to *Tradescantia hirsutianalis* Small are best considered as variants of *T. roseolepis* (R. Faden, pers. comm.). *Tradescantia hirsutianalis* is found to the north of our area and is excluded from our flora.

AGAVACEAE

AGAVE DESMETTIANA Jacobi. Probably originally native to Mexico, this species is cultivated in Florida and rarely escaped. The collections listed are cited by Gentry (1982). *Lee Co.*: *Brumbach 7798* (FLAS), *Brumbach 8459* (FLAS).

AMARYLLIDACEAE

Reexamination of our naturalized *Croton* species reveals specimens previously identified as *C. anabile* Donn should be provisionally determined as follows, pending further studies of this difficult genus (A. Meerow, pers. comm.).

CRINUM ASIATICUM L. A native of tropical Asia and cultivated in Florida where locally escaped. Lee Co.: *King* 111 (USF); *Todd* 126 (FLAS, USF).

CRINUM LATIFOLIUM L. var. *ZEYLANICUM* (L.) Hook. f. ex Trimen. A native of Asia, this species has been found as an escape from cultivation along roadsides and in pastures. Hillsborough Co.: *Wunderlin et al.* 9494 (USF). Pasco Co.: *Hansen & Hansen* 9948 (USF). Sumter Co.: *Wunderlin et al.* 9813 (USF).

ZEPHYRANTHES TUBISPATHA Herb. Native to the West Indies, this species is occasionally cultivated in Florida and rarely encountered as an escape. Pinellas Co.: *Beckner* 2620 (USF).

ORCHIDACEAE

ANACHEILUM COCHLEATUM (L.) Hoffsgg. var. *TRIANDUM* (Ames) Saulela, Wunderlin & Hansen = *Emyclia cochleata* (L.) Dressler. *Ananthelepis*, a segregate of *Emyclia*, is considered a distinct genus following Pabst et al. (1981). The Florida plants are triandrous and should be recognized at the varietal level.

MESADENUS POLYANTHUS (Reichenb. f.) Schlechter = *Spiranthes polyantha* Reichenb. f. Garay (1982) recognizes *Mesadenus*, a segregate of *Spiranthes*.

SACOLA LANCEOLATA (Aubl.) Garay = *Stenorbynchus lanceolatus* (Aubl.) L. C. Rich ex Spreng. Garay (1982) recognizes *Sacola*, a segregate of *Spiranthes* and *Stenorbynchus*.

SACOLA LANCEOLATA (Aubl.) Garay var. *LUTEOLBA* (Reichenb. f.) Saulela, Wunderlin, & Hansen. Materials of this tropical American taxon were previously seen from collections only to the south of our area in Florida. DeSoto Co.: *Beckner* 2255 (FLAS). Okcechobee Co.: *Saulela & Saulela* 8646 (USF).

CASUARINACEAE

CASUARINA EQUISETIFOLIA L. = *C. litorea* L. *Casuarina litorea* was published in the dissertation of Linnaeus' student Strickman in 1754. The names published in this work are now specifically rendered invalid according to Article 34, ICBN (Voss 1983). Therefore, the more familiar combination *C. equisetifolia* L. (Amoen. Acad. 4:143. 1759) is reinstated. There is still controversy concerning the author citation for both the genus and species. Bullock (1960) considers Linnaeus' description of *Casuarina equisetifolia* inadequate. Rogers (1982) concurs with this view. However, Friis (1980) considers the description of Linnaeus sufficient for valid publication. If the arguments of Bullock are accepted, the correct citations are: *Casuarina* L. ex Adans. and *Casuarina equisetifolia* L. ex J. R. & G. Forst.

JUGLANDACEAE

CARYA ALBA (L.) Nutt. ex Ell. This common tree of eastern U.S. has been overlooked in the northern counties. Sumter Co.: *Ober* 66 (FLAS). Volusia Co.: *Britchard s.n.* (FLAS).

The mockernut hickory has long been known as *Carya tomentosa* (Poir.) Nutt., due to confusion in the protologue of *Juglans alba* L. However, the typification of the later by Crantz (Inst. Rei Herb. 1:157. 1766) and subsequent clarifications by Rehder (1945) and Howard and Staples (1983) reveal that *Carya alba* is the correct name for this taxon. The earliest valid transfer of the epithet into *Carya* was that of Elliot (Sketch. Bot. S. Carol. 2:624. 1824). Although the description accompanying Elliot's transfer of Linnaeus' *Juglans alba* clearly refers to the shagbark hickory (*Carya wuta* (Mill.) K. Koch), the transfer is valid according to article 55.2, ICBN (Voss 1983).

FAGACEAE

QUERCUS LYRATA Walt. This oak of bottomlands in the southeastern United

STATES extends into our area along the Suwannee River. Levy Co.: *Skeen* 945 (FLAS, USF).

URTICACEAE

URTICA URENS L. A native of Europe, this species is adventive in our area in vegetable fields. Orange Co.: *Riffe s.n.* (FLAS).

POLYGONACEAE

ANTENORON VIRGINIANUM (L.) Robery & Vautier = *Tovara virginiana* (L.) Raf. (Fl. Ludov. 28, 1817) must replace *Tovara* Adans. (Fam. Pl. 2:276, 1763) since the latter is rejected in favor of the conserved later homonym *Tovaria* Ruiz & Pavon (Prodr. 49, 1794) of the Tovariaceae (Graham & Wood 1965; Voss et al. 1983).

ERRIGONUM LONGIFOLIUM Nutt. var. *GNAPHALIFOLIUM* Gandg. = *Eriogonum floridanum* Small. This taxon is best treated as a variety of the widespread lower great plains species *E. longifolium* (Reveal 1968).

Reevaluation by Nesom & Bates (1984) provides evidence that the following two taxa are best treated at the specific level.

POLYGONELLA BASRAMIA (Small) Nesom & Bates = *Polygonella ciliata* Meisn. var. *basiramae* (Small) Horton.

POLYGONELLA ROBUSTA (Small) Nesom & Bates = *Polygonella fimbriata* var. *robusta* (Small) Horton.

CARYOPHYLLACEAE

STIPULICIDA SETACEA Michx. var. *LACERATA* James. A study of the variability of *Stipulicida* in Florida results in the recognition of two varieties (var. *setacea* and var. *lacerata*) for our area (Judd 1983).

CERATOPHYLLACEAE

CERATOPHYLLUM MURICATUM Cham. = *Ceratophyllum whinatum* A. Gray—Based on a study of the neotropical species of the genus, the correct name for this species is *C. muricatum* (Lowden 1978). Further study by Donald Les (pers. comm.) supports this interpretation.

BRASSICACEAE

CORONOPUS DIDYMUS (L.) J. E. Smith. A native of Europe, this widespread weed of North America has been collected in Florida to the north and south of our range and was to be expected. Palm Beach Co.: *Correll et al.* 51528 (USF).

ROSACEAE

Duchesnea indica (Andrz.) Focke. This native of Asia is widely naturalized in Europe and eastern North America; the following is the southernmost in Florida. Marion Co.: *Norwan & Buchner s.n.* (USF).

FABACEAE

ALYSICARPUS OVALIFOLIUS (Schum. & Thonn.) J. Léonard. This is the correct name for the common weedy plant in Florida and must replace *Alysicarpus vaginalis* (L.) DC. which has been misapplied. *Alysicarpus vaginalis* is restricted in Florida to the southernmost counties, outside our range.

CENTROSEMA ARENICOLUM (Small) Hermann = *C. floridanum* (Britt.) Lakela. Small's name (Fl. SE U.S. 651, 1903) predates Britton's (*Torreya* 4:142, 1904) by one year.

Adoption of Irwin and Barneby's (1982) treatment of the New World Cassiinae necessitates changes for the central Florida species previously placed in *Cassia*, now redistributed in *Chamaecrista* and *Senna*.

CHAMAECRISTA FASCICULATA (Michx.) Greene = *Cassia chamaecrista* L.

CHAMAECRISTA NICTITANS (L.) Moench = *Cassia nictitans* L.

CHAMAECRISTA NICTITANS (L.) Moench var. ASPERA (Muhl. ex Ell.) Irwin & Barneby = *Cassia nictitans* L. var. *aspera* (Muhl. ex Ell.) Greene.

CHAMAECRISTA PILOSA L.

CHAMAECRISTA ROTUNDIFOLIA (Pers.) Greene = *Cassia rotundifolia* Pers.

CHAMAECRISTA SERPENS (L.) Greene = *Cassia serpens* L.

SENNA ALATA (L.) Roxb. = *Cassia alata* L.

SENNA LIGUSTRINA (L.) Irwin & Barnaby = *Cassia ligustrina* L.

SENNA MARIANDICA (L.) Link = *Cassia marilandica* L.

SENNA OBTUSIFOLIA (L.) Irwin & Barneby = *Cassia obtusifolia* L.

SENNA OCCIDENTALIS (L.) Link = *Cassia occidentalis* L.

SENNA PENDULA (Willd.) Irwin & Barneby var. GLABRATA (Vog.) Irwin & Barneby = *Cassia olateoides* Coll.

CORONILLA VARIA L. A native of Eurasia, this ground cover is infrequently planted in Florida and rarely escapes. Lee Co.: *Brownback* 8449 (FLAS); *Brownback* 8623 (FLAS).

A revision of *Crotalaria* for Africa and Madagascar (Polhill 1983) necessitates the following two nomenclatural changes.

CROTALARIA PALLIDA Ait. = *C. mucronata* Desv.

CROTALARIA BREVIDENS Benth. var. INTERMEDIA (Kotschy) Polhill = *C. intermedia* Kotschy.

CROTALARIA ROTUNDIFOLIA (Walt.) Gmel. There is little justification for maintaining var. *vulgaris* Windler.

KUMMEROWIA STRATA (Thunb.) Schindler = *Lepulezia striata* (Thunb.) Hook. & Arn. The acceptance of the genus *Kummerowia* as a segregate of *Lepulezia* (Ohashi et al. 1981) necessitates this change.

RUTACEAE

CITRUS X PARADISI Macf. = *C. paradisi* (L.) Macf. Recent studies by Scora et al. (1982) support the proposal that this is a hybrid between the sweet orange, *C. sinensis* (L.) Osbeck, and the Pummelo, *C. maxima* (Burm.) Merr. (= *C. grandis* (L.) Osbeck, fide Scora).

EUPHORBIACEAE

JATROPHA GOSSYPIFOLIA L. This species of tropical America is infrequently cultivated in Florida and locally escaped. The Pinellas County collection was made along the edge of a mangrove stand, conditions similar to the usual habitat for the species in tropical America. Pinellas Co.: *Beckner* 2627 (USF).

SAPINDACEAE

SAPINDUS SAPONARIA L. *Sapindus marginata* Willd. is distinguished from *S. saponaria* only by its unwinged leaf rachis. We feel the Florida material is best treated as a single species, following Little (1979).

RHAMNACEAE

ZAZYPHUS CELATA Judd & Hall. This species, possibly extinct, is known from only two collections from Highlands County, the type collected in 1948 (Judd and Hall 1984) and

the following made in 1955. Highlands Co.: *Bruce* 25333 (Archbold Biological Station Herbarium).

VITACEAE

CISSUS VERTICILLATA (L.) Nicols. & Jarvis = *Cissus sicyoides* L. The deletion of Article 71, ICBN (Voss et al. 1983) rejecting names based on monstrosities necessitates this change (Nicolson and Jarvis 1984).

VITIS ROTUNDIFOLIA Michx. The northern scuppernong grape is now known to extend into the northwestern part of our area. Hernando Co.: *Backner* 2670 (USF).

MALVACEAE

HIBISCUS CANNABINUS L. Native to Africa, this species is occasionally planted and found as an escape. Okeechobee Co.: *Backner* 1970 (FLAS).

SIDA SANTAREMENSIS Monteiro. A native of Brazil, Argentina, and Bolivia, this species is adventive in our area. This was first reported for North America from central Florida by Fryxell et al. (1984). The following collections were made from a second site in addition to the one from Hillsborough County cited by Fryxell et al. Hillsborough Co.: *Wanderlin & Van Hoek* 9819; *Van Hoek s.n.* (USF); *Moffler* 236 (USF).

CISTACEAE

LECHEA PULCHELLA Raf. A species of the Atlantic coastal plain, this was previously known in Florida to the north of our area. Volusia Co.: *Hansen & Richardson* 6235 (USF).

BEGONIACEAE

BEGONIA CUCULLATA Willd. var. *HOOKERI* (A. DC.) L. B. Smith & Schub. = *Begonia semperflorens* Link & Otto. According to *Hortus Third* (Bailey Hortorium 1976), this is the correct name for this taxon.

CACTACEAE

CEREUS GRANDIFLORUS (L.) Mill. var. *ARMATUS* (K. Schum.) L. Bens. = *Cereus conflorens* Weingart. This is the correct name for this taxon according to Benson (1982).

MYRTACEAE

MELALEUCA LINARIIFOLIA Sm. this is the second species of this predominantly Australian genus to become naturalized in Florida. Its potential as a noxious weed tree like *M. quinque-nervia* is unknown. Osceola Co.: *Santela & Santela* 8006 (USF).

ERICACEAE

LYONIA LIGUSTRINA (L.) DC. var. *FULGOSIFLORA* (Michx.) Fern. Judd's (1981) monograph of the genus indicates that the material in central Florida should be placed in this variety rather than the typical.

RHODODENDRON CANESCENS (Michx.) Sweet. This is the southernmost station for this species in Florida. Marion Co.: *Judd* 3228 (FLAS, USF).

PRIMULACEAE

ANAGALLIS MINIMA (L.) Krause = *Centunculus minimus* L. The differences between *Centunculus* and *Anagallis* are not sufficient in our opinion to maintain the former as a distinct genus. We are following Godfrey and Wooten (1981) and Ferguson (1972).

SAPOTACEAE

BUMELIA SALICIFOLIA (L.) Sw. = *Diphysa salicifolia* (L.) A. Rich. *Diphysa* is best united with *Bumelia* as discussed by Stearn (1968).

OLEACEAE

LIGUSTRUM SINENSE LOUR. Native to China, this commonly cultivated shrub is occasionally found as persistent and less commonly as an escape. Hillsborough Co.: *Wanderlin* et al. 9514 (USF).

GENTIANACEAE

NYMPHOIDES CORDATA (EIL.) Fern. This species enters our area from north Florida. Lake Co.: *Easterday* 279 (FLAS).

APOCYNACEAE

TABERNAEMONTANA DIVARICATA (L.) R. Br. = *Ervatania coronaria* (L.) Stapf. According to Leeuwenberg (1976), there is little justification for the splitting of the pantropical *Tabernaemontana* into segregate genera.

ASCLEPIADACEAE

MATELEA CONOCARPA (Walt.) Shinn. Drapelik (1970) reports that *M. suberosa* (L.) Shinn. is misapplied to the North American plants.

CONVOLVULACEAE

IPOMOEA CORDATOTRILoba DENNST. = *Ipomoea trichocarpa* EIL. This is the correct name for this common Florida species (Manitz 1983). Although the epithet was originally hyphenated ("cordato-triloba") by Dennstedt (1810), according to Article 73.9, ICBN (Voss et al. 1983) the hyphen should be deleted.

IPOMOEA IMPERATI (Vahl) Griseb. = *I. stolonifera* (Cyrillo) J. Fl Gmel. La Valva and Sabato (1983) show that *I. imperati* is the correct name for this species.

IPOMOEA VIOLACEA L. = *I. mayanthera* Roem. & Schult. Manitz (1977) shows *I. violacea* is the correct name for this well known species. (See also Powell et al. 1978; Powell 1979).

POLEMONIACEAE

PHLOX PILOSA L. A highly variable species for which subsp. *detonsa* (A. Gray) Wherry can not be maintained.

VERBENACEAE

GLANDULARIA CANADENSIS (L.) Nutt. Common north of here, this species is adventive in our area. Citrus Co.: *Arnold* et al. s.n. (FLAS); *Balzell* 4713 (FLAS); *Schmidt* A-165 (USF); *Wanderlin* 9403 (USF). Highlands Co.: *Brass* 15267. Seminole Co.: *Schallert* s.n. (FLAS).

The acceptance of *Phyla* as distinct from *Lippia* necessitates the following two changes.

PHYLA NODIFLORA (L.) Greene = *Lippia nodiflora* (L.) Michx.

PHYLA STOBCHADIFOLIA (L.) HBK. = *Lippia stobchadifolia* (L.) Small.

LAMIACEAE

LEONURUS SIBIRICUS L. This native of central Asia, introduced into North America for its medicinal properties, is occasional in north Florida and was to be expected in our range. Hillsborough Co.: *Lindsey & Arcuri* s.n. (USF).

MENTHA SPICATA L. Known from only two sites in central Florida and from sterile material, these collections are provisionally placed. Native to Europe, it is also naturalized in north Florida. Hillsborough Co.: *Beckner* 2602 (USF); *Wunderlin & Beckner* 9826 (USF).

SOLANACEAE

BRUGMANSIA SUAVEOLENS (Humb. & Bonpl. ex Willd.) Brecht. & J. Presl. This native of Brazil is occasionally cultivated in central Florida and has become locally naturalized. Hernando Co.: *Wunderlin & Beckner* 9447. County unknown; Eastern shore of Lake Okeechobee, 1924, *Small et al. s.n.* (FLAS).

PETUNIA × *HYBRIDA* Vilm. = *P. axillaris* (Lam.) BSP. The cultivated petunia, locally escaped in Florida, is believed to be a hybrid of *P. axillaris* and *violacea* Lindl. Evidence of partial segregation back to the parental types is frequent in our materials.

PHYSALIS WALTERI Nutt. Recent study of our collections by J. Sullivan, University of Oklahoma, indicates this is the correct name for Florida material previously identified as *Physalis viscosa* L. In addition, the previously recognized var. *elliottii* (Kunze) Waterfall and var. *maritima* (Curtis) Rydb. are reduced to synonymy.

PHYSALIS ANGSTIFOLIA Nutt. = *Physalis viscosa* var. *elliottii* f. *glabra* Waterfall. This taxon is recognized as a distinct species by J. Sullivan. Hybrids between *P. angustifolia* and *walteri* are common where the two species are sympatric.

SALPICHRON ORGANIFOLIA (Lam.) Baill. A native of southern South America, this species is sparingly naturalized in our area. Citrus Co.: *Koating s.n.* (FLAS); *Weber s.n.* (FLAS). Volusia Co.: *Evans et al.* 45513 (FSU).

SCROPHULARIACEAE

LIMNOPHILA INDICA (L.) Druce. This is the first report of this Old World species in Florida. Both this and the related species *L. scitiliflora* are grown as aquarium plants (Godfrey and Wooten 1981) which may account for their occasional occurrence in North America. Pinellas Co.: *Richardson* 891 (USF).

RUBIACEAE

GENIPA CLUSIFOLIA (Jacq.) Griseb. = *Casasia clusifolia* (Jacq.) Urban. If *Casasia* is submerged into *Genipa* as is advocated by most workers (e.g. Little 1979), *Genipa clusifolia* is the correct name for this taxon.

ASTERACEAE

ACMELLA REPENS (Walt.) L. C. Rich. = *Spilanthes americana* (Mutis ex L.f.) Hieron. R. Jansen (1981) segregates *Acemella* from *Spilanthes*. Recent study of our collections by Jansen shows that our plants are best referred to *Acemella repens* (= *Spilanthes americana* var. *repens* (Walt.) A. H. Moore).

ASTER FONTINALIS Alex. This taxon, previously placed in synonymy under *A. dumosus*, is considered specifically distinct (Jones 1984; J. Semple pers. comm.). Additional study is needed to determine if this species is distinct from *A. lasius* Britton from Cuba (Jones 1984). Lee Co.: *Bronsbach* 7049 (FLAS); *Bronsbach* 8701 (USF); *Bronsbach* 9131 (FLAS, USF).

ASTER SIMMONDSII Small. This taxon, previously placed in synonymy under *A. dumosus*, is considered specifically distinct (Jones 1980; J. Semple pers. comm.). The following representative specimens have been annotated by J. Semple: Brevard Co.: *Sewey & Poppleton* 1554 (USF). Broward Co.: *McCart* 11256 (USF). Citrus Co.: *Gemelle & Fleming* 1157 (USF). DeSoto Co.: *Fulton* 296 (USF). Hardee Co.: *Sewey* 2026 (USF). Hendry Co.: *Bras* 33407

(USF). Hernando Co.: *Cooley et al.* 8099 (USF). Hillsborough Co.: *Lakela* 25607 (USF). Indian River Co.: *Wanderlin & Bickner* 6414 (USF). Lee Co.: *Wanderlin et al.* 5383 (USF). Levy Co.: *Ray* 9690 (USF). Manatee Co.: *Lakela* 24883 (USF). Martin Co.: *Popenoe* 1032 (USF). Palm Beach Co.: *McCart* 10398 (USF). Polk Co.: *Lakela* 23726 (USF).

CENTRATHERUM PUNCTATUM Cass. A native of tropical America, this species is occasionally cultivated in Florida and rarely found as an escape. Volusia Co.: *Harrison s.n.* (FLAS).

DYSSODIA TENUILOBA (DC.) Robins. This western U.S. Plant in cultivation in St Petersburg has escaped locally and is spreading along roadsides. Pinellas Co.: *Burdett s.n.* (USF); *Chayer* 148 (FLAS).

ECLIPTA PROSTRATA (L.) L. = *Eclipta alba* (L.) Hassk. Roxburgh (Fl. Ind. 3: 438. 1832) united *E. prostrata* and *E. alba* under *E. prostrata* predating Hasskari (Pl. Jav. Rar. 528. 1848) who united the taxa under *E. alba*. (Koyama and Boufford 1981; Voss et al. 1983).

Following the publications of Sieren (1981) and Taylor and Taylor (1983), reexamination of our materials of *Euthamia* results in recognition of two rather than three species and the following two nomenclatural changes.

EUTHAMIA GRAMINIFOLIA (L.) Nutt. var. *HIRTIPES* (Fernald) C. & J. Taylor. Materials previously determined as *E. leptocphala* (Torr. & Gray) Greene and *E. tenuifolia* are best placed here. *Euthamia leptocphala* is excluded from the flora.

EUTHAMIA TENUIFOLIA (Pursh) Greene = *Euthamia minor* (Michx.) Greene.

SOLIDAGO ODORA Ait. var. *CHAPMANII* (A. Gray) Cronq. = *Solidago chapmanii* A. Gray. The slight differences between *S. odora* and *S. chapmanii* and the number of intermediates in the area of sympatry indicate the latter is best treated as a variety of the former (Cronquist 1977).

SOLIVA MUTISI HBK. Materials of this South American species were previously misidentified as *Soliva anthemifolia* (Juss.) R. Br. ex Less., a species not known to occur in central Florida (See Cabrera 1949; Correll & Johnston 1970; Gandhi and Thomas 1984).

SOLIVA PTEROSPERMA (Juss.) Less. This native of South America is a common turf weed in north and west Florida. Lake Co.: *Daubenmire & Daubenmire s.n.* (USF).

ACKNOWLEDGMENTS

The authors gratefully acknowledge the contributions of: Loran Anderson, Florida State University; Anthony Arcuri, Environmental Sciences and Engineering; Daniel Austin, Florida Atlantic University; Mary Barkworth, Utah State University; John Beckner, St. Petersburg; Allen Burdett, Florida Department of Environmental Regulation; David Crews, Florida Department of Natural Resources; Donovan† and Helen Correll, Fairchild Tropical Garden; Rexford and Jean Daubenmire, Sorrento; Robert Godfrey, Florida State University; Robert Faden, Smithsonian Institution; Duane Isely, Iowa State University; Walter Judd, University of Florida; Emmet Judziewicz, University of Wisconsin-Madison; Donald Les, Ohio State University; David Lindsey, Environmental Sciences and Engineering; Eliane Norman, Stetson University; John Popenoe, Fairchild Tropical Gardens; Donald Richardson, University of South Florida; Ruben Saulea, Fairchild Tropical Gardens; John Semple,

University of Waterloo; Allen Shuey, Bradenton; Gerould Wilhelm, Morton Arboretum.

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NOTES

DACTYLOCTENIUM AEGYPTIUM (GRAMINEAE) NEW TO BELIZE.—*Dactyloctenium aegyptium* (L.) Willd. has apparently not been recorded from Belize, as it is not listed among the monocots of Belize by Spellman et al. (*Rhodora* 77:105–140, 1975), nor in the plants of the Belize cays by Fosberg et al. (*Atoll Res. Bull.* No. 258, 1982). The discovery of this widespread, weedy species in Belize is, however, hardly surprising. I recently found *D. aegyptium* plentiful in disturbed areas in the central part of South Water Cay, ca 22.4 km SE of Dangriga, Stann Creek District, where it had apparently become established since my floristic survey of the site in 1979–1980. Voucher: *Pringle 2536*, 10 Jan 1985 (HAM) (*Contribution No. 57 from the Royal Botanical Gardens*).—*James S. Pringle, Royal Botanical Gardens, Box 399, Hamilton, Ontario, Canada L8N 3H8.*

ADDITIONAL NOTES ON *COREOPSIS*—In my recent paper on the Californian *Coreopsis* (*Sida* 10:276–289), several errors unfortunately were made. These errors were kindly called to my attention by John L. Strother (UC), and I want to thank him for his advice and attention to detail in these matters, for his review of a preliminary version of this note, and for the loan of selected microfiche (932 and 944) of the Candolle Prodromus herbarium. The errors were mostly in typification matters and require the following clarifications and emendations (page numbers refer to my *Sida* article pagination):

- p. 282—The TYPE for *Coreopsis calliopsidea* (DC.) A. Gray, *Bot. Mex. Bound.* 90, 1859.—*Agarista calliopsidea* DC., *Prodr.* 5:569, 1836, should be: California, *Douglas 49* (HOLOTYPE: G-DC, microfiche; ISOTYPES: BM!, K two sheets!). With the G-DC microfiche, lectotypification was unnecessary.
- The TYPE for *Leptosyne calliopsidea* var. *nana* A. Gray, *Synop. Fl. N. Amer.*, 2nd ed. 1(2):300, 1886 [1884], should be: California, San Bernardino Co.: "At Mohave Station etc.," May 1882, *Pringle s.n.* (LECTOTYPE, here designated: GH!; ISOLECTOTYPES, here designated: CAS!, F two sheets!, MO!, NY!, UC!). It is more likely that Gray saw the GH specimen than the CAS specimen.
- p. 283—The TYPE for *Coreopsis bigelovii* (A. Gray) H. M. Hall, *Univ. Calif. Publ. Bot.* 3:141, 1907.—*Pugiosappus bigelovii* A. Gray, *Pacif. Railr. Rep.* 4:104, 1857, should be: California, San Bernardino Co.: On the Mohave Creek, in the desert east [west] of Colorado [River], Mar 1854, *J. M. Bigelow s.n.* (HOLOTYPE: GH!; ISOTYPE: NY!). Lectotypification was unnecessary.
- The TYPE for *Pugiosappus breweri* A. Gray, *Proc. Amer. Acad. Arts*

8:660. 1873, should be: California. Ventura Co.: On dry hills at San Buenaventura, *Brewer 241* (HOLOTYPE: GH!; ISOTYPES: K!, UC!). Lectotypification was unnecessary.

- p. 285 — The section "Euleptosyne" should be section *Leptosyne* as follows: Section LEPTOSYNE (DC.) O. Hoffm., Nat. Pflanzenfam. 4(5):243. 1894 [1889]. TYPE: *Coreopsis douglasii* (DC.) H. M. Hall.

Leptosyne DC., Prodr. 5:531. (as genus). 1836.

Leptosyne sect. *Euleptosyne* A. Gray, Synop. Fl. N. Amer., 2nd ed. 1(2):299. 1886 [1884].

Coreopsis sect. *Euleptosyne* (A. Gray) Blake, Proc. Amer. Acad. Arts 49:341. 1913.

- The TYPE for *Coreopsis stillmanii* (A. Gray) Blake, Proc. Amer. Acad. Arts 49:342. 1913.—*Leptosyne stillmanii* A. Gray in E. Durand, J. Acad. Sci. Phil., 2nd Ser. 3:91. 1855, should be: California. In the valley of the Upper Sacramento [River], *Stillman s.n.* (HOLOTYPE: GH!; ISOTYPES: NY two sheets!, F photograph and fragment!). Lectotypification was unnecessary.

- p. 286 — The TYPE for *Coreopsis douglasii* (DC.) H. M. Hall, Univ. Calif. Publ. Bot. 3:140. 1907.—*Leptosyne douglasii* DC., Prodr. 5:531. 1836, should be: California, 1833, *Douglas 8* (HOLOTYPE: G-DC, microfiche!; ISOTYPES: BM plant C!, K two sheets!, GH plant I!, UC fragment!). With the G-DC microfiche, lectotypification was unnecessary.

—Edwin B. Smith, Department of Botany & Microbiology, University of Arkansas, Fayetteville, AR 72701, U.S.A.

SOLIDAGO SPATHULATA DC. VAR. NEOMEXICANA (GRAY) CRONQ. (ASTERACEAE) NEW TO TEXAS—A collection of *Solidago spathulata* DC. var. *neomexicana* (Gray) Cronq. (*Worthington 3366*, SMU, UTEP) from the Davis Mts., Jeff Davis Co., Texas, represents the first collection of this essentially Rocky Mountain species of goldenrod from the state. The nearest populations occur approximately 275 km to the northwest in the Sacramento Mts. of Otero and Lincoln cos., NM. The locality is on the forested crest of the mountain 1.6 km ESE of the top of Mt. Livermore (30°37'40"N-104°09'30"W), at 2285 m elev. Ponderosa pine, *Pinus ponderosa* Laws., is common on this ridge, but the forest is complex due to edaphic factors and includes *Pinus strobiformis* Engelm., *P. cembroides* Zucc., and oaks often growing in close proximity to one another. I would like to thank Mr. Darrell E. Ward for making the preliminary determination.—Richard D. Worthington, Department of Biological Sciences, The University of Texas at El Paso, El Paso, TX 79968, U.S.A.

NESTRONIA UMBELLULA RAF (SANTALACEAE) NEW TO MISSISSIPPI—*Nestronia umbellula* Raf. is a deciduous, dioecious, clonal

shrub which parasitizes the roots of pines and hardwoods. Previous records show a scattered distribution in the Piedmont, Coastal Plain, and Cumberland Plateau from southern Virginia to Alabama and Tennessee (Kral 1983; Horn & Kral 1984). During the course of field work to determine woody plant distribution in Mississippi's upper Pearl River Basin, I located a population of *N. umbellula* resulting in the first report of this monotypic genus from the state. The Mississippi location extends the western range of the species by ca 230 km.

Four clones of *N. umbellula* were found along a 0.4 km stretch of MS Hwy 19. The largest consisted of hundreds of shoots occupying a thinly wooded upland area of ca 1800 m². Two clones were found on each side of the highway with each extending from the edge of the ROW into the adjacent upland woods. All shoots were sterile with the exception of a few persistent peduncles from male inflorescences on a few shoots. Soils at the sites are sandy and consist of the Smithdale-Ruston and Lauderdale-Arundel associations (Galberry 1981). Future work will be directed toward determining the sex of each clone as well as toward looking for additional sites in the area.

Collection data are as follows: MISSISSIPPI, Neshoba Co.: ca 9.0 mi NW of Philadelphia (T12N R10E S10 NE4) side of Hwy 19 ca 2.7 mi SE of Winston Co. line. Near sandpit on sandy upland ridge. Up to 1.0 m shrubs, most covered with whitish powdery mildew, no fertile plants found, locally abundant under *Quercus incana*, *Q. margaretta*, and *Pinus echinata*, 1 Jul 1985, *Smith 1408* (IBE); same locality 8 Aug 1985, *Smith 1484* (IBE).

—*Timothy E. Smith, Institute for Botanical Exploration and Department of Biological Sciences, Mississippi State University, Mississippi State, MS 39762, U.S.A.*

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ALETIS FARINOSA, CYPERUS DIFFORMIS, AND CYPERUS PILOSUS NEW FOR FLORIDA.—Since recent reports by Anderson (1984) and Burkhalter (1984), three more plants collected in Escambia

County, Florida, have, upon examination of exsiccatae at FLAS and FSU, been determined to apparently be new additions to the vascular flora of Florida. These are noted below.

ALETIS FARINOSA L. Escambia Co.: near Barth, E of RR tracks at crossing near abandoned Bickerstaff Brickyard, 6 May 1978, *Burkhalter* 5835 (FLAS, UWFP); S of McDavid, E of U.S. Hwy 29 ca 200 ft S of jct with Pine Barren Rd, roadside, 18 Apr 1982, *Burkhalter* 8163 (UWFP); Barrineau Park, N side of Co Rd 196 ca ¼ mi E of jct with Co Rd 99, 28 Apr 1984, *Burkhalter* 9332 (UWFP); N of Barth, ca 0.2 mi N of Cotton Lake Rd along E side of L & N RR tracks, 19 May 1984, *Burkhalter* 9377 (UWFP).

CYPERUS DIFFORMIS L. Escambia Co.: near Pensacola, W side of Pensacola Blvd (U.S. Hwy 29) just N of Hill-Kelly Dodge, in water-filled roadside ditch, 18 Nov 1983, *Burkhalter* 9166 (FLAS, FSU, UWFP) [Determined by R. K. Godfrey, FSU]; near Pensacola, S side of Nine Mile Rd, W of jct with Holsberry Ln, roadside ditch, 17 Nov 1984, *Burkhalter* 9813 (FLAS, FSU, MOR, UWFP).

CYPERUS PILOSUS Vahl. Escambia Co.: near Pensacola, E side of Fairfield Dr just N of jct with Hestia Pl, roadside ditch, 12 Oct 1983, *Burkhalter* 9099 (FLAS, FSU, UWFP) [Determined by R. Kral, VDB].—*James R. Burkhalter, Herbarium, University of West Florida, Pensacola, FL 32514, U.S.A.*

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A WHITE-FLOWERED FORM OF *SPIGELIA MARILANDICA* L. (LOGANIACEAE) NEW TO TENNESSEE—A unique color form of *Spigelia marilandica* L. (Indian Pink) was discovered in 1968 growing in a suburban woodlot in Chattanooga, Hamilton Co., Tennessee. This new form has a corolla that is white on the outside, which contrasts with the scarlet outside of the typical form. Both forms have a yellow throat. The new form also differs from the typical Indian Pink by having a whorl of three leaves on some stems, but opposite leaves on other stems. Observations in the summer of 1984 of four stems producing white flowers revealed that all four stems grew from the same rhizome, which had 24 stem scars from previous seasons. Three of these stems had whorled leaves and one stem had opposite leaves. Pollen samples of the white form averaged about

95% fertility as determined by aniline blue in lactophenol solution. A description of this form is:

SPIGELIA MARILANDICA L., forma *eburnea* Van Horn and Freeman, forma nov.

Corolla alba extra, luteola intra; folia insolenter verticillaria, interdum opposita.

Spigelia marilandica forma *eburnea* differs from forma *marilandica* by its corollas being white on the outside and by most stems having leaves in whorls of threes.

TYPE: TENNESSEE. Hamilton Co.: growing among oaks, hickories, and dogwoods in lot adjacent to 3116 Lockwood Drive, Chattanooga, elev. 260 m, 19 May 1982, John Freeman 1. (HOLOTYPE: NCU)

—Gene S. Van Horn and John R. Freeman, Department of Biology, The University of Tennessee at Chattanooga, TN 37403, U.S.A.

NEW COMBINATIONS IN *ERIGERON* (ASTERACEAE)—In his studies of *Aster*, the second author recently examined types of *A. procumbens* Houston ex P. Miller and *A. scaberrimus* and found them to be the same species as *Erigeron myriomactis* Small and *E. longipes* DC., respectively; the names in *Aster* also are the earliest for these taxa. New combinations are proposed below, and the remainder of the nomenclature for species is presented. The first species occurs along the Gulf Coast from Mississippi through Louisiana and Texas and into Mexico as far south as the vicinity of the city of Veracruz. The second species is highly variable and occurs in Mexico from Veracruz westward to Durango and Nayarit and southward through Chiapas into Central America as far as Nicaragua.

ERIGERON procumbens (Houston ex P. Miller) Nesom, comb. nov.

Aster procumbens Houston ex P. Miller, Gard. Dict. ed. 8, *Aster* no. 32, plate 58, fig. 2, 1768. TYPE: MEXICO. [Veracruz], "growing in plenty in the sandy ground about Veracruz," 1729, W. Houston s.n. (HOLOTYPE: BM!).

Erigeron scaposus DC. "var. ? *conifolius*" A. Gray, Proc. Amer. Acad. Arts 16:94, 1881. *Erigeron repens* A. Gray, nom. nov., Syn. Fl. N. Amer. 1(2):217, 1884, non Weddell, 1855. *Erigeron myriomactis* Small, nom. nov., Fl. SE U.S. 1229, 1903. TYPE: UNITED STATES. Texas, [Galveston Co.], coast of Galveston, Nov 1842, F. Lindheimer s.n. (LECTOTYPE, designated here: GH!; ISOLECTOTYPE: MO!). In the description of *E. scaposus* var. *conifolius*, Gray referred to "Texas, sandy seashore" but simply cited two of his earlier publications for reference to specimens. Two collections at GH, Lindheimer s.n. and Wright s.n., were labeled by Gray as *E. scaposus* var. *conifolius* and both were later annotated by him as *E. repens* as vouchers for the Synoptic Flora. In the latter treatment, Gray referred to var. *conifolius* as a synonym of *E. repens* and cited

collections by Berlandier, Drummond, Wright, and Lindheimer. Because the label data on the Lindheimer collection specifically refers to the Texas coast, it is chosen as the lectotype.

Erigeron rufus A. Gray var. *psammophilus* Greenman, Proc. Amer. Acad. Arts 41:259, 1905. TYPE: MÉXICO, Veracruz, Lizardo, Dr. *Waters* 276 (Greenman cited sheets of this at GH and B; the GH collection could not be located and the B sheet has not been examined).

ERIGERON scaberrimus (Less.) Nesom, comb. nov.

Aster scaberrimus Less., Linnaea 5:143, 1830. TYPE: MÉXICO, [Veracruz], "in sylvaticis prope Jalapam," 28 Aug 1828, C. J. W. Schiede 308 (HOLOTYPE?: ISOTYPE: HAL!, fragments and tracing of B specimen-GH!).

Erigeron longipes DC., Prodr. 5:285, 1836. TYPE: MÉXICO, W. F. Karwinsky s.n. (HOLOTYPE: M, fide McVaugh, 1974; fragment of type at G-DC, microfiche!).

Erigeron scaposus DC., Prodr. 5:287, 1836. TYPE: MÉXICO, "circa Toluca," Apr 1834, G. Andrieux 277 (HOLOTYPE: G-DC, microfiche!, GH-photo!; ISOTYPE: GH!).

Erigeron scaposus DC. β *latifolium* DC., Prodr. 5:287, 1836. [*Erigeron marianthus* Schultz-Bip. ex Klatt, pro syn. sub. *E. scaposus* β *latifolium* (see comment following *E. affine*, below), Leopoldina 20:91, 1884; non Nurrall, 1840.] TYPE: MÉXICO, "environs de [Cd.] Mexico," 20 Jun 1827, J. L. Berlandier 375 (HOLOTYPE: G-DC, microfiche!, GH-photo!; ISOTYPE: US!).

Erigeron affine DC., Prodr. 5:289, 1836; non Badillo, 1946. [*Erigeron nitidus* Schultz-Bip. ex Klatt, pro syn. sub. *E. affine*, Leopoldina 20:91, 1884.] TYPE: MÉXICO, "environs de [Cd.] Mexico," Jun 1827, J. L. Berlandier 522 (HOLOTYPE: G-DC, fide McVaugh, 1974, microfiche!; ISOTYPE: B, pencil drawing ex herb. Klatt-GH!). Klatt clearly recognized the synonymy of Schultz's names with the earlier ones of De Candolle. We believe his publication of these epithets represented the use of barbarian names applied by Schultz to collections made by Schiede. It is possible, however, that Schulte already had validly published them in one of Linden's difficult-to-find sales catalogs (see Stafleu and Cowan 1981).

Erigeron orizabensis Schultz-Bip. ex Klatt, Leopoldina 20:91, 1884. TYPE: MÉXICO, [Veracruz], "Pic Orizaba," 11,000 ft, Liebmann 503 (HOLOTYPE?: drawing ex herb. Klatt at GH!).

—Guy Nesom, Dept. of Biology, Memphis State University, Memphis TN 38152, U.S.A. and Dept. of Botany, University of Texas, Austin TX 78712, U.S.A. and Scott Sundberg, Dept. of Botany, University of Texas, Austin TX 78712, U.S.A.

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DOCUMENTED PLANT CHROMOSOME NUMBERS 1985:

I. MISCELLANEOUS COUNTS FROM ONTARIO AND QUEBEC

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Chromosome number determinations for individuals predominantly from Ontario and representing 11 genera are reported; all support previously published counts for the respective taxa. The need for documentation of such reports has been stated many times (e.g., Strother 1972; Semple et al. 1983). I hope that these contributions will assist others in accomplishing their goals.

MATERIALS AND METHODS

Chromosome counts were made from freshly prepared material following the procedures of Chmielewski and Semple (1983). Root-tip cells were taken from transplanted material for plants collected in the wild. Mitotic metaphase-stage cells were examined. Voucher specimens were deposited in the Herbarium of the Department of Biology, University of Waterloo (WAT). In citation, *Chmielewski* is abbreviated to *C.*

RESULTS

BALSAMINACEAE

IMPATIENS CAPENSIS Meerb. $2n = 20$. CANADA. ONTARIO. Waterloo Reg. Mun.: Univ. Waterloo, Laurel Creek, *C. 1207*.

BERBERIDACEAE

PODOPHYLLUM PELTATUM L. $2n = 12$. CANADA. ONTARIO. Waterloo Reg. Mun.: Univ. Waterloo, North Campus, *C. 1159*.

CAMPANULACEAE

LOBELIA SPICATA Lam. $2n = 14$. CANADA. ONTARIO. Oxford Co.: East Zorra Township, 4.9 km W of Cassel, *C. 1645*.

COMPOSITAE

SOLIDAGO ALTESSIMA L. $2n = 54$. CANADA. ONTARIO. Huron Co.: 5 km NE of Ethel, *C. 1659*.

SOLIDAGO BICOLOR L. $2n = 18$. CANADA. ONTARIO. Haldimand-Norfolk Reg. Mun.: Seneca Township, Abbey Rd., 3.4 km N of Hwy 54, *C. 2131*.

SOLIDAGO CAESIA L. $2n = 18$. CANADA. ONTARIO. Frontenac Co.: Olden Township, Sharbot Lake, *C. 2165*, Lambton Co.: Bosanquet Township, Lake Rd., S of Grand Bend, *C. & Ringius 1982*. Waterloo Reg. Mun.: North Dumfries Township, River Rd., 0.6 km N of Dumfries North 13, *C. 2129*.

SOLIDAGO GIGANTEA Ait. $2n = 36$. CANADA. ONTARIO. Lennox-Addington Co.: Kaladar Township, 6 km E of Kaladar, *C. 2182*. Northumberland Co.: Seymour Township, E of Cambellford, *C. 2145*.

SOLIDAGO HISPIDA Muhl. $2n = 18$. CANADA. ONTARIO. Frontenac Co.: Hinchinbrooke Township, 0.8 km S of Parham, *C. 2164*.

SOLIDAGO JUNCEA Ait. $2n = 18$. CANADA. ONTARIO. Perth Co.: Blanshard Township, N of Townline Rd., *C. 1893*.

SOLIDAGO PTARMICOIDES (Nees) Boivin. $2n = 18$. CANADA. QUEBEC. Timiskaming District: Ile du College, 9.6 km NW of Ville Marie, *C. & C. 1287*.

SOLIDAGO RIDDELLII Frank. $2n = 18$. CANADA. ONTARIO. Kent Co.: Dover Township, Ferry crossing south of Wallaceburg, *C. & Leeder 2110*.

SOLIDAGO RUGOSA Mill. $2n = 18$. CANADA. ONTARIO. Haldimand-Norfolk Reg. Mun.: Townsend Township, 3.7 km S of Waterford, *C. 1927*. Huron Co.: Morris Township, 3.8 km NW of Brussels, *C. 1664*. Kent Co.: Orford Township, Orford Con. 12, E of Moravian Indian Reserve, *C. & Leeder 2087*. Kent Co.: Zone Twp. Zone Sd. Rd. 5, 0.5 km N of Zone Con. 7, *C. & Leeder 2095*. Lennox-Addington Co.: Kaladar Township, 6 km E of Kaladar, *C. 2181*. Middlesex Co.: Caradoc Township, intersection of Caradoc Con. 7 and Caradoc Sd. Rd. 4, *C. 2218*. Northumberland Co.: Percy Township, Warkworth Hill, *C. 2142*. Northumberland Co.: Seymour Township, 2.6 km E of Petherwick Corners, *C. 2150*. Simcoe Co.: Tecumseh Township, intersection of Simcoe Rd. 10 and Hwy 9, *C. & Ringius 2012*. Wellington Co.: Puslinch Township, Puslinch Con. 4, 1 km E of Rozell Rd., *C. 2047*.

SOLIDAGO RUGOSA Mill. $2n = 36$. Kent Co.: Camden Township, 5.6 km SE of Wabash, *C. & Leeder 2102*.

SOLIDAGO SQUARROSA Muhl. $2n = 18$. CANADA. ONTARIO. Nipissing District: 24 km E of Whitney, C. & C. 1581.

SOLIDAGO ULIGINOSA Nutt. $2n = 18$. CANADA. ONTARIO. Nipissing District: Hunstville, C. & C. 1578. Peterborough Co.: Smith Township, NW of Peterborough, C. 2177.

TANACETUM VULGARE L. $2n = 18$. CANADA. ONTARIO. Brant Co.: Onondaga Township, intersection of Hwy 54 and Brant Co. 22, C. 1566. Waterloo Reg. Mun.: St. Jacobs, C. 1569.

LILIACEAE

CLINTONIA BOREALIS (Ait.) Raf. $2n = 28$. CANADA. ONTARIO. Waterloo Reg. Mun.: Univ. Waterloo, Main Campus, C. 1160.

ERYTHRONIUM AMERICANUM Ker. $2n = 24$. CANADA. ONTARIO. Waterloo Reg. Mun.: Univ. Waterloo, Main Campus, C. 1158.

POLYGONATUM BIFLORUM (Walc.) Ell. $2n = 30$. CANADA. ONTARIO. Waterloo Reg. Mun.: Conservation Drive, 0.5 km W of Erbsville, C. 1174.

TRILLIUM GRANDIFLORUM (Michx.) Salisb. $2n = 10$. CANADA. ONTARIO. Waterloo Reg. Mun.: Univ. Waterloo, Main Campus, C. 1161.

PLANTAGINACEAE

PLANTAGO MAJOR L. $2n = 12$. CANADA. ONTARIO. Waterloo Reg. Mun.: Univ. Waterloo, North Campus, C. 1209.

RANUNCULACEAE

RANUNCULUS REPENS L. $2n = 32$. CANADA. ONTARIO. Waterloo Reg. Mun.: Hwy 24, 6.0 km SW of Cambridge, C. 1162.

ACKNOWLEDGEMENTS

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LECTOTYPIFICATION OF *LUPINUS SUBCARNOSUS* AND *L. TEXENSIS* (FABACEAE)

B. L. TURNER and JEAN ANDREWS

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Shinners (1953) correctly surmized that the name of our then and only state flower of Texas, *Lupinus subcarnosus* Hook., was perhaps typified by two or more discordant elements, noting that "It is possible that Hooker had more than one species among the collections..." upon which he based his name. In connection with a forthcoming book on the bluebonnets of Texas by the junior author (Andrews 1986), all collections of the Texas bluebonnets housed at The Royal Botanic Gardens, Kew, England (where Hooker worked), were borrowed so as to resolve any possible nomenclatural ambiguities with respect to the application of the correct scientific names of both *Lupinus subcarnosus* and *L. texensis*, the two most abundant bluebonnets of central Texas.

Lupinus subcarnosus was first described by Hooker in the Botanical Magazine in 1835. His description was accompanied by a colored plate (t. 3467), this being a fairly accurate drawing of what has long been accepted as the common clay-land bluebonnet of the more western portions of central Texas. Shinners (1953) notes that "despite the inaccurate illustration...his description leaves no doubt as to the application of the name *subcarnosus*." Nevertheless, examination of the possible type material available to Hooker shows that the only two specimens which he cited in his protologue of this species are, indeed, discordant elements.

The first cited collection in the protologue of *Lupinus subcarnosus*, a specimen from Bexar County, Texas made by *Berlandier* in 1828, is actually a specimen of what has long been called *L. texensis* Hook. The second and only other cited specimen is that of *Drummond* collected "between Brazoria and San Felipe" in 1835. This latter collection is what most workers have long called *L. subcarnosus*. The original description, as noted above, is accompanied by a hand-colored plate. The plate itself does not match the description. Apparently Hooker described *L. subcarnosus* largely from the pressed material at his disposal, the drawing having been rendered by a staff artist from plants of what Hooker subsequently described as *L. texensis*. When he described the latter species in the same year he was clearly befuddled by the very similar illustrations for he comments "Much

and closely as this plant resembles *Lupinus subcarneus* figured at tab. 3467, it nevertheless appears to me to be really distinct." Which it is! The problem is simply that *both* of the illustrations rendered are of the same species, *L. texensis*.

Under Article 7 of the International Code of Botanical Nomenclature, where a holotype has not been designated for a given taxon, a lectotype must be selected from among the syntypes cited or examined by the original author. This is especially critical where discordant elements make up the syntypes. Happily, in this instance, we are obliged to lectotypify *Lupinus subcarneus* by the aforementioned Drummond collection, which is the only such specimen in the Hooker Herbarium that is annotated by Hooker himself.

In his description of *Lupinus texensis*, which was also published in the Botanical Magazine of 1835, this too accompanied by a colored plate (t.3492), Hooker does not cite a specimen but rather merely notes the species to occur in Texas, citing specifically the city of San Felipe, which is in Austin County and about which both *L. subcarneus* and *L. texensis* may be found to this day.

Three herbarium sheets of *L. texensis* are found in the Hooker Herbarium housed at Kew. Two of these bear Drummond numbers 143 of his third collection made in 1835. The other sheet also bears this Drummond collection, along with a Lindheimer collection made in 1847.

From among these we have selected the Royal Botanic Gardens specimen number 2 (penciled loan number) as the lectotype. This sheet has both flowering and fruiting material of the species concerned and, in addition, upon this is a handwritten notation, presumably by Hooker, which reads, "similar to 142, but different." We selected Drummond 142, as noted above, as the lectotype of *Lupinus subcarneus*.

In summary, Hooker's descriptions of *Lupinus subcarneus* and *L. texensis* were accompanied by colored illustrations of the same taxon. This has caused some confusion with respect to the correct application of the names concerned. Study of the types and protologues of both species reveals that *L. subcarneus* is correctly applied to the more eastern sandy-land bluebonnet and that *L. texensis* applies to the more widespread, more western, clay-land bluebonnet.

It is altogether fitting that in this, our sesquicentennial year, the scientific names of our two most common official state flowers (*Lupinus* spp., cf. Andrews 1986), both described in the year 1835, can now be said to rest upon solid typifications.

ACKNOWLEDGEMENTS

We are grateful to Dr. Arthur Bell, Director, The Royal Botanic Gardens, Kew for the expeditious loan of the Hooker materials concerned.

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OBSERVATIONS ON THE VEGETATION OF THE MOSQUITIA IN HONDURAS

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ABSTRACT

Species lists and vegetational descriptions are given for sedge savannahs (primarily), colluvial creek swamps, and pine-oak-nance woods of the Mosquitia region along the eastern Caribbean coast of Honduras. This vegetation is contrasted with that of adjacent tropical wet forests.

INTRODUCTION

La Mosquitia is a lowland extending for about 480 km along the Caribbean coast from Cape Cameron, Honduras, nearly to Bluefields, Nicaragua. Approximately three-fourths of this area is characterized by savannahs. Savannah vegetation consists of open grassy stands of *Pinus caribaea* Morelet on the better drained sites and by low sedge prairies on the wetter sites. The vegetation of these Miskito pine savannahs, as they are sometimes called, contrasts markedly with the broadleaved tropical wet forests of all other regions of the Caribbean coast of Central America, except Belize, where savannahs also occur. The region is sparsely inhabited, mainly by Miskito Indians.

The purpose of this paper is to describe the vegetation of several plant communities, primarily the sedge savannahs, the colluvial creek swamps traversing these savannahs, and pine-oak-nance woods that are transitional between pine savannahs and tropical wet forest. The flora of the tropical wet forests is described briefly as it occurs at the inner edge of the Mosquitia and along an alluvial river within the Mosquitia.

PREVIOUS STUDIES

Carr (1950) briefly characterized this region, noting its foundation of marine Pleistocene deposits. Arnold (1954) described the geology, soils, and physiography of the Honduran Mosquitia and related his observations to recent changes in sea level. He gave few climatic data and noted the gross aspects of the vegetation. Parsons (1955) described the Mosquitia of both Honduras and Nicaragua with emphasis on the history and potential of land use. He included a map of the entire region and gave information on

climate, soils, fire, and vegetation. Radley (1960) described the climate, soils, geology, and physiography of Mosquita of Nicaragua. Holdridge (1962) mapped the Mosquitia as a wet tropical forest region. Taylor (1963) briefly described the pine savannahs in his survey of the vegetation of Nicaragua. Wagner (1964) compared the Mosquitia to the savannahs of Beliz and Yucatan. Munro (1966) discussed the vegetation of the Mosquitia of Nicaragua in relation to fire. The United Nations Development Program (UNDP, 1968) mapped and characterized the pine resources in the Honduran Mosquitia.

Systematic plant collecting began in the Honduran Mosquitia with several expeditions, including those reported herein, by personnel from the National University between 1970 and 1976. Nelson (1976, 1978) published check lists of most species collected on these expeditions. Proctor (1983) mentioned his having made subsequent collections in 1981 and described two species.

REGIONAL DESCRIPTION

The Mosquitia of Honduras is shown in Figure 1. The entire region is within the Department of Gracias a Dios, and the principal town is Puerto Lempira. The 100 meter contour, shown by the dotted line, is approximately the interior boundary of the Mosquitia. The actual boundary is at a slightly lower elevation, where steep mountains clothed with tropical wet forests abruptly meet the flat coastal plain. The savannahs of the Mosquitia occupy flat or gently rolling terrain. Several rivers, notably the Rio Patuca and the Rio Plátano, extend from the mountains through the savannahs. Fertile alluvium flanks each of these rivers and supports a corridor of tropical wet forest that extends from the mountains to the coast. These forests, with canopies 30–40 m tall, stand in sharp contrast and often without ecotone to the low, grassy savannahs.

Annual rainfall varies from about 200 to 400 cm. Parsons (1955) said that the region, "is probably the rainiest area of its size in the New World with a savanna-type vegetation." A 2–3 month dry season from March to May is mild in some areas but severe in others, sometimes with less than 3 cm of rain a month. Munro (1966) said that high temperatures (mean annual $>24^{\circ}\text{C}$) and low spring rainfall stressed the vegetation.

Upper soil horizons are highly leached and infertile, gravelly quartz sands and sandy loams lacking in organic matter. Subsoils are poorly drained, inhibiting root growth and thereby limiting that volume of soil from which nutrients can be exploited and in which anchorage can be attained. Pines lack tap roots and often topple in hurricanes (Munro 1966).

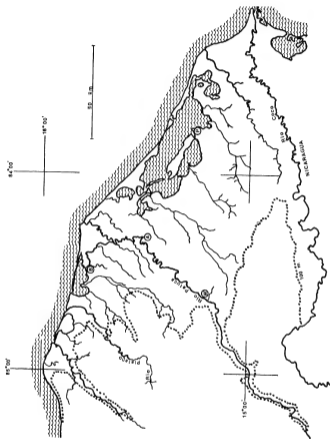


Fig. 1. Mosquitia region of Honduras, showing collecting locations. A - Ahuas, B - Brus Laguna, P - Puerto Lempira, W - Wampuisirpe.

Percolation is rapid in dry seasons, causing stress to the shallowly rooted vegetation.

Fires burn the savannahs frequently, often annually. The UNDP (1968) reported that 28% of the pine stands in the Mosquitia had been burned within the year of inventory. Fires are ignited at any season but particularly the dry season. At least some fires are set intentionally to provide fresh grass for livestock, to rid ticks and snakes, to facilitate hunting, or simply to provide entertainment (Arnold 1954, Munro 1966). Flames reach to the edges of the tropical wet forests but do not enter them for lack of graminaceous vegetation or other flammable materials. Frequent fires and infertile soils combine to prevent plants of tropical wet forests from colonizing the savannahs.

The predominant vegetation towards the coast is sedge prairie, dominated by species of *Rhynchospora*. Pinelands occur primarily in the interior of the Mosquitia, where soils are better drained and finer textured. The UNDP (1968) estimated that 76% of the Mosquitia was pineland but that much of this area had been logged. This report said that tree density was low but tree size was large, with 24% of the trees being over 50 cm in diameter. Most trees were reported as having defects, which were thought to have resulted from storms.

Thickets of shrubs and small trees occasionally interrupt the savannahs. These are usually dominated by palms (*Panrotis wrightii*) or by coppicing hardwoods (*Davilla kunthii*, *Quercus oleoides*). Nearer the alluvial rivers, thickets occur that are dominated by species of such genera as *Miconia*, *Isertia*, *Psychotria*, and *Helicteres*. Parsons (1955, citing R. L. Pendleton) said that these hardwood islands may have developed on former camp sites of Miskito Indians, where there had been protection from fire and where the soil had been enriched by refuse and ashes.

The Mosquitia contains many small creeks with headwaters within the flat coastal plain; some are shown in Figure 1. These minor drainages show little topographic relief and do not have enough flow for much alluvial transport of sediments. They are flanked by narrow ribbons of creek swamp, consisting of short, broadleaved trees. These creek swamps are floristically depauperate, compared to the much taller tropical wet forests along the large, alluvial rivers.

Near the base of the mountains, the pine savannahs contain a greater mixture of woody species than elsewhere. Although *Pinus caribaea* is generally the sole occupant of the overstory, the understory is distinctive for its open growth of broadleaved trees and shrubs. The most conspicuous understory species are an oak (*Quercus oleoides*) and nance (*Byrsonima crassifolia*). This pine-oak-nance woods appears to suffer less fire than the open

pinelands. Munro (1966) described similar vegetation in Nicaragua and said that it had a fire frequency of about every five years.

Vegetation at the coast is distinct from that of the savannahs and consists of beach strand vegetation, mangrove forests, tidal marshes, and scrubby woodlands, similar to that described by Sauer (1967). Ruderal and other obviously disturbed vegetation is restricted to the vicinity of the very few towns and settlements.

METHODS

Observations in this paper were made during three collecting trips totaling 15 days in 1972-73. The first trip was made on December 12-14, 1972, near Ahuas (Figure 1) in sedge prairies and creek swamps. The second trip was made May 17-23, 1973, with Gustavo Cruz and A. H. Gentry in the vicinity of the Rio Plátano. Collecting locations included sedge prairies, alluvial river swamps, tropical wet forests near the river 10 and 18 km inland, and tropical wet forests in low mountains 25 km inland. The third trip was taken August 30-September 3, 1973, to Ahuas, Brus Laguna, and Wampusirpe. Collecting locations included sedge prairies, colluvial creek swamps, pine savannahs, pine-oak-nance woods, and tropical wet forests, the latter near Wampusirpe at the foot of mountains bordering the savannah region.

Sedge savannahs were collected intensively on all three trips, allowing a rather thorough, systematic inventory of the flora. Creek swamps and pine-oak-nance woods were collected less intensively. Although tropical wet forests were visited on two trips, only a fraction of this rich vegetation could be collected.

The Mosquitia was reached by twice weekly scheduled flights from Tegucigalpa, weather permitting. Accommodations, electricity, and most logistical amenities were scarce. Transportation within the region was made difficult from the lack of roads and vehicles. River transportation was by piragua, including one called a tuk-tuk. This craft was a 40 foot long mahogany dugout and was named for the sound of its one-cylinder inboard engine. Several landing strips for light aircraft were scattered throughout the region. Rides were available from the Missionary Aviation Fellowship (*Alas de Socorro*) which served the Mosquitia.

The most complete sets of specimens were deposited at the National University (TEFH) and at the Escuela Agrícola Panamericana (EAP). A partial set containing specimens primarily from the savannahs was deposited at Florida State University (FSU). Another nearly complete set and all remaining duplicates were given to the Missouri Botanical Garden (MO) in exchange for a travel grant for one of the field trips. Plant names

follow Standley et al. (1958-1975) and Molina (1975) for most groups, Ames and Correll (1953) for orchids, and Clewell (1975) for composites.

RESULTS

Table 1 lists the flora of the grass-sedge savannahs. Table 2 lists the vascular flora of creek swamps along the colluvial streams with headwaters within the Mosquitia. Table 3 lists characteristic plants of the pine-oak-nance woods. Table 4 lists characteristic trees of tropical wet forests.

DISCUSSION

SEDGE SAVANNAHS. One hundred sixty-five species were recorded in the sedge savannahs (Table 1). The most abundant species was *Rhynchospora globosa*, and perhaps the next most abundant was *Paspalum pulchellum*. Other abundant species were *Rhynchospora chapmanii* and *R. barbata*. Particularly wet areas lacked grasses, but plants of *Tonina fluviatilis* and *Utricularia subulata* grew abundantly between the cespitose tussocks of *Rhynchospora globosa*. The relatively dry sedge savannahs contained much *Bulbostylis paradoxa* and *Declieuxia fruticosa*. Most herbaceous vegetation was 1-3 dm tall. Thickets of *Paurotis wrightii* were common in wet areas, and shrubs of *Davilla kunthii* and *Quercus oleoides* preferred higher ground.

Pine savannahs neighboring the sedge savannahs were characterized by much *Pteridium aquilinum*, *Rhynchospora rugosa*, and *Setaria geniculata*. Species denoted with an asterisk in Table 1 were those that occurred largely or entirely in disturbed horse pastures within the savannahs. These species may not be characteristic of the savannah flora but rather of ruderal habitats.

Parsons (1955) noted how, "the open, park-like Miskito savanna bears an extraordinary resemblance to the pine flats of Louisiana or Florida." Wagner (1964) reiterated Parson's observation. Twenty-two species (13.3%) listed in Table 1 are indigenous to northwestern Florida (Clewell 1985). Notable floristic dissimilarities between the two regions include the prominence of the Compositae and the unimportance of the Melastomataceae and Rubiaceae along the northern Gulf coast, as compared to the Mosquitia.

CREEK SWAMPS. The canopy of the creek swamp was dense, generally less than 10 m tall, and consisted mainly of broadleaved, evergreen species. Table 2 lists 52 species for the creek swamps. The Guttiferae provided the most important elements of the overstory, and *Symphonia globulifera* may have been the most abundant tree. Most species were trees and shrubs; most of the rest were epiphytes and woody vines. Terrestrial herbs were

TABLE 1. Plants of Sedge Savannas and Their Life Forms.

T - tree, S - shrub, V - woody vine, H - terrestrial herb, E - epiphytic herb, P - parasite. An asterisk (*) denotes species occurring largely or entirely in savannas used as pasture.

POLYPODIACEAE	
<i>Blechnum indicum</i> Burm.—H	
<i>Cochlidium rotundatum</i> (Hook.) Maxon—E	
<i>Pteridium aquilinum</i> (L.) Kuhn.—H	
CYATHEACEAE	
<i>Alsophila microdonta</i> Desv.—S	
<i>Trichopteris microdonta</i> (Desv.) Tryon—S	
LYCOPODIACEAE	
<i>Lycopodium carolinianum</i> L.—H	
<i>Lycopodium cernuum</i> L.—H	
PINACEAE	
<i>Pinus caribaea</i> Morelet—T	
GRAMINEAE	
<i>Andropogon bicornis</i> L.—H	
<i>Andropogon leucostachyus</i> HBK.—H	
<i>Andropogon virgatus</i> Desv.—H	
<i>Eragrostis acutiflora</i> (HBK.) Nees—H	
<i>Eragrostis elliptica</i> S. Wats.—H	
<i>Eragrostis nuytensis</i> (HBK.) Steud.—H	
<i>Hemipogon atrovirens</i> (HBK.) Chase—H	
<i>Isachne polygonoides</i> (Lam.) Doell.—H	
<i>Leptocoryphium lanatum</i> (HBK.) Nees—H	
<i>Melinis blakei</i> Swallen—H	
<i>Panicum cyanicent</i> Nees ex Trin.—H	
<i>Panicum hiemii</i> Ell.—H	
<i>Panicum pilosum</i> Sw.—H	
<i>Panicum polygonatum</i> Schrad.—H	
<i>Paspalum claviflorum</i> C. Wright—H	
<i>Paspalum minus</i> Fourn.—H	
<i>Paspalum plicatulum</i> Michx.—H	
<i>Paspalum pulchellum</i> Kunth—H	
<i>Sacciolepis nyarua</i> (Lam.) Chase—H	
<i>Setaria geniculata</i> (Lam.) Beauv.—H	
<i>Thysanotus paspaloides</i> HBK.—H	
<i>Trachypogon angustifolius</i> (HBK.) Nees ex Hack.—H	
<i>Tripsacum</i> sp.—H	
CYPERACEAE	
<i>Bulbostylis paradoxa</i> (Spreng.) Lindman—H	
<i>Cyperus diffusus</i> Vahl—H	
<i>Cyperus flavus</i> (Vahl) Nees—H	
<i>Cyperus hirtellus</i> L.—H	
<i>Cyperus odoratus</i> L.*—H	
<i>Elychalis filiculmis</i> Kunth—	
<i>Elychalis retrofracta</i> (Poir.) Urban—H	
<i>Fimbristylis autumnalis</i> (L.) R. & S.—H	
<i>Rhynchospora barbata</i> (Vahl) Kunth—H	
<i>Rhynchospora cephalotes</i> (L.) Vahl—H	
<i>Rhynchospora chapmani</i> Curtis—H	
<i>Rhynchospora cyperoides</i> (Sw.) Mart.—H	
<i>Rhynchospora divergens</i> Curtis—H	
<i>Rhynchospora globosa</i> (HBK.) R. & S.—H	
<i>Rhynchospora hirsuta</i> Vahl—H	
<i>Rhynchospora muricata</i> Nees—H	
<i>Rhynchospora rugosa</i> (Vahl) Gale—H	
<i>Rhynchospora setacea</i> (Berg) Boeckl.—H	
<i>Scleria cyperina</i> Kunth—H	
PALMAE	
<i>Passiflora virgata</i> (Griseb. & Wendl.) Britt.—S	
ARACEAE	
<i>Anthurium tarraibense</i> Engler—H	
XYRIDACEAE	
<i>Xyris ambigua</i> Beyr. ex Kunth—H	
ERIOCAULACEAE	
<i>Tonina flavescentis</i> Aubl.—H	
COMMELINACEAE	
<i>Ancistena geniculata</i> (Jacq.) Woodson*—H	
HYPOXIDACEAE	
<i>Carex nigricarpa</i> (Lam.) Baker—H	
IRIDACEAE	
<i>Cipura paludosa</i> Aubl.—H	
<i>Noumeaia tenuis</i> (Herb.) Baker—H	
BURMANNIACEAE	
<i>Burmanna capitata</i> (Walt.) Mart.—H	
ORCHIDACEAE	
<i>Habenaria pauciflora</i> (Lindl.) Reichb. f.—H	
<i>Loelia tibicensis</i> (Bazem. ex Lindl.) L. Wms.—E	
<i>Scaphyglottis cuneata</i> Schltr.—E	
<i>Schwarzburgia tibicensis</i> Bazem.—E	
<i>Spiranthes</i> sp.—H	
MYRICACEAE	
<i>Myrica cerifera</i> L.—S	
FAGACEAE	
<i>Quercus oleoides</i> S. & C.—T	
AMARANTHACEAE	
<i>Alternanthera tenuis</i> (L.) R. Br.—H	
CAPPARACEAE	
<i>Cleome serrata</i> Jacq.*—H	
DROSERACEAE	
<i>Drosera capillaris</i> Poir.—H	
CHRYSOBALANACEAE	
<i>Chrysobalanus icaco</i> L.—S	
<i>Hirtella racemosa</i> Lam.—S	

TABLE I (continued)

LEGUMINOSAE	
<i>Aechynomene histrix</i> Poit.—H	
<i>Cassia diphylla</i> L.—H	
<i>Cassia flexuosa</i> L.—H	
<i>Cassia tagera</i> L.—H	
<i>Crotalaria rubiginosa</i> Juss.—V	
<i>Crotalaria parviflora</i> DC.—H	
<i>Desmanthus virgatus</i> (L.) Willd.—H	
<i>Desmodium barbatum</i> (L.) Benth. & Oerst.—H	
<i>Eristonia diffusum</i> (HBK.) G. Don—H	
<i>Eristonia punctatum</i> Standl.—H	
<i>Eristonia viciatum</i> (Aubl.) G. Don—S	
<i>Galactia</i> sp.—H	
<i>Mimosa pudica</i> L.—H	
<i>Phaseolus linearis</i> HBK.—H	
<i>Stylosanthes gyanensis</i> (Aubl.) Sw.—H	
<i>Topobria nitens</i> Benth.—H	
<i>Zornia reticulata</i> Sw.—H	
MALPIGHIACEAE	
<i>Byrsonima crassifolia</i> (L.) HBK.—T	
POLYGALACEAE	
<i>Polygala adenophora</i> DC.—H	
<i>Polygala hygrophylla</i> HBK.—H	
<i>Polygala salviniiana</i> Bennett.—H	
<i>Polygala tinctoria</i> Aubl.—H	
EUPHORBIACEAE	
<i>Acalypha arvensis</i> P. & E.*—H	
<i>Caperonia palustris</i> (L.) St. Hil.—H	
<i>Croton trinitatis</i> Millsp.*—H	
<i>Euphorbia amygdaloides</i> Boiss.—H	
<i>Euphorbia hirsutifolia</i> L.—H	
<i>Phyllanthus niruri</i> L.—H	
MALVACEAE	
<i>Ahutilon benjeyanum</i> Rose—H	
<i>Urena lobata</i> L.*—H	
STERCULIACEAE	
<i>Melochia villosa</i> (Mill.) Fowc. & Rendl.—S	
DILLENIACEAE	
<i>Davilla kunthii</i> St. Hil.—S	
OCHNACEAE	
<i>Saussurea erecta</i> L.—H	
TURNERACEAE	
<i>Piriqueta cirtoides</i> (L.) Mey. ex Steud.—H	
<i>Tournefortia</i> sp.—H	
PASSIFLORACEAE	
<i>Passiflora foetida</i> L.—H	
MYRTACEAE	
<i>Psidium guianense</i> Sw.—S	
<i>Psidium salutare</i> (HBK.) Breg.—S	
MELASTOMATACEAE	
<i>Acicis reticulata</i> (Naud.) Triana*—H	
<i>Acicantbera bisulcis</i> (Aubl.) Cogn.—H	
<i>Acicantbera quadrata</i> Pers.—H	
<i>Clidemia capitellata</i> (Bonpl.) D. Don—S	
<i>Clidemia densiflora</i> (Standl.) Gl.—S	
<i>Miconia albicans</i> (Sw.) Triana—S	
<i>Miconia ciliata</i> (L. Rich.) DC.—S	
<i>Miconia bondarensis</i> D. Sm.—S	
<i>Miconia landelliana</i> L. Wms.—S	
<i>Miconia prasina</i> (Sw.) DC.—T	
<i>Miconia schippii</i> Standl. S	
<i>Nepenthes aquatica</i> (Aubl.) Naud.—S	
<i>Pterulopsis stenophylla</i> Gl.—H	
<i>Rhynchospora paludicola</i> (D. Sm.) Gl.—H	
<i>Tibouchina aspera</i> Aubl.—S	
ONAGRACEAE	
<i>Jussiaea repens</i> Poit.—S	
GENTIANACEAE	
<i>Crotalaria pringlanum</i> (Witttr.) Rob.—H	
<i>Schultesia brachyptera</i> Cham.—H	
APOCYNACEAE	
<i>Tabernaemontana coryscarpa</i> Blake—S	
CONVOLVULACEAE	
<i>Cuscuta</i> sp.—HP	
VERBENACEAE	
<i>Citharexylum candicans</i> L.—S	
<i>Stachytarpheta angustifolia</i> (Mill.) Vahl—H	
<i>Tournefortia spicata</i> Aubl.—H	
LABIATAE	
<i>Hyptis atrovirens</i> Poit.—H	
<i>Hyptis capitata</i> Jacq.*—H	
<i>Hyptis confertiflora</i> Pohl. ex Benth.—H	
<i>Ocimum micranthum</i> Willd.*—H	
SCROPHULARIACEAE	
<i>Angelonia cilivaris</i> Rob.—H	
<i>Bombarea pusilla</i> HBK.—H	
<i>Gerardia albida</i> (B. & R.) Standl.—H	
<i>Gerardia hispida</i> Mart.—H	
<i>Gerardia spiciflora</i> Engelm.—H	
LENTIBULARIACEAE	
<i>Utricularia hispida</i> Lam.—H	
<i>Utricularia subulata</i> L.—H	
RUBIACEAE	
<i>Alibertia edulis</i> (L. Rich.) A. Rich. ex DC.—H	
<i>Anisomeris prostrata</i> (Bartl.) Standl.—S	
<i>Borreria laevis</i> (Lam.) Griseb.—H	
<i>Borreria oxymeris</i> (Burm.) DC.—H	
<i>Borreria swartziana</i> Mey.—H	
<i>Coccycoloba boritana</i> Bartl.—H	
<i>Dactyloctenium aegyptium</i> (Willd.) Kuntze—S	
<i>Drosera rotundifolia</i> Sw.*—H	
<i>Urtica hirsuta</i> DC.—S	

TABLE 1 (continued)

<i>Palicourea galottiana</i> Mart.—S	<i>Spilanthes americana</i> (Mutis) Hieron.—H
<i>Palicourea triphylla</i> DC.—SV	<i>Spilanthes merrillii</i> Standl. & Wms.—H
<i>Psychotria capitata</i> R. & P.—S	<i>Spilanthes polialepidica</i> Moore—H
<i>Psychotria officinalis</i> (Aubl.) Sandw.—S	<i>Veronica cinerea</i> (L.) Less.—H
COMPOSITAE	<i>Wedelia trilobata</i> (L.) Hitchc.—H
<i>Erechtites hieracifolia</i> (L.) Raf.*—H	<i>Zexmenia poutarou</i> Standl. & Sreyerm.—S
<i>Orthopappus angustifolius</i> (Sw.) Gl.—H	

represented mainly by a few ferns and dense patches of the clambering *Scleria secans*.

Many shrubs of the sedge savannahs (Table 1) were increasingly common with proximity to creek swamps. Some of these shrubs rightfully could be included as components of both communities, although they were restricted to the sunny edges of creek swamps. *Calliandra houstoniana* commonly flanked creek swamps.

In physiognomy, these swamps resembled creek swamps along the northern Gulf coast that are dominated by species of *Cliftonia*, *Cyrilla*, *Ilex*, *Lyonia*, and *Magnolia*. These Gulf coastal swamps share little in common floristically with Honduran creek swamps.

PINE-OAK-NANCE WOODS. As noted above, this ecotonal community is named for its three most conspicuous woody species, *Pinus caribaea*, *Quercus oleoides*, and *Byrsonima crassifolia* (nance). The pines comprised an open overstory 20–25 m tall. One pine stump 56 cm in diameter contained more than 100 annual rings. Oaks were upwards to 12 m tall and typically formed an open understory along with small trees and large shrubs of other species. Nance was the most common of these other species and grew to a height of 5 meters. *Calliandra houstoniana* was common, and a tree fern, *Alsophila myosuroides*, was conspicuous. Grasses and forbs generally comprised a continuous ground cover. This ground cover became sparse or absent in the occasional dense thickets of understory trees.

Table 3 lists 28 species characteristic of the community. Many other species belong to this community that also occur in the pine savannahs. Unfortunately, the site that was examined had been recently burned, making a thorough inventory impossible. The most common herb was *Paspalum pectinatum*. Grasses, rather than sedges, predominated in the ground cover. Notable by its absence was *Rhynchospora globosa*, the most abundant species of the sedge savannahs. The soil was loamy and probably more fertile than in the savannahs. The community resembled the pine-oak-hickory woods of the Tertiary highlands near the northern Gulf coast, both in physiognomy and with respect to soil type and fire frequency.

TABLE 2. Plants of the Creek Swamps and Their Life Forms

POLYPODIACEAE		STERCULIACEAE	
<i>Lindsaea striata</i> (Sw.) Dryand.—H		<i>Helicteres gazzanafolia</i> HBK.—S	
<i>Nephrolepis biserrata</i> (Sw.) Schott.—E		DILLENIACEAE	
<i>Polypodium palmieri</i> Maxon.—H		<i>Caratella americana</i> L.—T	
<i>Polypodium polyposoides</i> (L.) Watt.—E		GUTTIFERAE	
<i>Polypodium triseriale</i> Sw.—E		<i>Clusia flava</i> Jacq.—T	
<i>Vittaria limata</i> (L.) J. Smith.—E		<i>Clusia salvinii</i> D. Sm.—T	
CYPERACEAE		<i>Synplocis globalifera</i> L.f.—T	
<i>Scleria swani</i> (L.) Urban.—H		<i>Vimba camparagay</i> Sprague & Riley—TV	
ARACEAE		COCHLOSPERMACEAE	
<i>Syngonium podophyllum</i> Schott.—H		<i>Cochlospermum vitifolium</i> Willd. ex Spreng.—T	
BROMELIACEAE		MYRTACEAE	
<i>Anchusa bracteata</i> (Sw.) Griseb.—E		<i>Eugenia aeruginosa</i> DC.—T	
<i>Bromelia pinguis</i> L.—E		MELASTOMACEAE	
<i>Tillandsia balbisiana</i> Schult.—E		<i>Clidemia strigillosa</i> (Sw.) DC.—S	
<i>Tillandsia bulbosa</i> Hook.—E		<i>Cavendishia istandra</i> (Sw.) DC.—S	
PIPERACEAE		<i>Henrietta sacosa</i> (Aubl.) DC.—T	
<i>Piper aduncum</i> L.—T		<i>Miconia borealis</i> Gl.—T	
LORANTHACEAE		<i>Miconia ibaguenis</i> (Bonpl.) Triana—T	
<i>Phoradendron quadrangulare</i> (HBK.) Krug. & Urban.—PS		<i>Miconia schlechterdalis</i> Cogn.—S	
<i>Strathanthus orbicularis</i> (HBK.) Blume.—PV		<i>Tooca guianensis</i> Aubl.—S	
ANNONACEAE		ONAGRACEAE	
<i>Xylopia aromatica</i> (Lam.) Mart.—T		<i>Jussiaea linifolia</i> Vahl.—H	
LEGUMINOSAE		SAPOTACEAE	
<i>Calliandra hastata</i> (Mill.) Standl.—S		<i>Chrysophyllum lacinia</i> L.—T	
<i>Cassia bacillaris</i> L.f.—V		APOCYNACEAE	
<i>Pithecellobium donnell-smithii</i> (B. & R.) Standl.—T		<i>Mondorville subcaginata</i> (R. & P.) Woodson—V	
MALPIGHIACEAE		CONVOLVULACEAE	
<i>Byrsonima crassifolia</i> (L.) HBK.—T		<i>Cuscuta</i> sp.—HP	
EUPHORBIACEAE		VERBENACEAE	
<i>Pera arborea</i> Mutis.—T		<i>Cithorexylum caudatum</i> L.—T	
AQUIFOLIACEAE		<i>Laetia canara</i> L.—S	
<i>Ilex guianensis</i> (Aubl.) Kuntze.—T		SOLANACEAE	
VITACEAE		<i>Solanum jamaicense</i> Mill.—S	
<i>Cissoceros L. Rich.—V</i>		RUBIACEAE	
<i>Cissoceros salutaris</i> HBK.—V		<i>Alibertia edulis</i> (L. Rich.) A. Rich.—S	
MALVACEAE		<i>Anacardium corymbosum</i> HBK.—T	
<i>Hibiscus ferrellatus</i> Lam.—S		<i>Cephaelis tomentosa</i> (Aubl.) Vahl.—S	
		<i>Chisoceros pachyphylla</i> Wernham—V	
		<i>Guettarda cumbis</i> Urban.—T	

TROPICAL WET FOREST. As mentioned earlier, the flora of the tropical wet forests contrasted markedly with that of the savannahs, including the creek swamps and the pine-oak-nance woods. Since a systematic inventory of tropical wet forest was not possible, only a few trees have been

TABLE 3. Plants Characteristic of the Pine-Oak-Nance Woods and Their Life Forms.

T - tree, S - shrub, V - woody vine, H - terrestrial herb, E - epiphytic herb, P - parasite.

POLYPODIACEAE	GUTTIFERAE
<i>Polypodium lycopodioides</i> L.—H	<i>Vismia canparaguay</i> Sprague & Riley—TV
<i>Polypodium triseriale</i> Sw.—H	MELASTOMACEAE
<i>Vittaria lemata</i> (L.) J. Smith —E	<i>Bellucia castariensis</i> Cogn.—T
CYATHEACEAE	<i>Clidemia capitellata</i> (Bonpl.) D. Don—S
<i>Alsophila neyraudoides</i> Liebm.—S	<i>Henrietta fascicularis</i> (Sw.) Gomez—T
PINACEAE	<i>Miconia borulii</i> Gleason—T
<i>Pinus caribaea</i> Moench—T	<i>Miconia ibaguensis</i> (Bonpl.) Triana—T
GRAMINEAE	<i>Miconia lacera</i> (Bonpl.) Naud.—S
<i>Axonopus purpusii</i> (Mez) Chase—H	<i>Miconia prasina</i> (Sw.) DC.—T
ARACEAE	ARALIACEAE
<i>Anthurium scandens</i> (Aubl.) Engler—H	<i>Didymopanax neruense</i> (Aubl.) Dcne. & Planch.—T
ORCHIDACEAE	CLETHRACEAE
<i>Epidendrum nocturnum</i> Jacq.—E	<i>Clethra macrophylla</i> Mart. & Gal.—T
FAGACEAE	RUBIACEAE
<i>Quercus strobila</i> S. & C.—T	<i>Alibertia edulis</i> (L. Rich.) A. Rich.—S
LEGUMINOSAE	<i>Palicourea triphylla</i> DC.—V
<i>Calliandra basitoniata</i> (Mill.) Standl.—S	<i>Pryobotria caespitosa</i> Bredem. ex R. & S.—S
<i>Cassia bacillaris</i> L.f.—V	<i>Sabicea panamensis</i> Wernham—V
MALPIGHIACEAE	COMPOSITAE
<i>Byrsonima cratifolia</i> (L.) HBK.—T	<i>Zexmenia pinetorum</i> Standl. & Seeyerem.—S
AQUIFOLIACEAE	
<i>Ilex guianensis</i> (Aubl.) Kuntze—T	

TABLE 4. Trees Characteristic of the Tropical Wet Forest.

SWAMP FOREST, NEAR MOUTH OF RIO PLÁTANO	RIVERINE FOREST 10-25 KM FROM MOUTH OF RIO PLÁTANO
<i>Montrichardia arborescens</i> (L.) Schott	<i>Pavonia aspera</i> Trecul.
<i>Coccoloba barbadensis</i> Jacq.	<i>Vochysia hondurensis</i> Sprague
<i>Annona glabra</i> L.	<i>Capania aviculata</i> Standl.
<i>Inga sparia</i> H. & B. ex Willd.	<i>Apios membranacea</i> Spruce ex Benth.
<i>Pithecolobium latifolium</i> (L.) Benth.	<i>Protium glabrum</i> (Rose) Engler
<i>Carapa guianensis</i> Aubl.	<i>Annona muricata</i> L.
<i>Pachira aquatica</i> Aubl.	<i>Sloanea zuluensis</i> Pitt.
<i>Synphonia globulifera</i> L.f.	<i>Bixa orellana</i> L.
<i>Pleuranthodendron mexicana</i> (Gray) L. Wms.	<i>Apidisperma neogalcarpor</i> Muell.-Arg.
<i>Grias integrifolia</i> (Standl.) Kunth	<i>Miconia hondurensis</i> D. Sm.
<i>Tournefortia bicolor</i> Sw.	
<i>Pavonia stenura</i> Standl.	
<i>Hamelia rostrata</i> Wernham	
<i>Palicourea fastigata</i> Benth.	

listed to introduce the tropical wet forest and to indicate the considerable floristic differences with savannas. Table 4 lists trees collected in a swamp near the mouth of the Río Plátano and in the floodplain and associated slopes of this river at collecting stations 10, 18, and 25 km inland from the coast. *Symphonia globulifera* was the only species common to the tropical wet forest and savannah flora listed in Tables 1-3.

The same degree of floristic contrast is evident along the northern Gulf coast, where hardwood forests of floodplains and ravines differ substantially from adjacent pinelands and savannas (Clewell 1977, Clewell et al. 1982).

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SYSTEMATICS OF NAMA (HYDROPHYLLACEAE):
COMPARISON OF SEED MORPHOLOGY OF SECTS.
ARACHNOIDEA AND CINERASCENTIA WITH FIVE
SPECIES OF ERIODICTYON AND
TURRICULA PARRYI

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ABSTRACT

Nama lobbii and *N. rothrockii*, members of the monotypic sects *Arachnoidea* and *Cinerascenia*, respectively, are divergent elements in *Nama* and their relationships with the genus have been questioned. Alternative genera with which the two might be allied are *Eriodictyon*, traditionally allied with *Nama*, or possibly, *Turricula*, historically associated with both genera. Utilizing scanning electron microscopy, seeds from five distinctive species of *Eriodictyon*, *E. crassifolium* var. *denudatum*, *E. tomentosum*, *E. traskiae* subsp. *smithii*, *E. angustifolium* and *E. californicum*, *Turricula parryi* and the two *namas* were examined for implications resident in seed morphology that might bear on placement of *N. lobbii* and *N. rothrockii*. Seeds of the *namas* are distinct from both *Eriodictyon* and *Turricula*, while seeds of the latter taxa are quite similar. Seed morphology combined with other available evidence suggests that *N. lobbii* and *N. rothrockii* are distinct phyletic elements within the Hydrophyllaceae.

INTRODUCTION

Nama is the second largest genus in the Hydrophyllaceae, housing about 50 species ranging from short-lived annuals to robust subshrubs. Distributionally, species occur predominantly in western and southwestern United States and Mexico but three venture into South America and one is endemic to Hawaii. They occupy a variety of habitats ranging from arid, alkaline-gypseous flats in the central Chihuahuan Desert to more mesic, but seasonally dry slopes and higher elevations in the sierras of western North America and eastern Mexico.

As treated by Hitchcock (1933), the genus is structured of five sections; *Arachnoidea*, *Cinerascenia*, *Conanthus*, *Zonolacus* and *Nama* (as *Eunama*). Much the largest, sect. *Nama* comprises an extremely diverse group of

species unified by their entire leaves, styles that are free or connate less than half their length, a superior ovary, membranous, loculicidally dehiscent capsules and axillary, extra-axillary or terminal, one, two or few-flowered cymose inflorescences. Each of the smaller sections is separated from the largest by clearly distinctive features; sect. *Conanthus*, (3 sp.), houses dichotomously branched annuals with styles connate over half their length; sect. *Zonolacus*, (1 sp.), exhibits a half inferior ovary; sect. *Arachnoidea*, (1 sp.), produces cartilaginous, loculicidally and septicidally dehiscent capsules; sect. *Cinerascentia*, (1 sp.), displays crenate leaves and capitate inflorescences.

Species of sects. *Arachnoidea* and *Cinerascentia*, *Nama lobbii* Gray and *N. rothrockii* Gray, respectively, are critical elements in *Nama*. They are the most divergent namas, morphologically, and thus, set the limits of *Nama*. Moreover, it is through *N. lobbii* that the nearest relative of *Nama* has traditionally been identified as *Eriodictyon*, so the former taxon serves in positioning *Nama*, as well. However, a growing body of evidence portrays these taxa as more distant from *Nama* proper than was reckoned by Hitchcock (1933) and their inclusion in *Nama* lately has been questioned (Bacon 1984, 1974; Chance and Bacon 1984; Raven and Axelrod 1978). For, not only do they diverge from the bulk of *Nama* in gross morphology, they also diverge in seed morphology (Chance and Bacon 1984), chromosome number (Bacon 1984, Cave and Constance 1947, 1959; see Constance 1963, for summary) and flavonoid chemistry (Bacon, Fang and Mabry, in review). Thus, placement of *N. lobbii* and *N. rothrockii* appears seriously challenged and their positioning elsewhere must be considered. Since *N. lobbii* has been closely associated with *Eriodictyon*, traditionally, the latter taxon is a logical alternative genus with which the former species and, perhaps, *N. rothrockii* might be more closely allied. A second alternative is the monotypic *Turricula*, historically associated with both *Nama* and *Eriodictyon*. Since seed morphology has proven informative in suggesting relationships not previously evident, morphologically, in *Nama* (and other groups, see Chance and Bacon 1984, and references therein), it follows that comparison of seed morphology among these four taxa might provide insight relevant to positioning of *N. lobbii* and *N. rothrockii*. Therefore, we have examined seed morphology of the two species of *Nama*, five distinctive species of *Eriodictyon*, *E. crassifolium* Benth. var. *dennudatum* Abrams, *E. tomentosum* Benth., *E. traskiae* Eastw. subsp. *smithii* Munz, *E. angustifolium* Nutt., *E. californicum* (H. & A.) Torr., and *Turricula parryi* (Gray) Macbr. We report herein results of that survey and implications as they bear on placement of *N. lobbii*, *N. rothrockii* and systematics of *Nama* proper.

MATERIALS AND METHODS

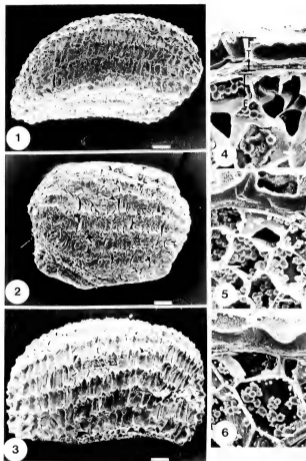
Mature, whole seeds removed from herbarium specimens were mounted on brass stubs with double-stick carpet tape. For examination of internal features of the testa, seeds were sectioned free-hand with a razor blade and mounted as for whole seeds. Specimens were coated to a thickness of approximately 25–30 nm in a Polaron E5100 sputter coater using gold-palladium target and examined with a JEOL JSM 35-C SEM at an accelerating voltage of 15 kV. A minimum of five seeds per collection was examined.

RESULTS

Seeds of examined species of *Eriodictyon* and *Turricula* are remarkably homogeneous. While there are variations in precise shape and size, as noted for seeds in other plant groups (see Chance and Bacon 1984, and references therein), generally, seeds of both taxa are irregularly oblong (Figs. 1,2,3,7,8,9) in outline, more or less angulate-wedge shaped in cross section and average over 1 mm in length (Table 1). The outer testa in all is clearly cellular in composition and surface patterning in all is shallowly reticulate, following the terminology of Chance and Bacon (1984). Reticulum cells are arranged into definite rows, with each cell elongated at right angles to the long axis of the seed. The longer radial walls in each cell are conspicuously concave. This organization accounts for their "transverse corrugations" as seen under the light microscope. In section (Figs. 4,5,6,10,11,12), the lower tangential wall of each reticulum cell appears weakly to strongly undulate suggesting thickenings or, perhaps, compres-

TABLE 1. Seed characteristics of *N. lobtii*, *N. rostrckii*, *Eriodictyon* and *Turricula*.

Taxon	Length (\bar{X} ,mm)	Width (\bar{X} ,mm)	Coat Thickness (min-max, μ)
<i>N. lobtii</i>	1.26	0.82	12–40
<i>N. rostrckii</i>	1.52	1.01	30–58
<i>E. angustifolium</i>	1.02	0.65	15–24
<i>E. crassifolium</i> var. <i>denticulatum</i>	1.22	0.78	4–8
<i>E. tomentosum</i>	1.09	0.70	3–6
<i>E. traskiae</i> subsp. <i>smithii</i>			
Hannan 65	1.11	0.80	6–12
Hannan 60	1.29	0.71	10–12
<i>E. californicum</i>	1.03	0.62	6–8
<i>T. parryi</i>	1.10	0.70	10–16



Figs. 1-6. Seeds of *Eriodictyon*. (Bar in whole seed figures = 100 μ ; bar in section figures = 10 μ ; bars apply to all figures) 1. *E. crassifolium* var. *denudatum*, whole seed, 2. *E. tomentosum*, whole seed, 3. *E. smithii* subsp. *traskiae*, whole seed. 4. *E. crassifolium* var. *denudatum*, seed section (T = seed coat, E = endosperm, applies to all sections). 5. *E. tomentosum*, seed section. 6. *E. smithii* subsp. *traskiae*, seed section.

sion ridges. Radial walls, however, lack thickenings, with the possible exception of *E. tomentosum* (Fig. 5, upper left corner); however, additional examination is required to confirm or deny this possibility since potential thickenings do not occur in each reticulum cell in this species. The seed coat in these taxa varies in thickness among species and at different points within a single seed section (Table 1) and ranges from a low of 3μ in *E. tomentosum* to a high of 24μ in *E. angustifolium*.

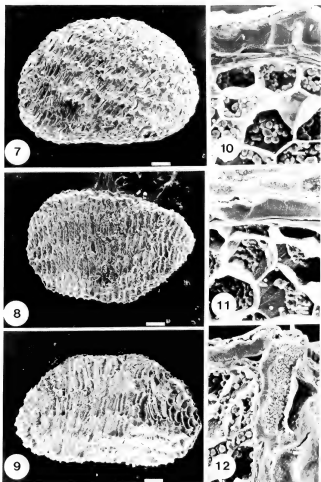
Seeds of *N. rotbrockii* and *N. lobbii* (Figs. 13, 14) essentially conform with those as reported by Chance and Bacon (1984) except that seed coat thickness and average seed length of both is slightly less for seeds examined in this study. Seeds of the former taxon exhibit a foveolate-alveolate surface patterning and a solid outer testa $30\text{--}58\mu$ in thickness (Fig. 15; Table 1); those of the latter exhibit a papillose surface (Fig. 14) and a solid outer testa $12\text{--}40\mu$ in thickness (Fig. 16; Table 1).

Seeds of both *N. lobbii* and *N. rotbrockii* are distinctive when compared with *Eriodictyon* or *Turricula*. Neither of the former species exhibits the chambered, ordered reticulum of the latter and the seed coat is generally much thicker in the former. In this last respect, however, the thinner areas in the testa of *N. lobbii* are within the range of variation in thickness of the testa in *Eriodictyon* and *Turricula*. Nevertheless, in overall morphology there is little similarity among seeds of *N. lobbii* or *N. rotbrockii* and those of the latter genera.

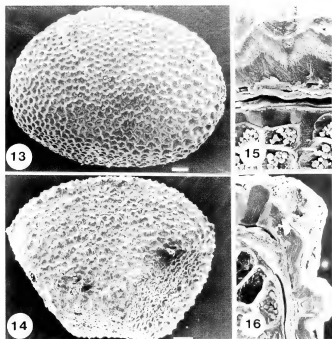
DISCUSSION

The lack of similarity in seed features of *N. lobbii*, *N. rotbrockii* and *Eriodictyon* is accentuated by the striking similarity among seeds of the latter and *Turricula*; seed features clearly countenance an alliance of these two genera. However, neither of the names can be closely allied to *Eriodictyon* or *Turricula* based on seed characteristics, nor can they be closely allied one to another on these features. Indeed, seed morphology implies that both *N. lobbii* and *N. rotbrockii* are elements phylogenetically distinct from *Eriodictyon*, *Turricula* and *Nama* (see Chance and Bacon 1984) and, therefore, distinct elements within the Hydrophyllaceae, as suggested by Bacon, Fang and Mabry (in review). Moreover, such a view is consistent with other available evidence and reconciles the lack of agreement in past dispositions of *N. lobbii*.

In structuring *Nama* into five sections, Hitchcock (1933) was recognizing the unique features exhibited by species forming the four smaller sections. Indeed, features of these species had long been appreciated, but there had been little agreement as to their systematic significance. Various workers had subjectively appraised one or another of these taxa as distinct



Figs. 7-12. Seeds of *Eriodictyon* and *Torrivala*. 7. *E. angustifolium*, whole seed. 8. *E. californicum*, whole seed. 9. *T. parryi*, whole seed. 10. *E. angustifolium*, seed section. 11. *E. californicum*, seed section. 12. *T. parryi*, seed section.



Figs. 13–16. Seeds of *N. rustroclivii* and *N. lobbii*. 13. *N. rustroclivii*, whole seed. 14. *N. lobbii*, whole seed. 15. *N. rustroclivii*, seed section. 16. *N. lobbii*, seed section.

genera (e.g., Peter 1897, Gray 1875), as subgenera of *Nama* (Brand 1913, Jepson 1925) or as members of other recognized genera (Greene 1885, Hall 1906). In positioning *N. lobbii*, Hitchcock (1933) was aware that the taxon had been transferred to *Eriodictyon* by Greene (1885), accepted there by Hall (1906), but excluded from that genus in its then most recent treatment by Abrams and Smiley (1915). Entering into Hitchcock's (1933) deliberations, too, was the positioning of the problematical *Turricula*; originally described as a *Nama* (Gray 1880), the taxon was transferred to *Eriodictyon* by Greene (1889), where it was accepted by Hall (1902), but was rejected there by Abrams and Smiley (1915) and subsequently established as the monotypic *Turricula* by Macbride (1917). Hitchcock

concluded, nevertheless, that *T. parryi* was more appropriately housed in *Eriodictyon*; he retained *N. lobbii* as a section of *Nama* and then allied *Nama* and *Eriodictyon* through these two taxa.

Subsequent to Hitchcock's work, Cave and Constance (1942, 1944, 1947, 1950, 1959) and Constance (1963) have extensively surveyed chromosome numbers within Hydrophyllaceae. All species of *Eriodictyon* exhibit $n = 14$; *T. parryi* has $n = 13$, supporting its recognition as a monotypic genus. In contrast, *Nama*, including sects. *Conanthus* and *Zonolacus*, is strikingly diploid with $x = 7$ (only three species of *Nama* proper are consistently tetraploid; all are herbaceous and clearly to be related to other species in *Nama* proper; see Bacon 1984). However, *N. lobbii* exhibits $n = 14$, while *N. rotrockii* has $n = 17$ (Bacon 1974, 1984; Constance 1963), marking them as distinct within *Nama*. Chromosome number of *N. lobbii* supports its potential alliance with *Eriodictyon*; however, the number in *N. rotrockii* is known elsewhere in the family only in the South African *Codon*.

Chance and Bacon (1984) have found that seed morphology identifies six species groups within *Nama*. Species of sect. *Nama* compose five groups; importantly, species of sects. *Conanthus* and *Zonolacus* are separately accommodated in two of these five groupings. Species of sects. *Arachnoidea* and *Cimerascentia*, in contrast, form the sixth seed group; their seeds are much larger, exhibit a thicker seed coat and possess distinctive sculpturing patterns when compared with other groups. However, as evident herein, seeds of each taxon are distinctively organized, and Chance and Bacon (1984) noted that any relationship between the two should be viewed as distant with relationships to the bulk of *Nama* even more remote. Results presented in this report substantiate the views of Chance and Bacon (1984) and, furthermore, suggest that the two *namas* should be positioned some distance from both *Eriodictyon* and *Turricula*.

Flavonoid chemistry of *N. lobbii* and *N. rotrockii* has been determined (Bacon, Fang and Mabry, in review), and it is unique within *Nama*, as well; both taxa accumulate 6-oxygenated flavone aglycones, whereas other *namas* accumulate flavonoids with usual oxygenation patterns. However, flavonoids of three species of *Eriodictyon*, *E. tomentosum*, *E. californicum* and *E. angustifolium*, also have been resolved (Bacon et al., in review), and all accumulate 6-oxygenated flavone aglycones; chemistry of the two *namas* and three *eriodictyons* is quite similar, arguing that they are to be allied, nevertheless.

Morphologically, *Eriodictyon* is one of the more homogeneous genera of Hydrophyllaceae. All species are rhizomatous shrubs with scorpioid inflorescences, except for *E. capitatum* Eastw., and loculicidally and septicidally

dally dehiscent capsules (Munz and Keck 1959, Carlquist et al. 1983). As well, their uniform chromosome number and the uniformity in flavonoid chemistry and seed morphology among examined species argues convincingly that the genus represents a single phyletic element. To position *N. lobbii*, as suggested by Greene (1885), or *N. rotbrockii* within *Eriodictyon* would destroy the homogeneity of the latter; although *N. lobbii* is woody and both *nama*s are rhizomatous (Bacon, pers. obs.; Jepson 1943), neither is a shrub, both tend to be spreading and mat-forming, and neither exhibits scorpioid inflorescences. Moreover, seed morphology of these taxa does not contenance such a union. Considering *Turricula*, its seed morphology clearly suggests a close alliance with *Eriodictyon*; however, while it possesses scorpioid inflorescences and its capsules dehisce in the same manner as do those of *Eriodictyon*, this perennial's upright, herbaceous habit and its chromosome number argue that it is correctly recognized. Seed morphology clearly distinguishes *N. lobbii*, in particular, and *Nama* proper, in general (see Chance and Bacon 1984), from *Turricula*. Therefore, any relationship between *Nama* and *Eriodictyon* is portrayed as less direct and more remote than surmised by Hitchcock (1933); in fact, how *Nama* proper relates to *N. lobbii*, *N. rotbrockii* or *Eriodictyon* is not clear. Indeed, accumulated evidence suggests that *N. lobbii* and *N. rotbrockii* are distinct phyletic elements within the Hydrophyllaceae. Their affinities, as suggested by their flavonoid chemistry and rhizomatous habit, lie nearer to *Eriodictyon* than to *Nama*, although *N. lobbii*, with its capsular dehiscence pattern, woody habit and chromosome number is nearer *Eriodictyon* than is *N. rotbrockii*. Such a view renders *Nama*, although still diverse, more homogeneous and acknowledges the distinctive characteristics of *N. lobbii* and *N. rotbrockii*. A treatment formalizing this view is forthcoming.

ACKNOWLEDGEMENTS

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APPENDIX: Source of Seed Samples

Vouchers for *Eriodictyon* are deposited at EMC;
those for *Nama* will be deposited at TEX.

Nama lobbii: CALIFORNIA: Eldorado Co.: 14 mi N of South Lake Tahoe on Hwy 89, near Emerald Bay, Bacon 1700. *N. rotbrockii*: CALIFORNIA: Inyo Co.: 1.9 mi below Onion Creek Campground, 10.1 mi W of Independence, Bacon 1699. *Eriodictyon angustifolium*: UTAH: Washington Co.: 1 mi S of Pintura, Hannan 503. *E. crassifolium* var. *denudatum*: CALIFORNIA: Ventura Co.: California Hwy 33, 20.4 mi N of jet with California Hwy 150, Hannan

64. *E. tomentosum*: CALIFORNIA: Kern Co.: Park Hill Rd, 3.7 mi S of California Hwy 58, *Hannan* 58. *E. smithii* ssp. *traskiae*: CALIFORNIA: Santa Barbara Co.: E Camino Cielo Road, 7 mi W of Gibraltar Road, *Hannan* 60; California Hwy 1, 2.8 mi N of Burton Mesa Rd., Purisima Hills near Lompoc, *Hannan* 65. *E. californicum*: CALIFORNIA: Calaveras Co.: Old Priest Grade (California Hwy 120) W of Chinese Camp, *Hannan* 57. *Torrucula parryi*: CALIFORNIA: San Diego Co.: Pine Valley, *Rise* 35306 (MICH).

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VEGETATIVE APOMIXIS IN *MUHLENBERGIA REPENS* (POACEAE: ERAGROSTIDEAE)

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Vegetative apomixis in grasses refers to the production of bulbils (a small bulb or bulblike structure produced on above ground parts, Radford et al. 1974, p. 92) in flowers by modification of spikelet structures (lemma, palea, androecium, and/or gynoecium). The term "vivipary", which is the germination of a seed within the flower (Stebbins 1941), has often been misapplied to describe this phenomenon (Nygren 1954, Gould 1968). Vegetative apomixis is known to occur in the families Agavaceae, Liliaceae, Poaceae, Polygonaceae, and Saxifragaceae. In grasses, it is most commonly associated with the tribes Poeae (*Poa* and *Festuca*) and Aveneae (*Deschampsia* and *Agrostis*). However, it has also been described in the Chlorideae for *Bouteloua* (Hill 1982), the Eragrostideae for *Eleusine* (Nygren 1954), and in the Paniceae for *Setaria* (Nygren 1954). This condition has been previously mentioned in the Eragrostideae for *Muhlenbergia richardsonis* (Trin.) Rydb. (Cronquist et al. 1977) although not described. In the course of field collections, three populations of *M. repens* (Presl) Hitchc. were collected that had spikelets exhibiting vegetative apomixis. Two of these populations were separated by approximately 50 kilometers and disjunct from the third by approximately 600 kilometers. Collection data for the specimens are given in Table 1. Following is a description of the spikelet parts of the three populations.

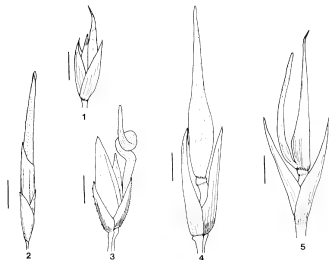
Spikelet structures of non-apomictic spikelets have glumes 1.6–2.4 mm long, lemmas 2.6–3.2 mm long, and paleas 2.1–2.7 mm long (Fig. 1). The vegetative apomictic specimens of *Morden et al.* 518 have spikelets with dimensions that are average for the species (Figs. 2 and 3). The rachillas of these spikelets are not elongated. The androecia and gynoecia are modified into bulbils and the leaf of the bulbil either extends out the top of the spikelet between the lemma and palea, or grows through the palea and curves upward, usually twisting.

The production of bulbils in *Morden et al.* 521 and *Morden* 684 is similar to that of population 518. However, the appearance of these spikelets are greatly modified. The glumes are greater than 3 mm long (longer than many sexual spikelets). The rachilla is also elongated, in most cases 1–2

mm long, resulting in the floret being exposed well above the glumes. The lemma is elongated to 5 mm or more in length and the palea appears to be absent or modified forming the outer leaf of the developing bulbil. The appearance of the bulbil in other respects is similar to that previously described.

Vegetative apomixis in these populations was not present in all spikelets of the inflorescence. Apomictic conditions are usually limited to several spikelets within an inflorescence and only a few individuals from each population.

There are several postulations as to why vegetative apomixis develops in populations. There is a strong correlation between the presence of this condition and the ploidy level of the species involved such that as ploidy level



Figs. 1-5. Vegetative apomixis in *Mahlenbergia repens*. 1. A non-vegetative apomictic spikelet of *M. repens* with average spikelet dimensions (Morales *et al.* 521). 2. Vegetative apomictic spikelet with the leaf of the bulbil extending out the top of the spikelet (Morales *et al.* 518). 3. Vegetative apomictic spikelet with the leaf of the bulbil extending through the palea and upwards (Morales *et al.* 518). 4. Vegetative apomictic spikelet with elongated glumes, rachilla, and lemma. Bulbil is not evident (Morales 684). 5. Vegetative apomictic spikelet with elongated glumes, rachilla, and lemma. Bulbil is extending through the palea and upward (Morales *et al.* 521).

TABLE 1. Collection data for vegetative apomictic populations in *Muhlenbergia repens*. Specimens are deposited at TAES.

MEXICO. NUEVO LEON. Scattered patches along hillside, 8 km W of "Y" intersection in Galeana, 1740 m elev., 27 Aug 1981, *Morden, Hatch, & Valdes R. 518*; in low areas along Hwy 57, 32 km N of San Roberto, 18 km S of San Rafael, small patch associated with *M. utilis* and *M. villosa*, 1740 m elev., 27 Aug 1981, *Morden, Hatch, & Valdes R. 521*. UNITED STATES. TEXAS. Jeff Davis Co.: 17 mi S of Kent in canyon along Hwy 118, 1730 m elev., 13 Oct 1982, *Morden 684*.

increases, vegetative apomixis becomes more prevalent (Stebbins 1941, Nygren 1954). This is found either within a single species with various ploidy levels or within a genus. In his work on *Deschampsia*, Nygren (1954) found vegetative apomixis to be caused by a single recessive gene. Nygren also reported that for *Poa alpina* this condition was either gene related or environmentally stimulated. Because of the presence of two such distinct morphological forms, we feel that vegetative apomixis in *Muhlenbergia repens* is the result of two independent evolutionary occurrences. Since it is seldom found in natural populations, it is possibly the result of a recessive gene that is prompted by environmental stimulation resulting in a low frequency of occurrence in the population.

Another means by which this may have become incorporated into *M. repens* is through hybridization. *Muhlenbergia richardsonis* is closely related to *M. repens* and independent studies by the first author have shown there to be intergradation of morphological characteristics in eastern Arizona and western New Mexico where the two species overlap in distribution. It is possible that genes carrying traits for vegetative apomixis were passed from one species to the other and introgressed into the other populations. This process could have happened in either direction. However, it does not seem likely because of the two differing morphological types.

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ANISACANTHUS QUADRIFIDUS SENSU LATO (ACANTHACEAE)

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Studies of a third linear-leaved taxon of *Anisacanthus* from the Chihuahuan Desert Region [see Henrickson and Lott, 1982 for discussion of *Anisacanthus linearis* (Hagen) Henrickson and Lott, and Daniel and Henrickson, 1982 for discussion of *A. junceus* (Torr.) Hemsl.] have lead to a re-evaluation of two wide-spread species: *A. wrightii* (Torr.) Gray and *A. quadrifidus* (Vahl) Nees. *Anisacanthus wrightii* and *A. quadrifidus* were distinguished by Hagen in his 1941 monograph of the North American species of the genus on the basis of calyx size and calyx lobing. *Anisacanthus quadrifidus*, which ranges from San Luis Potosi south to Hidalgo, Puebla and Oaxaca, has calyces 7–10 mm long with attenuate lobes 5–6 mm long while *A. wrightii* of Texas, Coahuila, Nuevo Leon, Tamaulipas has shorter calyces under 5 mm in length with acute lobes 1–3 mm long. In his monograph, Hagen named a new variety of *A. wrightii* from near Saltillo, Coahuila with narrow leaves and very short calyx lobes as *A. w.* var. *brevilobus* Hagen.

A similar, and even more distinct taxon with shorter calyces and even narrower leaves is here separated from Hagen's *A. quadrifidus*. The new taxon, from the states of San Luis Potosi and Zacatecas, was hidden within Hagen's *A. quadrifidus*. A total of six specimens referable to the taxon were cited by Hagen (1941) in his specimens examined, but their measurements were neither included in the species description nor in the key, and until his cited specimens were seen, recent collections of the taxon were considered novelties. The taxon is here referred to by its manuscript name "*potosinus*."

Hagen (1941) considered vestiture, corolla size and particularly calyx characters as important features in distinguishing taxa of *Anisacanthus*. While *A. quadrifidus* and *A. wrightii* differ in some quantitative leaf and calyx features, they are similar in a large number of both qualitative and quantitative features including growth habit, stem and leaf vestiture, leaf texture, inflorescence and bract size, orientation, and structure, calyx vestiture and corolla size, structure and orientation etc. (see descriptions

below). In contrast, other North American species in the genus have some complex of character states that set them apart from these and other species (see Hagen 1941).

In addition to the calyx characters indicated by Hagen, *A. quadrifidus* and *A. wrightii* also differ in leaf size and petiole length. *Anisacanthus wrightii* tends to have broader leaves [(7-)11–20 mm wide] and longer petioles [(2.5-)5–10 mm long] than *A. quadrifidus* which typically has mature leaves only 3–11 mm wide and petioles only 1–4 mm long.

The quantitative differences between these taxa are illustrated by means of bivariate plots in Fig. 1a, b, and by line drawings in Fig. 2. Figure 1a is a simple bivariate plot showing petiole length (in mm) as y-axis and maximum leaf width (in mm) as x-axis for each of the four recognized taxa and an intermediate population. Leaf width-petiole length measurements were taken from 1 leaf per herbarium specimen (from 1 per collection when duplicates were present) from "typical" large leaves. While it is recognized that this neither represents a statistical sample nor necessarily represents the largest leaves present on the plant, it does reflect the characters available to a taxonomist working with herbarium material.

Figure 1b is a similar bivariate plot for calyx features with the y-axis showing calyx-tube length, the x-axis showing calyx-lobe length for the same specimens and taxa. Calyx measurements were taken from flowers at or near anthesis as calyx tubes are slightly accrescent. There always is some variation among these measurements on any specimen and the data presented here are intended to show only the trends in variation.

Data in Fig. 1a, depicting leaf width vs. petiole length, show a continuous range of variation from the broad-leaved, long-petioled *A. wrightii* to the progressively narrower-leaved, shorter-petioled *A. quadrifidus*, and taxa *brevilobus* and "*potosinus*" with some overlap between each taxon. Figure 1b, showing calyx tube vs. calyx lobe lengths, illustrates a similar pattern. However, in these characters, *A. quadrifidus* has the longest calyx lobes, 2 to 4 times longer than the calyx tubes, and *A. wrightii* and taxon "*potosinus*" both have shorter calyx lobes, 1 to 2 times longer than the tubes. Calyx lobes of taxon *brevilobus*, in contrast, are as long as or shorter than their calyx tubes (Fig. 1b).

When both data sets are considered, one sees that each taxon has its own unique quantitative characters. *Anisacanthus wrightii* has broader leaves and longer petioles; *A. quadrifidus* has the longest sepal lobes, relatively short petioles; taxon *brevilobus* has moderately narrow leaves, and very short calyx lobes; while taxon "*potosinus*" has very narrow leaves, small calyces but with moderately long lobes. These characters, however, are not discrete from those of the other taxa. Rather the character states are contiguous or

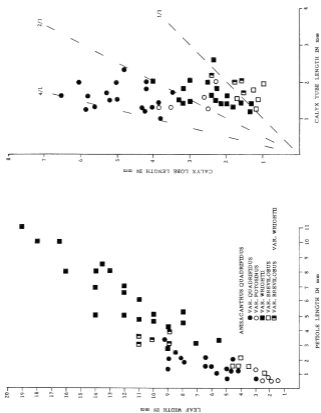


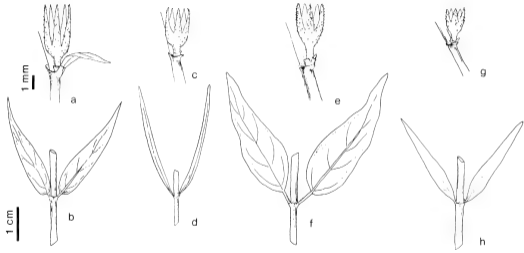
Fig. 1. Bivariate plots of leaf and calyx characters of *Anisacanthus quadrifidus*. a. — Standard plot of petiole length (in mm) vs. maximum leaf width (in mm). Data obtained from largest leaf present in herbarium specimens of collections available for study. Designation of infraspecific taxa are indicated as shown. Plants near Galeana, Nuevo Leon with leaves as in *A. q.* var. *wrightii* but calyces as in *A. q.* var. *brislobius* are indicated as intermediate between these taxa. b. — Standard plot of calyx tube length vs. calyx lobe length in mm of calyces of flowers at or very near anthesis. Dashed lines indicate ratios of lobe vs. tube lengths where lobes are equal to tube length (1/1), two times tube length (2/1), and four times tube length (4/1).

slightly overlapping with those of related taxa (Fig. 1a, b). The fact that these four taxa share a large number of vegetative and floral characteristics and that other North American taxa in the genus differ to some degree from these taxa in various quantitative or qualitative characteristics supports the contention, presented here, that the four taxa are best ranked at the infraspecific level rather than as distinct species.

Each taxon also has its own geographical range. *Anisacanthus quadrifidus* is known from arid deciduous scrub in southern Mexico from Oaxaca, Puebla north to the states of Mexico, Hidalgo and Queretaro from 1000–2400 m elevation (Fig. 3). In contrast, *A. wrightii* occurs in the Tamaulipan scrub from southern Texas through Coahuila, Nuevo Leon south into Tamaulipas mostly from 320–900 m elevation. Although these two allopatric taxa are sometimes quantitatively similar, identification of herbarium specimens is never a problem as the taxa easily can be distinguished geographically. Hagen's *A. wrightii* var. *brevilobus* occurs locally in canyons and drainages east of Saltillo, Coahuila in the transition between semi-arid plains and chaparral scrub vegetation on the slopes from 1500–1800 m elevation (Fig. 3). There are populations combining the characters of *A. wrightii* and taxon *brevilobus* in the Sierra Madre Oriental about 110 km southeast of this area near Galeana and Pablillo, Nuevo Leon that have the short calyx lobes of taxon *brevilobus* and the long-petioled, broader leaves typical of *A. wrightii*. They also occur at an elevation more characteristic of taxon *brevilobus*—1700–2000 m. These intermediate plants are designated in Figs. 1, 3 by intermediate (half-darkened) symbols. Not all collections from this area have short calyx lobes however. The origin of the short calyx lobes may be related to past introgression between *A. wrightii* and the taxon *brevilobus*.

The connecting link between *A. quadrifidus* and *A. wrightii* is provided by the narrow-leaved taxon "*potosinus*" which occurs along the southern border of the Chihuahuan Desert Region and in more montane areas within the southern portion of the Chihuahuan Desert proper from San Luis Potosi to northern Zacatecas (Fig. 3). The taxon occurs in an arid scrub mostly from 1800–2100 m elevation. With its very narrow, linear-lanceolate leaves and relatively short calyces, it appears very much like a more xeric-adapted derivative of *A. quadrifidus*. While taxon "*potosinus*" is disjunct from *A. quadrifidus* in the south, its northern range shows a geographical link with *A. wrightii*.

The question arises whether the short calyx-lobe character of *A. wrightii* var. *brevilobus* could have arisen from past introgression with northern populations of short-calyced "*potosinus*." As noted above, populations of "*potosinus*" currently occur at relatively high elevations along the southern



border of, and in scattered montane islands within the southern Chihuahuan Desert. It is probable that during the Holocene "*potosinus*" was more widespread and may have come into contact with other taxa of *Anisacanthus*.

Daniel (1982) reports that while natural hybrids are not known in *Anisacanthus*, he has successfully made artificial crosses between *A. wrightii* and the longer-flowered *A. linearis* and *A. thurberi*. The progeny of these crosses exhibited pollen stainability of 99 and 91 percent respectively. If one finds such high cytological compatibility between these diverse species, may we expect the same from the four taxa dealt with in this paper?

The striking vegetative similarity between "*potosinus*" and the linear-leaved *A. linearis* (Henrickson and Lott 1982) and *A. junceus* (Daniel and Henrickson 1982) of the northern Chihuahuan Desert is very apparent. Vegetatively these three taxa are difficult to distinguish, however, *A. linearis* and *A. junceus* belong to a separate lineage within the genus that has much longer corollas (40–56 mm long) with longer lobes and filaments (18–35 mm long) than those of the *A. quadrifidus-wrightii* taxa whose corollas and filaments measure 30–38 mm (rarely to 45) and 9–11 mm respectively. They also differ in a number of other characteristics involving vestiture, pedicels, calyx structure etc., characters that are not in evidence in "*potosinus*." Whether the linear-leaved characteristics of these taxa and our "*potosinus*" is due to convergent adaptation to xeric habitats or is due to past introgression with these taxa is unknown. But the lack of *A. linearis* and *A. junceus* characteristics in "*potosinus*" suggests the independent development of linear leaves by "*potosinus*."

As noted above, the occurrence of "*potosinus*" in the Chihuahuan Desert was unknown to me until recently. A collection from northern Zacatecas (Henrickson 6222) was confused with *A. junceus* and illustrated as *A. junceus* by Henrickson in Daniel and Henrickson (1982, Fig. 1c). As noted in the paper it differed from true *A. junceus* in its more distinctly glandular calyx.

Fig. 2. Line drawings of calyces and leaves of varieties of *Anisacanthus quadrifidus*. a-b. — *A. q.* var. *quadrifidus*. a. — Calyx showing persisting bract. Note position of line of abscission above persisting bract base and long calyx lobes. b. — Leaves. Note relatively short petiole. Both Lott & Wendt P35 (TEX). c-d. — *A. q.* var. *potosinus*. c. — Calyx showing moderate long lobes. d. — Leaves are consistently narrow in this variety. Both Wendt et al. 2233 (TEX). e-f. — *A. q.* var. *wrightii*. e. — Calyx with moderate long lobes. Note decurrent lines of decurved hairs. f. — Leaves. Note large size, long petioles. Both Smith 229 (TEX). g-h. — *A. q.* var. *brevilobus*. g. — Calyx showing characteristic short lobes. h. — Leaves which tend to be narrow. Both Waterfall & Wallis 13246 (F). All calyces and leaves drawn to scale. Magnification indicated in a and b. Drawing by K. Cook.

While some questions remain as to the role of past introgression in northern Mexican *Anisacanthus*, the data presented here indicates that *A. quadrifidus* and *A. wrightii*: (1) share a large number of characteristics; (2) as a unit they are well distinguished by these characteristics from other species in the genus (see Hagen 1941); (3) their distinguishing characteristics tend to grade into those of other taxa (Figs. 1, 2); (4) while each taxon has its own geographical range, there is some indication of introgression in the short calyx-lobed populations of *A. wrightii* near Galeana in Nuevo Leon. To reflect this pattern, the taxa in *Anisacanthus quadrifidus* and *A. wrightii* are here combined into a single species which takes the name of the oldest specific epithet and the type of the genus *Anisacanthus quadrifidus* (Vahl) Nees and the other taxa are reduced to varieties of this species.

ANISACANTHUS QUADRIFIDUS (Vahl) Nees

Moderately to strongly branched, erect to spreading shrubs 0.5 – 1.5 (-2.6) m tall; young stems with internodes (5-)10–45(-65) mm long, 0.7 – 1.5 mm wide, terete, non to weakly striate, yellow-green, with decurved to more or less straight hairs 0.1 – 0.4 (-0.6) mm long in 2 broad decurrent lines extending from leaf-petiole margins across a stipular ridge and down the complete internode, this well developed or sparse, otherwise glabrous or sometimes sparsely hirtellous, rarely sparsely glandular but soon to tardily glabrate; older stems tan to grayish, with bark not peeling in sheets. Leaves opposite, lanceolate, linear-lanceolate to linear, (8-)15 – 35(-65) mm long, (0.8)1.0 – 16(-20)[-30] mm wide, (reduced above), tapering to an acute tip, rounded to cuneate, sometimes oblique, subsessile or with petioles (0.5-)1 – 7(-10) mm long at base, unevenly entire at yellowish, sometimes revolute (when dry) margins, glabrous to glabrate on both surfaces except for few to many antrorsely curved hairs along lower impressed midrib above and along lower leaf and petiole margins; leaf-blades yellow-green, more or less glandular-punctate, with midvein raised, yellowish beneath; leaves abscising at base above a yellowish, broad, persisting leaf-base 0.3 – 0.5 mm high, 0.8 – 1.6 mm wide, with abscission line often appearing black. Flowers 1 (-3) at upper nodes borne on elongate, slender, secund, upwardly arching, spicate racemes along terminal (2-)5 – 14 cm of seasons shoots; inflorescence internodes 2 – 14(-18) mm long, vestitured as stems or more hirtellous; bracts (reduced leaves) lanceolate-deltate, 2 – 7 mm long to 0.5 – 1.3 mm wide at base, acute to attenuate; paired bracteoles similar, 2 – 3 mm long, both rather soon caducous leaving distinct protruding bract-bases topped with conspicuous tan, corky-rimmed abscission scars; peduncles broad, (0.5-)1 – 2(-3) mm long; calyces (3-)4 – 8(-10) mm long, tube 0.9 – 2.5(-3)

mm long, lobes lanceolate, oblong-lanceolate to deltate, (1.2-)2-6.5 mm long, 0.9-1.2 mm wide at base, lobes 0.8-4.8 times as long as tube at anthesis; pedicels, calyces hirtellous with erect hairs more or less 0.03 mm long particularly at tube base, and with more or less conspicuous yellow-headed, stipitate glands 0.05-0.1 mm long with heads 0.03-0.07 mm wide outside, margins and tips of lobes weakly pilose with hairs 0.1-0.2 mm long, these often tufted at tip, inner lobe surfaces weakly to densely sessile glandular and weakly strigose with scattered antrorse hairs near tube; corollas red to orange-red, often yellowish where shaded in bud, (29-)32-38(-45) mm long, tube expanded at base around ovary, slightly ampliate distally, 19-25(-28) mm long, upper (posterior) lobe 14-17 mm long, separating 3-7 mm proximal to lower 3-lobes, lower 3 lobes 9-13 mm long, all lobes flaring, oblong to strap-shaped, 2-3 mm wide, acute; corollas pilose-pubescent externally with multicellular, tapering, retrorsely bent-spreading hairs 0.2-0.3 mm long; stamens 2, inserted in lower lobe distal to separation of upper lobe; filaments glabrous (7-)9-11 mm long, orange-yellow, glabrous, straight; anthers (2.3-)2.7-3.4 (-3.7) mm long, thecae subequal to equal, parallel, separate for 1-1.5 mm at base, sporangia reddish, connective dull yellowish; style 26-35 mm long, glabrous, exserted; stigmatic lobes ca 0.2 mm long, acute. Capsules 13-16 mm long, glabrous, tan, basal flattened stipe 5-8 mm long, head ovoid, 6-8 mm long, apiculate, retinacula 2.5-3 mm long; seeds (2-)3-4, notched basally, 4.5-5.6 mm long, 4-4.5 mm wide, to 1 mm thick, at maturity brown, more or less bullate and tuberculate on both faces, or mainly on inner face, with thickened margins.

Four varieties are separable by the following key:

- A. Calyx lobes (1-)1.5-4.3 times as long as calyx tubes at anthesis; leaf-blades linear to lanceolate.
- B. Petioles of larger leaves 0.5-3(-4) mm long; larger leaf-blades linear-lanceolate, to 1-9(-13) mm wide.
- C. Leaf-blades lanceolate, to (3-)4.5-9(-13) mm wide; petioles (1-)2-3(-4) mm long; calyx lobes (1.6-)3-4.3 times as long as calyx tubes at anthesis; Hidalgo, Queretaro, south to Oaxaca
..... *A. q. var. quadrifidus*
- CC. Leaf-blades linear-lanceolate, to (0.9-)1.5-3(-5) mm wide; petioles 0.5-1.2 mm long; calyx lobes (1.1-)1.5-2(-3) times longer than calyx tubes at anthesis; San Luis Potosi to northern Zacatecas
..... *A. q. var. potosinus*
- BB. Petioles of larger leaves (3.5-)4-7(-11) mm long; larger leaf-blades lanceolate to lance-ovate, 7-15(-20) mm wide; calyx lobes 1-2.3 times as long as calyx tubes at anthesis; Texas, Coahuila, Nuevo Leon to Tamaulipas
..... *A. q. var. wrightii*

- AA. Calyx lobes 0.5–0.8(–1.2) times as long as calyx tubes at anthesis; leaf-blades lanceolate to linear-lanceolate, 2.3–4.5 (–5.5) mm wide; Coahuila (southeast of Saltillo, and with intermediates with *A. g.* var. *wrightii* near Galeana, Nuevo Leon) *A. g.* var. *brevilobus*

1. **ANISACANTHUS QUADRIFIDUS** (Vahl) Nees var. **QUADRIFIDUS**, Linnaea 16:307. 1842. *Justicia quadrifida* Vahl, Enum. Pl. 1:124. 1804, based on *Justicia coccinea* Cav. Icon. Pl. 2:77, pl. 199. 1793, non Aublet 1775. *Anisacanthus quadrifidus* (Vahl) Standley, Contr. U.S. Nat. Herb. 23:1343. 1926. TYPE: Nuevo Hispanica. LECTOTYPE here designated: MA (photo!); ISOLECTOTYPE: F!

Anisacanthus virgularis (Salisb.) Nees in DC. Prod. 11:445. 1847. *Justicia virgularis* Salisb., Parad. London. pl. 50. 1806. TYPE: HOLOTYPE: plate 50 in Parad. London. (see Hagen 1941, p. 405, a.). Correspondence with K and BM indicate no specimens referable to this collection exist. It was probably described and illustrated from garden material.

Justicia superba Hort. ex Nees in DC. Prod. 11:445. 1847. TYPE: (in herb. Hort. Berol. fide Nees).

Justicia byssofolia Gouan ex Nees in DC. Prod. 11:445. 1847, non L. 1753, pro syn. (in herb. Hooker fide Nees).

Siphonoglossa glabrescens Lindau, Bull. Herb. Boiss. 2:546. 1894. TYPE: MEXICO, OAXACA. DIST. Tlacolula, prope Zoquitlan, Jun 1888, *Seler* 76 (HOLOTYPE: B, destroyed; PHOTOTYPES: GH, MICH, NY fide Hilsenbeck, pers. comm.).

Plants strongly branched; stems and inflorescence with decurrent lines of erect to decurved hairs (0.03–)0.1–0.2(–0.4) mm long, otherwise glabrous; petioles (1–)2–3(–4) mm long; leaves lanceolate, (1.4–)2.0–4.0(–5.0) cm long, (3.0–)4.5–9.0(–13.0) mm wide, margins more or less revolute when dry; calyces at anthesis (3.4–)4–7(–8) mm long, lobes (3.5–)4–5.5(–6.5) mm long, tube 1.5–2 mm long, lobes (1.6–)3–4.3 times as long as tubes, sparsely to densely hirtellous and with stipitate glands 0.06–0.12 mm long, their glands 0.04–0.06 mm wide outside, lobes densely glandular inside; corollas 33–40 mm long; anthers 2.7–3.4 mm long. Central Oaxaca to Puebla, Mexico, Hidalgo, Queretaro; 1000–2400 m elevation (Figs. 2a–b, 3).

Anisacanthus quadrifidus var. *quadrifidus* is readily recognizable by its long, lanceolate sepal lobes and relatively narrow leaves with short petioles. In describing *Justicia quadrifida*, Vahl (1804, page 124) cites Cavanille's (1793) *Justicia coccinea* as a synonym and appears to make a superfluous name for the taxon in a manner contrary to ICBN Article 63. However, on page 120, Vahl recognizes Aublet's (1775) *Justicia coccinea* as a species indicating that he considered the Cavanille name to be a later tautonym.

Representative specimens: MEXICO, OAXACA: 1.4 mi E of Tlacolula, 1670 m, 13 Nov 1980, *Fryxell and Lott* 3415 (TEX); road to Yagul, between Oaxaca and Miacla, 1 Mar 1960,

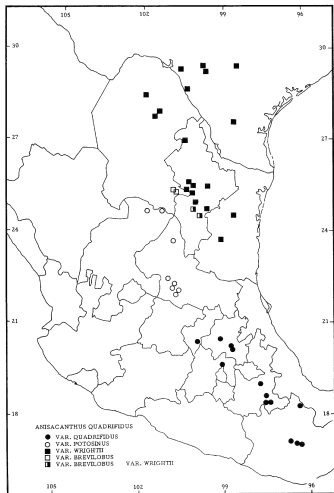


Fig. 3. Distribution of varieties of *Anisacanthus quadrifidus* in Mexico and Texas.

Carlson 3698 (F - 2 sheets); Oaxaca Valley, 5000 ft, 7 Nov 1894, *Smith* 713 (F). PUEBLA: San Bartolo, 15 km al NW de Tehuacan, 1700 m, 9 Jan 1959, *Rzedowski* 9501 (TEX); 7.7 km al N de Tehuacan, 1900 m, 13 Sep 1980, *Lott and Wendt* P35 (TEX). MEXICO: Cerro de Santa Cruz, N de Sierra de Guadalupe, 2300 m, 2 Nov 1963, *Mattala* 37329 (LL - 2 sheets). HIDALGO: Cerros al N de Pachuca, 2450 m, 18 Sep 1966, *Rzedowski* 23177 (TEX).

2. *ANISACANTHUS QUADRIFIDUS* var. *potosinus* Henrickson var. nov.

A. A. quadrifida var. *quadrifida* foliis linearis-lanceolatis (non lanceolatis), (0.9-)1 - 3(-5) [non (3-)4.5 - 9(-11)] mm latis, petiolis 0.5 - 1.2 [non (1-) 2 - 4] mm longis differt; a *A. linearis* et *A. juncea* corollis 29 - 36(-43) [non 40 - 56] mm longis, filamentis brevioribus id est 7 - 11 [non 18 - 35] mm longis differt.

Plants strongly branched, twiggy, erect to widely spreading, 0.5 - 1.5 m tall, often wider than tall; stems, inflorescence glabrous or with decurrent lines of decurved hairs 0.03 - 0.1 mm long, sometimes more striate; petioles 0.5 - 1.2 mm long; leaves linear-lanceolate to linear, (1.5-) 2 - 4(-5) cm long, (0.9-) 1.5 - 3(-5) mm wide, attenuate, at margins often more or less revolute with sparse decurved hairs, otherwise glabrous; leaf-blade typically conduplicate along midrib; calyces at anthesis 3.5 - 5(-5.5) mm long; lobes 2 - 3(-4) mm long, tube 1.3 - 2 mm long, lobes (1.1-)1.5 - 2 (-3) times as long as tube, weakly to strongly hirtellous and with stipitate glands 0.06 - 0.12 mm long, their glands 0.05 - 0.07 mm wide, mostly glandular and strigose inside lobes, marginal hairs 0.2 - 0.3 mm long; corollas 29 - 36 (-38) mm long; anthers 2.8 - 3.2 mm long. San Luis Potosi to northern Zacatecas. 1800 - 2100 m. (Figs. 2c-d, 3, 4).

TYPE: MEXICO. SAN LUIS POTOSI: Mpio. Villa de Reyes 3.9 km. al O. de la Carretera San Luis Potosi-Queretaro, por Carretera que va a Villa de Reyes. Km 20 de carretera S.L.P.-Queretaro, 1950 m, 8 Oct 1979, *J. Garcia, T. Wendt and E. J. Lott* 1297 (HOLOTYPE: MEXU; ISOTYPES: TEX, CHAP and to be distributed).

Specimens examined: MEXICO. SAN LUIS POTOSI: Chiefly in region of San Luis Potosi, 6000 - 8000 ft, 1878, *Parry and Palmer* 706 (F); San Luis Potosi, 1879, *Schiffner* 367 (F); gravel washes, Bocas, 17 Aug 1891, *Pringle* 3820 (F); Zaragoza, 2050 m, 7 Jul 1954, *Rzedowski* 3516 (F); 13 mi NE of San Luis Potosi, 20 Aug 1954, *Waterfall* 15679 (F); same location as type, 8 Oct 1979, *Garcia P. et al.* 1297 (TEX, CHAP); 11 Oct 1979, *Wendt et al.* 2235 (TEX, CHAP); on road between Real de Catorce and Doc de Catorce, ca 2100 m, near 23° 43'N lat, 100° 52'W long, 18 Sep 1980, *Henrickson & Behey* 18615, 18616, 18617 (TEX). ZACATECAS: *sic loc.*, *Lloyd* 10 (F); 0.4 mi S of Zacatecas-Coahuila border along Hwy 54, near 24° 43'N lat, 101° 13'W long, 6100 ft, 30 Aug 1971, *Henrickson* 6222 (TEX).

3. *ANISACANTHUS QUADRIFIDUS* var. *wrightii* (Torr.) Henrickson comb.

nov. *Dryas wrightii* Torr. in U.S. and Mex. Bound. Surv. Bot. 123. 1859. *Anisacanthus wrightii* (Torr.) Gray, Syn. Fl. N. Am. 2(1):238. 1878. TYPE: UNITED STATES. NEW MEXICO: May - Oct, 1848. *C. Wright* 435 (HOLOTYPE: NY; ISOTYPE: TEX!).



Fig. 4. *Anisacanthus quadrifidus* var. *potosinus* Henrickson. a. — Stem showing linear leaves and flowers. This was drawn from a dried specimen and several flowers have fallen off distorting the second nature of the inflorescence. b. — Node with leaves showing line of abscission at base and distinctive stipular ridge connecting opposite leaf margins. c. — Calyx with associated bractlets. Calyx shown in dried condition with lobes flaring. d. — Corolla showing expanded base that surrounds ovary, strap-shaped lobes and position of anthers and style. e. — Anther, adaxial view (left) and abaxial view. f. — Open capsule showing retinacula. All from Garcia *P. et al.* 1297 (TEX). Scale bars = 1 cm except in e where bar = 1 mm. Drawing by B. Angell.

Plants moderately branched, erect to spreading; stems mostly with dense decurrent lines of decurved hairs (0.1-)0.2-0.4(-0.6) mm long; inflorescences rather strongly hirtellous with erect hairs 0.03 mm long with or without decurrent longer hairs; petioles (3-)4-7(-11) mm long; leaf-blades lanceolate to broadly lanceolate (25-)30-50(-62) mm long, 7-15(-20)[-30] mm wide, margins mostly revolute when dried; calyces at anthesis (2.6-)3.5-4.5 (-5) mm long, lobes (1.3-)1.8-3.2(-4) mm long, tubes (1.2-)1.4-2(-2.0) mm long, lobes (0.9-)1.1-2.3 times as long as tubes, both hirtellous and with stipitate glands 0.03-0.08 mm long, their glands 0.03-0.06 mm wide, marginal hairs 0.1-0.2 mm long; corollas 31-40 mm long; anthers 2.5-3.2 mm long. Texas, Coahuila, Nuevo Leon and Tamaulipas. 300-900 m. (Figs. 2e-f, 3).

Representative specimens: UNITED STATES. TEXAS. Uvalde Co.: Con Can, along Rio Frio, 22 Jun 1963, *Correll and Washburn 28016* (LL). MEXICO. NUEVO LEON: Lampazos, 21 Jun 1937, *Edwards 282* (E TEX); 12 mi W of Linares, 1200 ft, 26 Jul 1956, *Fearing and Thompson 25* (TEX); behind Cola de Caballo, Monterrey, 29 May 1960, *Smith M229* (E TEX); Alamar to Puerto Blanco, 15 mi SW of Galeana, 23 Jul 1934, *Muller and Muller 1197* (TEX); Rayones, 900 m, 9 Jun 1980, *Hinton 17824* (TEX). COAHUILA: Muzquiz, Sabinas, 7 Nov 1936, *Marb 408* (TEX); Rancho Babia, 18 May 1938, *Marb 1209* (E TEX). TAMAULIPAS: vicinity of San Jose, La Vegonia, 20 Jul 1930, *Bartlett 10526* (E TEX); vicinity of Victoria, 320 m, 1 Feb-9 Apr 1930, *Palmer 120* (F).

4. *ANISACANTHUS QUADRIFIDUS* var. *brevilobus* (Hagen) Henrickson
comb. nov. *Anisacanthus wrightii* var. *brevilobus* Hagen, Ann. Missouri Bot. Gard.
28:400, 1941. TYPE: MEXICO. COAHUILA: Chojo Grande, 27 mi SE of Saltillo, 16
Jul 1905, *Palmer 719* (HOLOTYPE: NY!; ISOTYPES: CB, F!, MO).

Plants moderately branched, spreading to erect; stems more or less striate, mostly with decurrent lines of decurved hairs 0.1-0.3 mm long; inflorescences more or less decurrently, sulcately grooved, with short decurved hairs in sulci, otherwise glabrous; petioles (1-)1.5-2.1 mm long; leaf-blades narrowly lanceolate to linear-lanceolate, (17-)20-35(50-) mm long, 2.3-4.5(-5.5) mm wide, margins more or less revolute; calyces at anthesis 2.5-3.6 (-4.0) mm long, lobes 1-1.7 mm long, tubes (1.3-)1.5-2 mm long, lobes 0.5-0.8(-1.2) times as long as tubes, hirtellous and with mostly many stipitate glands 0.03-0.06 mm long, their heads 0.04-0.05 mm wide, strongly glandular and strigose inside, marginal hairs few, limited to a terminal tuft of hairs 0.1-0.2 mm long; corollas 33-37 mm long; anthers 2.2-2.9 mm long. Coahuila, in canyons southeast of Saltillo, 1700-2000 m. (Figs. 2g-h, 3).

Representative specimens: MEXICO. COAHUILA: Paso del Aguila, E of Saltillo, 12 Jul 1946, *Barkley et al. 16M496* (TEX); same location, 2 Jul 1947, *Barkley et al. 7244* (TEX-2 sheets); 12 air mi E of Saltillo, lower Canon de Chorro, 1900 m, 27 Sep 1980,

Henrickson and Bekey 18643, 18644 (TEX); 18 mi NE of Saltillo, 6 Aug 1957, *Waterfall and Wallis 13246* (F-2 sheets).

Collections from near Galeana, Nuevo Leon have relatively broad leaves as in *A. q.* var. *wrightii* and short sepals as in *A. q.* var. *brevilobus* and are considered intermediate between the two taxa. While these characters tend to be uniform through this area, some specimens from the area have longer sepals (see *Muller and Muller 1197*).

Specimens examined: MEXICO. NUEVO LEON: Taray to Alamar, about 15 mi SW of Galeana, 20 Jul 1934, *Muller and Muller 1108* (F, TEX); Hacienda Pabillo, Galeana, 27 Aug 1936, *Taylor 262* (F, TEX); Mcpo. Galeana, 5400 ft, 2 Aug 1939, *Chase 7731* (F-2 sheets); 1 mi W of Galeana on road to Cerro Potosi, 5400 m, 16 Sep 1980, *Henrickson and Bekey 18540* (TEX).

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TAXONOMY OF *FLYRIELLA* (ASTERACEAE-EUPATORIEAE)

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ABSTRACT

A taxonomic treatment of the genus *Flyriella* is rendered including information relating to its generic relationship, phyletic arrangement of its four species, chromosomal, and chemical data. Illustrations of the species are presented along with a map showing distributions.

INTRODUCTION

Flyriella King & Robinson is a North American genus of four species which is largely confined to north central and northeastern México, but extends into the United States in the border regions of Trans-Pecos Texas. The genus was proposed by King & Robinson (1972b). It is named in honor of Dr. David Flyr, plant systematist from The University of Texas (Turner 1972), who placed the generitype (*Eupatorium parryi*) in the genus *Brickellia* (as *B. sbineri*) after removing it from its original position in *Eupatorium*. This placement by Flyr (1968) was based upon a number of morphological features which he took to be brickellioid. Flyr noted that *B. sbineri* did, however, differ from other species of *Brickellia* (with the exception of *B. fendleri* Gray) in having only five-ribbed rather than ten-ribbed achenes as is typical of *Brickellia*.

The dissociation of *Eupatorium parryi* from *Brickellia* by King & Robinson left *B. fendleri* as anomalous in *Brickellia* in possessing five-ribbed achenes. Gray, as noted by Flyr, was uncertain as to the proper placement of *B. fendleri*; it remained for King & Robinson (1972a) to place the latter in a newly erected monotypic genus, *Brickelliastrum*. In their establishment of *Flyriella*, King & Robinson recognized five species: *F. chrysostylis*, *F. sphenopoda*, *F. leonensis*, *F. parryi*, and *F. stanfordii*. In 1982, they added an additional species, *F. barrimanii*.

In the present treatment we have recognized only four species: 1) *F. parryi*, a wide-ranging, variable, taxon that includes *F. chrysostylis* and *F.*

sphenopoda; 2) *F. leonensis*, a weakly differentiated taxon from near Monterrey, México; 3) *F. stanfordii*, a species along the Sierra Madre Oriental; and 4) *F. harrimanii*, a very distinct local endemic in the lower montane regions about Gómez Farías, Tamaulipas.

CHROMOSOMAL STUDIES

Chromosome counts are available for only two species, *F. leonensis* and *F. parryi*, both diploid, as indicated in Table 1. The base number $x = 10$, is not known to occur in *Brickellia* (King et al. 1976). The latter genus has a base chromosome number of $x = 9$. *Eupatorium* has a base number of $x = 10$, as does *Alomia* (Mabry et al. 1981), near which we would position *Flyriella*.

FLAVONOID STUDIES

Mabry et al. (1981) have made the only chemical study of *Flyriella*. They examined three of the four species, (*F. parryi*, *F. leonensis*, and *F. stanfordii*) as shown in Figures 1 and 2. Unfortunately, only two populations of *F. parryi* were examined and only one population each of *F. leonensis* and *F. stanfordii*. All the species examined produce glycyolated quercetins. *Flyriella stanfordii* differs significantly from *F. parryi* and *F. leonensis* in producing only monoglycosidic forms.

Mabry et al. (1981) treated *F. sphenopoda* as a distinct taxon, and the chromatographic profiles of plants referable to this name lacked the monoglucosides (Fig. 1). However, in view of the considerable morphological variability in its flavonoid components, no significant taxonomic import is given the chromatographic profile concerned.

SPECIES RELATIONSHIPS WITHIN *FLYRIELLA*

Flyriella parryi, a wide-ranging variable species, appears to be most closely related to *F. leonensis* and is sympatric with it in the vicinity of

TABLE 1. Chromosome Numbers in *Flyriella*

Species	Chromosome Number (2n)	Location and Voucher
<i>F. leonensis</i>	20	MÉXICO: Nuevo León. 17 mi by road W of Horsetail Falls. <i>Turner 10037</i> (LL).
<i>F. parryi</i>	20	MÉXICO: Coahuila. Above Las Delicias. <i>Powell 2699</i> (TEX)
<i>F. parryi</i>	20	MÉXICO: Nuevo León. 5 mi W of El Alamo. <i>Turner 10007</i> (LL).

Monterrey, Mexico. Additional work in this area is needed to ascertain if they grow in close proximity which might occasion hybridization. Chemical analysis reveals that *F. leonensis* is almost identical with *F. parryi*, sharing three of the four flavonoids concerned: quercetin 3-arabinoside, ombuaside, and tamarixetin 3-rhamoglucoside (Mabry et al. 1981, Figs. 1, 2).

Flyriella stanfordii is believed to be more closely related to *F. harrimanii* than are *F. parryi* and *F. leonensis*. Both *F. stanfordii* and *F. harrimanii* possess short glandular trichomes and winged petioles and both occur in the more mesic habitats of southern Tamaulipas. Nevertheless, *F. stanfordii* is probably more closely related to *F. parryi* and *F. leonensis* than it is to *F. harrimanii* to judge from its involucrel characters.

Relationships among the four species are shown in Figures 3 and 4. This is largely derived from consideration of hypothetical polarized character states as shown in Table 2. That is, we have erected an imaginary primitive state for the characters concerned, based on a wide experience with what appears to be specialized characters in the tribe Eupatorieae generally. We do not believe that arbitrary selection of an out-group for cladistic analysis

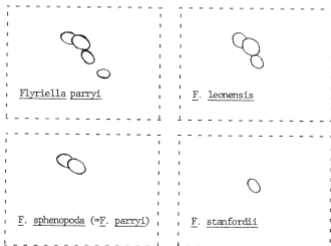


Fig. 1. Two-dimensional chromatographic flavonoid patterns for *Flyriella* (modified from Timmerman 1980).

TABLE 2. Hypothetical primitive versus advanced character states in *Flyriella* (P = *F. parryi*; L = *F. leonensis*; S = *F. stanfordii*; H = *F. harrimanii*).

PRIMITIVE (0)	ADVANCED (1)	SPECIES			
		P	L	S	H
1. Leaves with glandular trichomes	1. Leaves without glandular trichomes	0	1	0	0
2. Petioles alate (clearly winged)	2. Petioles not alate (poorly winged)	1	1	0	0
3. Involucral bracts not scarious	3. Involucral bracts scarious	1	1	1	0
4. Outer involucral bracts leafy	4. Outer involucral bracts reduced	1	1	1	0
5. Involucral bracts numerous	5. Involucral bracts reduced	1	1	1	0
6. Numerous florets/head 50 - 100 = 0 30 - 49 = 1 10 - 29 = 2	6. Fewer florets/head	2	2	1	0
7. Corolla flared	7. Corolla tubular or constricted	1	1	0	0
8. Carpodia mostly not contorted	8. Carpodia mostly contorted	1	1	0	0
9. Habitat mesic	9. Habitat xeric	2	1	0	0
	Totals	10	10	4	0
Mesic = 0					
Sub-mesic = 1					
Desert = 2					

at this time would be a meaningful phyletic exercise, although it might reduce the circularity of our premise.

Based upon the characters in Table 2, *F. harrimanii* appears to be the most primitive species in the genus. Its leafy involucral bracts as well as other "primitive" or less advanced features suggest that the remaining taxa evolved out of similar ancestral prototypes, culminating in the more xeric *F. parryi* (Fig. 4) whose involucre and florets evolved so as to "mimic" species of *Brickellia*.

As can be seen from the cladogram (Fig. 4), character states 2, 6, 7, 8, and 9 are synapomorphies linking *F. leonensis* and *F. parryi*. Character states 9² and 1 are automorphies for *F. parryi* and *F. leonensis* respectively. Character states 3, 4, 5, and 6 are synapomorphies for the three species *F. leonensis*, *F. parryi*, and *F. stanfordii*. *Flyriella harrimanii* appears to be, as noted above, the most primitive species.

It will be interesting to obtain additional chemical data for *F. stanfordii* and *F. harrimanii*, for it appears from current analyses that the more highly evolved diglycosidic flavonoids might be missing from the latter species, substantiating the suggestions made here, which are largely based upon morphological data.

GENERIC RELATIONSHIPS OF *FLYRIELLA*

In his transfer of *Eupatorium parryi* into the genus *Brickellia*, Flyr (1968) largely emphasized its narrow, erect-lobed, constricted corollas and

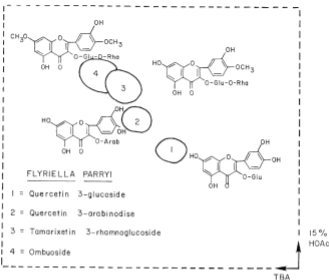


Fig. 2. Two-dimensional chromatographic profile of *Flyriella parryi*: TBA = *t*-BuOH-HOAc-H₂O, 3:1:1 (modified from Mabry et al. 1981).

narrow, green and white, seriate phyllaries. Indeed, in these and in certain microfeatures, chiefly the hirsute stylar node, it is very similar to *Brickellia*. *Flyriella*, however, lacks fringed pappus setae and, of course, possesses fewer ribs on its achenes and has a base chromosome number of $x = 10$. Nevertheless, *Flyriella* shares a close relationship with *Brickellia* and both genera are placed in the subtribe *Alomiinae* by Robinson & King (1977).

Mabry et al. (1981), upon completion of a series of chemical analyses, found no support for a close link between *Flyriella* and *Brickellia*. They note that the flavonoid chemistry of *Flyriella parryi* and *Brickellia laciniata* (Timmerman et al. 1979) reveal very different patterns. *Brickellia* species contain 6-methoxylated glycosides, sulfates, and aglycones, none of which is found in *Flyriella* (Figs. 2, 3).

Turner, in Mabry et al. (1981), suggest that *Flyriella* is more closely related to *Alomia* rather than *Brickellia*. There is much evidence to support this hypothesis, and it comes from several lines of investigation, as noted below.

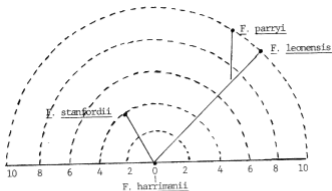


Fig. 5. Wagnerian diagram showing hypothetical relationships among the four species of *Flyriella*. Character states for the construction shown in Table 2.

In addition to the chemical data, two of the four species of *Flyriella* have been shown to be diploid with $2n = 20$ or $x = 10$ (Table 1). This base number also characterizes *Alomia* (Mabry et al. 1981). *Brickellia*, on the other hand, has a base chromosome number of $x = 9$.

Both *Flyriella* and *Alomia* are spring-flowering. *Brickellia* is predominately a fall-flowering genus as are the majority of its close relatives. Because most Eupatorioid genera of the Chihuahuan Desert region are fall-flowering, it can be suggested that *Flyriella harrimanii*, which appears to be the most primitive member of the genus on morphological grounds, is the species which lies geographically nearest the hypothetical center-of-origin of the group. The more advanced features of *F. parryi* are perhaps adaptations to drier habitats. Even so, label data and observations in the field by the junior author show the species to be largely confined to more mesic sites in the desert regions (along perennial streams mostly in cool, moist canyons).

In short, since *Flyriella* appears not to be closely related, phyletically speaking, to *Brickellia*, and since it has no extant desert relatives from which it might have evolved, the most likely ancestral candidate at this time appears to be *Alomia* or a close relative of the latter (Table 3). *Alomia* may have had a double origin, partly Ageratoid and partly Trichonioid, as noted by both B. L. Robinson (1913) and Robinson and King (1977). Indeed, the junior author has suggested that *Flyriella* and *Alomia* might be better positioned in the subtribe Ageratinae. This implies that the

TABLE 3. Comparison of selected characters of *Alomia* and *Flyriella*. *Brickellia* is not compared here since it is exceedingly variable and such a litany would be beyond the scope of this study. If compared, it would differ from *Alomia* and *Flyriella* largely by its base chromosome number, $x = 9$, fall-flowering, and more xeric habitats.

	ALOMIA	FLYRIELLA
Distribution	Subtropical regions of México & South America	Subtropical to drier temperate regions of north central and northeastern México
Habitat	Mesic	Mesic to semi-xeric
Habit	Perennial herbs	Perennial herbs
Stem vestiture	Long non-glandular trichomes or glandular trichomes	Long non-glandular trichomes or glandular trichomes
Leaves	Mostly opposite	Mostly opposite
Petiole	Alate or non-alate	Alate or non-alate
Phyllary shape	Mostly acute to acuminate	Mostly acute to acuminate
Corolla	Flaring or tubular	Flaring, or tubular with or without apical constriction
Stylar node	None	Present
Carpopodium	Concurred	Contorted or "turbinate"
Achene	4-5-ribbed	4-5-ribbed
Pappus bristles	None or reduced	Well-developed
Chromosome no.	$x = 10$	$x = 10$
Anthesis	Spring	Spring

morphological characters which relate it to *Brickellia* (discussed above) are convergent. Additional study, especially chemical, is needed to confirm or refute the close relationship of *Flyriella* and *Alomia*.

TAXONOMY

FLYRIELLA K. & R., *Phytologia* 24:69. 1972.

Perennial herbs, 0.5-2.0 m tall; stems erect, puberulent to viscid from a tap root or short rhizome. Leaves opposite below, often becoming alternate above. Capitulescence a terminal corymboid panicle. Heads turbinate to hemispheric, the florets yellowish-white. Involucral bracts in 3-5 imbricated series, striated green and white, occasionally tinged with purple. Receptacle plane, naked. Corollas tubular, gradually flaring upward but often constricted just below the lobes. Lobes 5, short, narrowly triangular. Anthers included, appendages ovate. Style branches linear, yellowish-white, sometimes turning rusty colored upon drying. Achenes 4-5-ribbed, sparsely pubescent, carpopodium short to elongate, often contorted. Pappus of 20-40, white, ciliate setae. Base chromosome number, $x = 10$.

TYPE SPECIES: *Eupatorium parryi* A. Gray

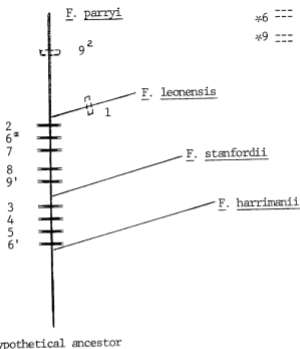


Fig. 4. Cladogram constructed from results obtained from computerized method (Wagner 78, Version 25/8/79, James Farris, State University of New York, Stony Brook, IBM 370/178 Computer). Data utilized based on character states from Table 2.

*Change in characters number 6 & 9 from character states 1 & 2.

KEY TO SPECIES

- A. Outer involucre bracts somewhat leaf-like, as long or longer (10–15 mm) than the innermost bracts; florets 70–100 per head 1. *F. harrimanii*
- A. Outermost involucre bracts not leafy, much reduced (3–6 mm long); florets 10–49 per head (B)
- B. Corolla throat narrowly funnelform, not constricted below the lobes; petioles conspicuously winged throughout; montane subtropical areas of southern Tamaulipas and Nuevo León 2. *F. stanfordii*
- B. Corolla throat tubular (ca 0.5 mm across), not conspicuously constricted below the lobes; petioles only partially winged, if at all; montane mostly desert areas of north central México (C)

- C. Stems and branches of capitulescence with glandular trichomes or these intermixed with long, straight mostly stiff hairs; widespread variable species of north central México and adjacent areas of Texas 3. *F. parryi*
- C. Stems puberulent, without glandular trichomes, the hairs crisped and variously recumbent; restricted species about Monterrey, México 4. *F. lesmeisii*

1. *FLYRIELLA HARRIMANII* K. & R., *Phytologia* 50:380. 1982. TYPE: MÉXICO, TAMAULIPAS: on route B-5, 3 mi E of Gómez Farias, across from gravel pit, 600 ft, woods on pitted limestone, 31 Mar 1975, *Harriman et al.* 10698 (HOLOTYPE: US!).

Erect perennial herb to 200 cm tall. Leaves opposite; blades ovate-deltoid, 4.0–13.5 cm wide, 5–17 cm long, irregularly serrate, both surfaces glandular; petioles 3–11 cm long, glandular pubescent, winged. Capitulescence in ultimate pedunculate units of 1–3 heads, each head on a bracteolate pedicel 1–3 cm long. Involucre campanulate, 1.5–2.0 cm long, ca 2 cm wide; bracts herbaceous, imbricate in 3–5 series, glandular, 10–15 mm long, ca 1.4 mm wide. Florets 70–100; corolla white, funnelliform, ca 4 mm long, ca 1 mm wide; lobes narrowly triangular, acute, 0.5–0.7 mm long, 0.2–0.4 mm wide. Anthers ca 2.2 mm long. Style branches (when dried) amber, linear-oblanccolate, 1.0–1.5 mm long, sometimes unequal. Achenes 4–5-ribbed, ca 4 mm long, brown-black, very sparsely pubescent throughout; pappus 5.0–5.5 mm long, composed of 30–35, filiform, ciliate setae.

Distribution and Habitat (Fig. 5): Subtropical, lower montane regions in the area of Gómez Farias in Tamaulipas. Flowering Mar. and Nov.

Additional specimen examined: MÉXICO, TAMAULIPAS: Gómez Farias area: Rancho Del Cielo below Aguacates turnoff, 24 Nov 1968, *Richardson* 958 (TEX).

Flyriella harrimanii is readily distinguished from other species in the genus by its larger, fewer heads that are composed of 70–100 florets and by its larger leafy outer involucral bracts (Fig. 6). Nevertheless, it is presumably most closely related to *F. stanfordii*, as noted in the section on Species Relationships.

2. *FLYRIELLA STANFORDII* K. & R. *Phytologia* 24:69. 1972. TYPE: MÉXICO, TAMAULIPAS: 4 km W of Miquihuana in canyon with luxuriant vegetation, 4 Aug 1941, *Stanford et al.* 675 (HOLOTYPE: GH!).

Erect "rhizomatous" herb, 50–100 cm tall. Leaves becoming alternate above; blades deltoid, 2.0–8.5 cm wide, 3–11 cm long, irregularly serrate, short-glandular on both surfaces; petioles 2–5 cm long, winged throughout; capitulescence in ultimate pedunculate units of 10–25 heads, each head on a bracteolate, glandular, pedicel, 3.0–6.5 mm long.

Involucre campanulate, 6.0–8.0 mm long, 5.0–7.0 mm wide; bracts imbricate in 3–5 series, glandular, tinged with purple, lanceolate-ovate, 2.5–6.5 mm long, ca 1 mm wide. Florets 20–30; corolla white, tinged with purple, tubular to narrowly funnelform, 4–5 mm long, 0.4–0.6

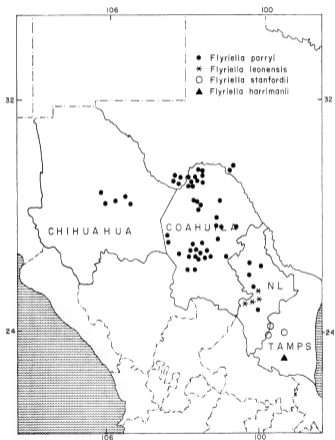


Fig. 5. Distribution of the four species of *Flyriella*.

mm wide, not constricted near the apex, glabrous; lobes narrowly triangular, acute, ca 0.3 mm long, minutely atomiferous-glandular. Anthers ca 1.2 mm long. Style branches linear-oblancoolate, brownish-yellow, ca 0.4 mm long. Achenes 4–5-ribbed, ca 2.3 mm long, black, sparsely pubescent throughout. Pappus 4–5 mm long, composed of 25–35 filiform, ciliate setae.

Distribution and Habitat (Fig. 5): Subtropical montane areas along the Sierra Madre Oriental from 1850–2320 m. In limestone along crags, in oak-pine forest clearings and along stream beds. Flowering: Jun–Jul.

Additional specimens examined: MÉXICO. NUEVO LEÓN/TAMAULIPAS: Nuevo León and just E into border of Tamaulipas, 28 Jun 1948, *Meyer & Rogers* 2687 (US); Dulces Nombres, 20 Jul 1948, *Meyer & Rogers* 2831 (MO, US); Zaragoza, Encantada, 17 Jun 1979, *Hinton* 17544 (TEX); ca 10 km SSW of Zaragoza, Jul 1977, *Wells & Nesom* 554 (LL).

Flyriella stanfordii is distinguished from other species in the genus largely by its narrowly funnellform corolla throat that is not abruptly constricted and by its conspicuously winged petioles (Fig. 7). Additional comments on its relationship are given in the section on Species Relationships.

3. *FLYRIELLA PARRYI* (A. Gray) K. & R. *Phytologia* 24:69, 1972. *Eupatorium parryi* A. Gray, in *Torr. Bot. Mex. Bound.* 75, 1859. TYPE: MÉXICO. COAHUILA: "Sierra de Carmel", probably an error for Sierra del Carmen in Coahuila, 16 Nov 1852, *Parry* 3 (HOLOTYPE: GH!).

Eupatorium chryostylum Robinson, *Proc. Amer. Acad. Arts.* 41:274, 1905. TYPE: MÉXICO. COAHUILA: dry ledges, rocky hills near Chihuahua City, 17 Apr 1885, *Pringle* 135 (HOLOTYPE: GH!; ISOTYPES: DS!, MICH!, NY!, US!). *Flyriella chryostyla* (Robinson) K. & R. *Phytologia* 24:69, 1972.

Eupatorium sphenopodum Robinson, *Proc. Amer. Acad. Arts.* 43:35, 1907. TYPE: MÉXICO. COAHUILA: above Monterrey on shaded cliffs of limestone, 16 Jul 1906, *Pringle* 10259 (HOLOTYPE: GH!; ISOTYPES: CAS!, F!, LL!, MO!, US!). *Flyriella sphenopoda* (Robinson) K. & R. *Phytologia* 24:69, 1972.

Brickellia shineri M. E. Jones ex Flye, *Sida* 5:254, 1968. TYPE: MÉXICO. NUEVO LEÓN: "Sabinal", Ojo de Agua, ca 2.5 mi W Sabinas Hidalgo, [26] 25 Mar 1932, *M. E. Jones* 29411 (HOLOTYPE: POM; PICTHOLOTYPE: US!; ISOTYPE: UC!). (date and specific locality from Blake 1945). *Brickellia shineri* M. E. Jones, *Contr. W. Bot.* 18:22, 1933. Nom. illegit., with our Latin diagnosis.

Erect herb from perennial tap root, 0.5–1.0 m tall. Leaves mostly opposite, alternate and reduced just below the capitulescence; blades predominately deltoid to cordate, 3–10 cm wide, 5–11 cm long, irregularly serrate, dentate to lobed, glandular on both surfaces, especially along edges and veins; petioles 3–7 cm long, glandular, abruptly winged, just below blade. Capitulescence in ultimate pedunculate units of 3–16 heads, each head on bracteolate pedicel 3–7 mm long. Involucre turbinate, 8–10 mm long, 4–5 mm wide; bracts in 3–5 series, ovate to

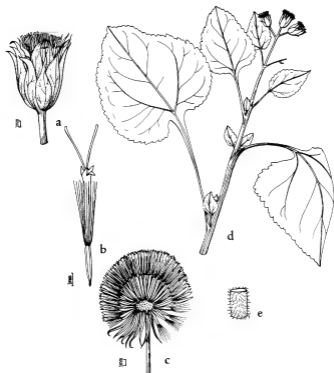


Fig. 6. *Flyriella harrimanii*: a) flowering head; b) floret; c) mature fruiting head, longitudinal section; d) flowering branch; e) portion of stem showing glandular trichomes.

linear lanceolate, 2.5–9.5 mm long, ca 1 mm wide, the apices acute to acuminate. Florets 10–25; corolla yellowish-white or tinged with purple, tubular with constriction ca 1.0 mm long, 0.2 mm wide at top of tube; lobes narrowly triangular-acute, ca 0.2 mm long, ca 0.1 mm wide. Anthers ca 1 mm long. Style branches yellowish-white, linear oblanceolate, 5–7 mm long. Achenes 4–5-ribbed, ca 3.5 mm long, black, sparsely pubescent throughout; pappus 4–5 mm long, composed of 20–30 ciliate setae. Chromosome number, $n = 10$ pairs.

Distribution and Habitat (Fig. 5): wide ranging, highly variable species occurring in mesic habitats of the Chihuahuan desert regions of north central Mexico and adjacent Trans-Pecos areas of Texas, mostly in calcareous soils at elevations from 900–2200 m. Flowering: Apr–Jul.

Additional specimens examined: UNITED STATES. TEXAS. Brewster Co.: end of Pine Canyon Trail, 12 Nov 1976, *Correll 35402* (LL, MO); Cattail Falls, 9 Nov 1964, *Correll & Correll 30592* (LL); Juniper Canyon, 16 Jun 1964, *Correll et al. 29721* (LL); Big Bend National Park, Chisos Mts., Pine Canyon, 17 Jun 1963, *Correll & Wasshausen 27865* (CAS, LL, MO); Chisos Mts. Aug 1935, *Marb 149* (F); Cattail Springs, 7 Jul 1931, *Moore & Steyermark 3408* (CAS, GH, LL, MO, US); Chisos Mts., 5 Aug 1931, *Mueller 8179* (GH, TEX, US); Pine Canyon, near waterfall under oaks and pines, 24 Sep 1977, *Powell et al. 3229* (LL, US); Lower Pulliam Canyon, 4 Jul 1936, *Sperry 193* (LL, US); Lower Pulliam Canyon, 26 Aug 1936, *Sperry 293* (LL, US); Cattail Falls, 19 Apr 1955, *Wallus 7* (LL); waterfalls in Pine Canyon, 1 Jul 1937, *Warnock 760* (GH, TEX, US); mid Green Gulch, 23 Jul 1950, *Warnock 9146* (LL); upper Green Gulch, 28 Jun 1941, *Warnock 20975* (GH, LL, MO, TEX); Green Gulch, 22 Aug 1947, *Warnock & Thorp 4005* (US). Val Verde Co.: 3.5 mi S of Pandale, 9 May 1967, *Correll 34150* (GH, LL); Eagle Cave Canyon E of Langtry, 21 Apr 1966, *Correll & Rollins 32610* (GH, LL, UC); 5 mi N of Langtry on Ozona road, 8 May 1947, *McVaugh 8232* (E GH).

MEXICO. CHIHUAHUA: Mouth of Majalca Canyon, 11 May 1959, *Correll & Johnston 21758* (LL); near Chihuahua, 22 Jun 1936, *LeSueur 963* (F); vicinity of Chihuahua, 8–27 Apr 1908, *Palmer 40* (E GH, NY, US); Mapula Mts., 27 Apr 1887, *Pringle 1595* (MICH, MSC, UC).

COAHUILA: Sierra Mojada, just S of Esmeralda, above Sociedad Cooperativa Minera, 1 Sep 1972, *Chiang et al. 9070f* (LL); middle of upper reaches of Canon de la Hacienda, almost due S of Rancho Cerro de la Madera, N slope of Sierra de la Madera, 21 Sep 1972, *Chiang et al. 9449* (LL); ca 32 air mi NE of San Pedro, 1 mi SW of Las Delicias, 27 Aug 1971, *Henrickson 6072* (LL); ca 64 air mi SE of Big Bend National Park basin along highway 22 towards Múzquiz, 4 Aug 1976, *Henrickson & Prigge 14910* (LL); ca 35 air mi W of Cuatro Ciénegas, in mid-canyon de la Hacienda of Sierra de la Madera, 6 Aug 1973, *Henrickson & Wendt 11988* (LL); SW end of Sierra de la Fragua, 1–2 km N of Puerto Colorado, 2 Sep 1941, *Johnston 8784* (LL); Canon de Jara, 30–40 km W of Cuatro Ciénegas, 4–5 Sep 1941, *Johnston 8857* (LL); Rio Grande, side canyons at upper Madison Falls, 10 Apr 1973, *Johnston et al. 10611* (LL); Sierra San Marcos, N part jutting into Ciénegas basin, higher slopes, just reaching the lowest ponderosa pines, 9 May 1973, *Johnston et al. 10943* (LL); ca 5 km SW of Mina El Popo, dissected E slope of Sierra del Carmen, 28 Jul 1973, *Johnston et al. 11891* (LL); El Popo, ca 2 km S of Cañon El Diablo, 29 Jul 1973, *Johnston et al. 11929j* (LL); southern part of Sierra de los Organos, 8 Aug 1973, *Johnston et al. 12132* (LL); Múzquiz, Spring 1935, *Marb 203* (TEX); Múzquiz, 8 Jul 1936, *Marb, Jr. 346* (TEX); Múzquiz, 1939, *Marb s.n.* (F); Múzquiz, 12–13 Apr 1936, *Marb 2136* (GH, TEX); 92.5 mi NW of Múzquiz on highway 53 to Boquillas del Carmen, 29 Jun 1982, *Pool & Watson 2531* (TEX); near the spring (pool) above Las Delicias at base of bluffs, 20 May 1974, *Powell & Turner 2699* (TEX); canyons in the Sierra del Sobaco, a few km W of Las Delicias, 1 Oct 1942, *Santos 2804* (GH); Sierra Mojada, above San Salvador Mine near Esmeralda, 4 Aug 1941, *Stewart 1078* (E GH, LL); Cañon del Milagro, ca 12 Km W of Hacienda de la Encantada, 10–16 Sep 1941, *Stewart 1717* (GH, LL); Sierra del Carmen, Pico de Cerda, 12 Aug 1974, *Wendt 578* (LL); Cañon de la Barrica at base of

southern cliffs of Picacho El Pajarito, 28 Aug 1975, *Wendt & Lott 1366* (LL); Sierra de la Fragua, 6 Jan 1976, *Wendt et al. 1428* (LL); Sierra de la Gloria, Cañon Oscuro Chiquillo, 7 Sep 1976, *Wendt & Riskind 1720* (LL); Múzquiz, Hacienda Mariposa, E slope of the Sierra de Puerto Santa Ana, 23 June 1936, *Wynđ & Mueller 254* (GH, MICH, MO, MSC, NY, US).

Nuevo León: Sabinas Hidalgo, Ojo de Agua, 16 Jun 1939, *Chase 7020* (GH, NY); Sabinal, 26 Mar 1932, *Jones 29411* (CAS); Sierra Madre above Monterrey, 25 May 1908, *Pringle 15615* (LL, US); 5 mi W of El Alamo, 1 Jun 1978, *Turner 10007* (E, LL).

Flyriella parryi is readily distinguished from other species by its glandular trichomes which are often interspersed with long straight eglandular

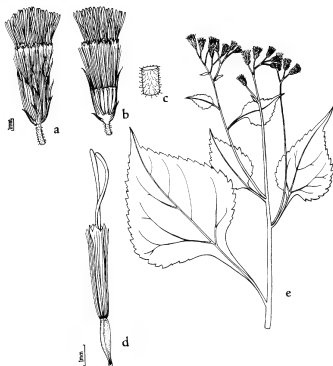


Fig. 7. *Flyriella stanfordii*: a) flowering head; b) longitudinal section of head; c) portion of stem showing glandular trichomes; d) floret; e) flowering branch.

hairs. In addition, as noted by King and Robinson (1972b), it is marked by its conspicuously constricted corolla throat and relatively few-flowered heads (Fig. 8).

Flyriella parryi is quite similar to *F. leonensis*, but the latter does not possess glandular trichomes. No doubt the two species are closely related and perhaps hybridize in the area of Monterrey since both species have been collected on Chipinque Mesa to the west of the city. *Flyriella parryi* occurs at lower, more xeric, habitats in this region, while *F. leonensis* occurs at more elevated mesic habitats (e.g., the *Quercus*-dominated forest at ca 2000 meters above Chipinque Mesa).

4. *FLYRIELLA LEONENSIS* (Robinson) K. & R. *Phytologia* 24:69. 1972.
Eupatorium leonensis Robinson, Proc. Amer. Acad. Arts. 36:479. 1901. TYPE:
MEXICO. NUEVO LEÓN: on the Sierra Madre near Monterrey, 16 Jun 1887, C. G.
Pringle 2277 (HOLOTYPE: GH!).

Eupatorium chrysoxyloides Robinson, Proc. Amer. Acad. Arts. 43:50. 1907. TYPE:
MEXICO. NUEVO LEÓN: Sierra Madre above Monterrey, limestone, 915 m, 27 Apr
1906, C. G. Pringle 10231 (HOLOTYPE: GH!; ISOTYPE: US!).

Erect perennial herb 25–50 cm tall. Leaves mostly opposite, alternate and reduced just below the capitulescence; blades predominately deltoid, 3–6 cm wide, 3.5–7.0 cm long; irregularly serrate to lobate, minutely puberulent on both surfaces, often glabrate; petioles 3–8 cm long, puberulent, abruptly winged just below the blade. Capitulescence of ultimate pedunculate units of 10–25 heads, each head on a bracteolate pedicel, 2–8 mm long. Involucre narrowly campanulate, 5–7 mm long, ca 5 mm wide; bracts imbricate in 3–5 series, linear-lanceolate, 3–7 mm long, 1 mm wide or less. Florets 30–40; corolla "yellowish-white", tubular throughout, ca 5 mm long, 0.5 mm wide, glabrous; lobes narrowly triangular, acute, ca 0.3 mm long, minutely atomiferous glandular. Anthers ca 1 mm long. Style branches linear-oblongate, yellowish-white, smooth, 5–8 mm long. Achenes 4–5-ribbed, 2.0–2.5 mm long, black, sparsely pubescent mostly near the apex; pappus 4–5 mm long, composed of 40–50 filiform, ciliate setae. Chromosome number, $n = 10$ pairs.

Distribution and Habitat (Fig. 5): Mostly eastern Nuevo León along the front range of the Sierra Madre Oriental from 600–1700 m where it occurs in limestone soils mostly in mesophytic habitats, along streams and cool moist areas. Flowering: Apr–Jul.

Additional specimens examined: MEXICO. NUEVO LEÓN: Chipinque Park, N facing slopes in pine-oak forest, 11 Jun 1978, Poole & Watson 1394 (TEX); Horsetails Falls, ca 35 km SSE of Monterrey, 26 Apr 1976, Sanders & Harborne 76060 (TEX); Cola de Caballo, 6 Apr 1971, Siegler & Baker D13133 (MSC); Cola de Caballo, 31 May 1970, Siegler et al.

DS-2570 (MSC); Monterrey, 22 May 1960, *Swish M219* (TEX); Chipinque Mesa, slopes just above motel, ca 6000 ft, 2 Jun 1978, *Turner 10019* (LL); 17 mi by road W of Horsetail Falls, 2 Jun 1978, *Turner 10037* (CAS, LL).

Flyriella leonensis is readily distinguished from other species in the genus by its puberulent, non-glandular, foliage. In addition, it can be distinguished by its sparsely ciliate achenes (mostly near apex) and generally smaller and broader heads (Fig. 9).

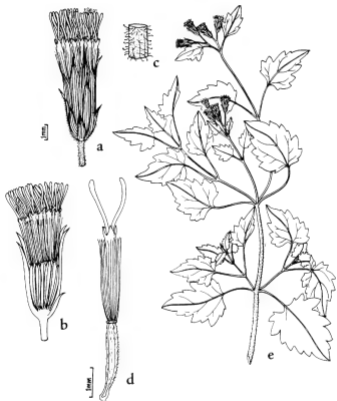


Fig. 8. *Flyriella parryi*: a) flowering head; b) longitudinal section of head; c) a portion of stem showing glandular trichomes; d) floret; e) flowering branch.

Eupatorium chrysostyloides Robinson (not to be confused with *E. chrysostylum* Robinson, which is a synonym of *Flyriella parryi*), clearly belongs to this species. King and Robinson (1972) also treated these as synonymous. According to B. L. Robinson, in his original description, *E. chrysostyloides* is distinguished by its "mixed pubescence." Actually the pubescence is puberulous, much as in *Flyriella leonensis*.

As noted above, *F. leonensis* appears to occur at higher elevations, up to 1700 m, and in more mesic habitats than *F. parryi*, at least in the Monterrey area.

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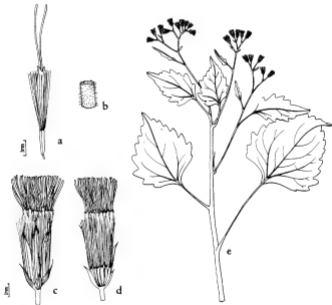


Fig. 9. *Flyriella leonensis*: a) floret; b) portion of stem showing eglandular trichomes; c) flowering head; d) longitudinal section of head; e) flowering branch.

help with the cladistic analysis. Dr. Guy Nesom, as reviewer, added assorted pungent criticisms which proved helpful.

This study is based upon approximately 130 specimens deposited in the following herbaria: CAS (2); DS(1); F (10); GH (19); LL (38); MICH (6); MO (6); MSC (5); NY (7); TEX (20); US (16).

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DISTRIBUTION OF *PORTULACA OLERACEA* L. (PORTULACACEAE) SUBSPECIES IN FLORIDA

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ABSTRACT

Range maps for the subspecies of *P. oleracea* (Portulacaceae) in Florida are provided. The collections are enumerated. Unusual specimens are noted and their seeds illustrated with scanning electron micrographs.

INTRODUCTION

The cosmopolitan *Portulaca oleracea* L. is an aggressive weedy colonizer. Chromosomally, the species is $x = 9$, and diploids, tetraploids, and hexaploids are known. The different cytotypes have distinctive seed size and seed coat texture, which makes subspecies determinations relatively easy (Danin et al. 1978). Matthews and Levins (1985a) stated: "Seed surface markings must be correlated with other morphology features when used in delimiting taxa," and they did not recognize subspecies or varieties of *P. oleracea* (1985b). Apparently they were not aware that seed size, shape, and markings were correlated with different chromosome numbers in this species.

The subspecies are not evenly distributed throughout the world (Danin et al. 1978; Danin 1983, 1985), but sympatric populations are frequently encountered.

Matthews and Levins (1985a) noted *Portulaca* has a large concentration of species in South America. They suggested *P. pilosa* entered Florida from the Carribean and spread northeast into North Carolina and westward along the Gulf Coast with evidence of recent migration into Arkansas (probably from Texan populations rather than coastal populations). Study of the distribution of *P. oleracea* in Florida is warranted because the state is strategically placed in possible migration zones between tropical and temperate regions. In this study, only a few specimens were found in primary habitats, such as *Godfrey* 72166 from mangrove flats in Monroe County. Most specimens reported here were collected in secondary synanthropic habitats such as gardens, patches in lawns, and along roadsides.

METHODS

Ripe seeds were obtained from living plants or from herbarium specimens (principally from FLAS, FSU, and USF). Identifications were made from seed size and seed coat texture as determined with the dissecting microscope under diffused light. A key to the subspecies is in Danin et al. (1978). The subspecific epithets *granulatostellulata* and *papillatostellulata* were originally hyphenated, but according to Article 73.9, ICBN (Voss 1983), the hyphen should be deleted.

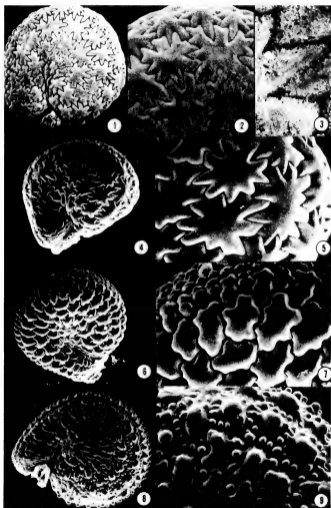
Seeds were mounted on stubs, vacuum dried, then sputter coated with 100–200 Å of AuPd (60/40). SEM micrographs were taken on a Cambridge Stereoscan S4-10 at 20 keV.

Seeds are illustrated to show diagnostic surface features (Figs. 1–9). The stellulae (plate-like epidermal cells) may have stellate radiating arms (Figs. 2, 5) or have irregularly lobed margins (Fig. 7). Stellulae may have prominently raised centers (tubercles) and papillae on the stellular arms (Fig. 9), but these features do not always occur together. The cell surfaces are usually smooth, but they may be covered with wax in some specimens (Figs. 2, 3).

DISTRIBUTION

The known distribution of *Portulaca oleracea* in Florida as determined from specimens from selected herbaria is mapped by subspecies in Figure 10 and enumerated below. It probably occurs in every county in the state, but fleshy, weedy plants (such as this species) are often neglected by collectors. Chromosome numbers are noted for each subspecies (Danin et al. 1978); no counts were made in the present study.

P. OLERACEA subsp. *GRANULATOSTELLULATA* (Poebln.) Danin & Baker ($n = 18$). **Broward Co.:** 10 mi W of Deerfield, 31 Aug 1969, *Carr 10866* (FLAS). **Hendry Co.:** Clewiston (mixed with subsp. *papillatostellulata*), 29 Dec 1984, *Danin s.n.* (FSU). **Hernando Co.:** Weeki Wachee, 25 Oct 1971, *Genella & Fleming 1062* (USF). **Hillsborough Co.:** Tampa (mixed with subsp. *nicaragoensis*), 9 Jul 1977, *Cruz 1097* (USF). **Lake Co.:** 0.5 mi W of Yalaha (mixed with subsp. *papillatostellulata*), 12 Oct 1980, *Baltzell 11235* (FLAS). **Lee Co.:** Fort Myers, 26 Dec 1984, *Danin s.n.* (FSU); Florida Forests Foundation, 20 Aug 1963, *Hoffman 11* (FLAS). **Leon Co.:** N of Tallahassee, 30 Aug 1984, *Danin s.n.* (FSU); Tallahassee (mixed with subsp. *nitida*), 11 Sep 1984, *Danin s.n.* (FSU); Tallahassee, 22 Mar 1985, *Danin s.n.* (FSU); Tallahassee, 21 Jul 1942, *Karz s.n.* (FLAS). **Manatee Co.:** Bradenton, 18 Nov 1947, *Burgis s.n.* (FLAS). **Marion Co.:** 2 mi NW of Weirsdale, 18 Nov 1973, *Baltzell 5619* (FLAS). **Monroe Co.:** Cape Sable, 7 May 1965, *Lahela & Long 28566* (USF). **Okaloosa Co.:** Eglin Air Force Base, 21 Nov 1983, *Wilhelm 11915* (USF). **Pinellas Co.:** Clearwater, 25 Jul 1984, *Danin s.n.* (FSU); Belleair Bluffs to Belleair Shores, 24 Jul 1975, *Senple et al. 1663* (USF). **Wakulla Co.:** Panacea, 27 May 1985, *Danin s.n.* (FSU).



P. OLERACEA subsp. **NICARAGUENSIS** Danin & Baker ($n = 9$). **Brevard Co.:** Malabar Cape, 31 Dec 1974, *Lakela & Long* 28072 (USF); North Merritt Island, 12 Dec 1972, *Shwey* M0684 (USF). **Clay Co.:** 2.5 mi E of Middleburg, 31 May 1981, *Sauleda & Ragan* 5380 (USF). **Collier Co.:** NW of Naples, 29 May 1965, *Lakela* 28681A (USF). **Dade Co.:** old field, 1 Nov 1979, *Alexander s.n.* (USF); Coral Gables, 26 Dec 1984, *Danin s.n.* (FSU); Miami Beach, 29 Dec 1984, *Danin s.n.* (FSU); Miami, 19 Sep 1980, *Sauleda* 4631 (USF); Key Biscayne, 2 Nov 1965, *Craighead s.n.* (USF). **Flagler Co.:** Marineland, 18 Nov 1961, *Godfrey* 61693 (FSU). **Franklin Co.:** Apalachicola, 30 Aug 1984, *Anderson* 7545 (FSU). **Hendry Co.:** Clewiston, 30 Jun 1967, *Smith* 1648 (FLAS). **Hillsborough Co.:** Tampa (mixed with subsp. *granulatosstellulata*), 9 Jul 1977, *Crews* 1097 (USF); 6 mi S of River View, 1 Apr 1976, *Wunderlin et al.* 5607 (USF). **Lake Co.:** Mt. Plymouth, 1 Aug 1983, *Danbennire s.n.* (USF). **Lee Co.:** S tip Sanibel Island, 13 Mar 1954, *Cosley* 2568 (FLAS, USF); Sanibel Island, 30 Mar 1968, *Brownbach* 6190 (FLAS), 28 Oct 1978, *Wunderlin et al.* 6188 (USF); Fort Myers, *Correll* 30330 (GH); Mound Key, 13 Jul 1974, *Todd* 127 (FLAS, USF). **Levy Co.:** 3.3 mi NE of Cedar Key, 11 June 1976, *Baltzell* 8551 (FLAS). **Martin Co.:** 11.5 mi N of Port Mayaca, 25 Nov 1976, *Baltzell* 9130 (FLAS). **Monroe Co.:** Flamingo, 1 Jan 1956, *Craighead s.n.* (FLAS); Flamingo (mixed with subsp. *papillatosstellulata*), 28 Dec 1984, *Danin s.n.* (FSU); Cudjoe Key, 16 Sep 1972, *Godfrey* 72166 (FSU); Key West, 25 Oct 1974, *Godfrey* 74027 (FSU), 14 Sep 1979, *Hawen* 6265 (USF); Long Key 14 Nov 1964, *Lakela* 27929 (USF); Big Pine Key, 7 Aug 1966, *Long et al.* 2241 (USF); Content Keys, 4 Jun 1967, *Long* 2675 (FSU); Spanish Harbor Key, 29 Nov 1969, *Long* 3026 (USF); Marathon, 27 Aug 1961, *Rosbach* 2887 (FLAS). **Palm Beach Co.:** Palm Beach, 29 Jun 1967, *Casew* 99 (USF). **Pinellas Co.:** Clearwater, 25 Jul 1984, *Danin s.n.* (FSU); NE of Clearwater, 28 Sep 1970, *Genella & Fleming* 349 (USF); Dunedin, 3 Oct 1976, *Genella & Fleming* 2490 (USF). **Putnam Co.:** Welaka, 26 Jun 1940, *Loeisle s.n.* (FLAS). **Volusia Co.:** 9 mi S of New Smyrna Beach, 27 Apr 1961, *Ray* 10787 (FSU, USF).

P. OLERACEA subsp. **NITIDA** Danin & Baker ($n = 18$). **Alachua Co.:** Gainesville, 15 May 1975, *Fleck* 48 (FLAS). **Collier Co.:** Marco Island, 20 Aug 1965, *Lakela* 29079 (USF). **Leon Co.:** Tallahassee (mixed with subsp. *granulatosstellulata*), 11 Sep 1984, *Danin s.n.* (FSU).

P. OLERACEA subsp. **PAPILLATOSTELLULATA** Danin & Baker ($n = 27$). **Duval Co.:** Holly Oaks Forest, 17 May 1965, *Craiger* 424 (FLAS). **Escambia Co.:** Pensacola, 16 Aug 1983, *Wilhelm* 11741 (USF). **Hendry Co.:** Clewiston (mixed with subsp. *granulatosstellulata*), 29 Dec 1984, *Danin s.n.* (FSU). **Indian River Co.:** 4 mi S of Vero Beach, 9 Apr 1962, *Godfrey & Reinert* 61480 (FSU). **Lake Co.:** 0.5 mi W of Yalaha (mixed with subsp. *granulatosstellulata*), 12 Oct 1980, *Baltzell* 11235 (FLAS). **Pinellas Co.:** Clearwater, 25 Dec 1984, *Danin s.n.* (FSU). **Monroe Co.:** Flamingo (mixed with subsp. *nicaraguensis*), 28 Dec 1984, *Danin s.n.* (FSU).

P. OLERACEA subsp. **STELLATA** Danin & Baker ($n = 27$). **Hillsborough Co.:** Egmont Key, 1 Sep 1978, *Crews* 1480 (USF).

Figures 1–9. Scanning electron micrographs of selected *Portulaca oleracea* seeds. 1. *Lakela* 27374 (subsp. *stellata* X subsp. *nicaraguensis*?). 2. *Lakela* 27374, with typical stellulae of subsp. *stellata*. 3. *Lakela* 27374, surface detail showing waxy covering characteristic of many subsp. *nicaraguensis* specimens. 4. *D'Arcy* 2942 (affin. subsp. *nitida*?). 5. *D'Arcy* 2942, with non-waxy stellulae that are individually much larger than those in Fig. 2. 6. *Godfrey* 61693 (subsp. *nicaraguensis*, the non-waxy form). 7. *Godfrey* 61693, with perforations along the sutures between the stellular arms. 8. *Danin s.n.* in 1985 (subsp. *granulatosstellulata*). 9. *Danin s.n.* in 1985, with tubercles and papillae on the epidermal plates.

PROBLEMATIC SPECIMENS

The following specimens are not comfortably assigned to any subspecies. They are not mapped in Fig. 10, but are illustrated in Figs. 1–5. They possibly represent new subspecific taxa or hybrids.

Lakela 27374 (FLAS, USF) from Fort de Soto Park in Pinellas County has rather diverse seed size. A few seeds have size and shape like those of subsp. *stellata* but are covered with wax as in subsp. *nicaraguensis*. Figures 1–3 are of an unusually small seed of *Lakela 27374* with the stellate epidermal cells of subsp. *stellata* and the waxy covering (and smaller seed size) of subsp. *nicaraguensis* (Fig. 3). These specimens probably represent hybrids between the two subspecies.

D'Arcy 2942 (FLAS) from Indian River Island in Indian River County has seeds similar to those of subsp. *nitida* in size and shape, but the specimen has linear rather than obovate leaves. The epidermal cells of the seeds are stellate as in subsp. *nitida* (Figs. 4, 5), but the individual cells are much larger in D'Arcy's specimen (i.e. there are fewer cells across the face of the seed) than they are in typical subsp. *nitida*.

DISCUSSION

Legrand, in a study of American species of *Portulaca* (1962), noted variation in seed surface features in *P. oleracea*, but he did not recognize any varieties or subspecies taxonomically. Matthews and Levins (1985a) found that seed surface markings were not helpful in distinguishing some other species of *Portulaca*. They did not cite the study of Danin et al. (1978) in either of their papers, and even though they noted some variability in seed coat features in *P. oleracea*, they followed the taxonomy of Legrand. We have found that seed size and surface texture are of considerable taxonomic utility in distinguishing subspecies of *P. oleracea*. All the Florida collections were easily assigned subspecies with the exception of the two mentioned as problematic specimens. Unfortunately, the different subspecies (cytotypes) are not distinguishable vegetatively, and chromosome numbers and seed ultrastructure are not useful for identification of subspecies in the field.

The cytotypes of *P. oleracea* are not evenly distributed on a world-wide basis, and they show an uneven distribution in Florida as well. The subtropical subsp. *nicaraguensis* is the most frequently collected in Florida (Fig. 10). Its range in Florida is apparently part of the original distribution of the subspecies rather than due to human interference. Migration routes for this subspecies from central America and the Caribbean into Florida appear to be similar to those noted for *P. pilosa* (Matthews and Levins 1985a). Subspecies *stellata* is generally found at higher latitudes; its

occurrence in Florida is surprising and does not reflect migration from the tropics.

Putative hybrids are known from Yucatan (Danin et al. 1978) and Florida (interspecific and intraspecific, respectively). This suggests the Gulf of Mexico region is an area of active speciation for *Portulaca oleracea*. This species is well suited for detailed cytogenetic studies at the population level because sympatric subspecies occur.

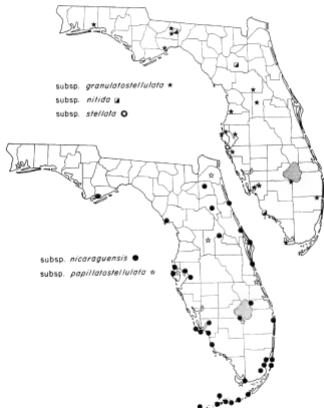


Figure 10. Distribution of *Portulaca oleracea* subspecies in Florida.

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SOME OBSERVATIONS ON *PINUS GLABRA* WALTER (PINACEAE)

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ABSTRACT

Pinus glabra Walter is the least common of the southeastern pines. It rarely if ever grows in pure stands. Quadrats were established at 14 sites in the southeastern United States wherever *P. glabra* was abundant throughout its range. Importance values of trees found in sample plots indicate that *P. glabra* had a higher importance value in Mississippi than had been previously reported.

INTRODUCTION

Pinus glabra Walter, spruce pine, the least common of the southeastern pines, rarely if ever grows in pure stands. It occupies soils that are loamy, low in organic content, and acid in reaction. *Pinus glabra* may be found in all stages of its life history in mature forests within its range, an unusual occurrence for a pine. Its seedlings and saplings have been reported growing where light intensity was as low as 250 foot candles (Dial et al. 1976).

Dial et al. (1976) have studied *P. glabra* on sites in the lower coastal plain of South Carolina where *P. glabra* is locally abundant. They sampled six areas in Colleton and Dorchester counties, South Carolina and found *P. glabra* to be associated with *Liquidambar styraciflua*, *Pinus taeda*, and *Quercus virginiana*.

Harrar (1964) reported that *P. glabra* reaches its maximum development within an area in northwest Florida between the Choctawhatchee and Chattahoochee rivers. Observations by the present authors in this area indicate that *Pinus clausa*, sand pine, not *P. glabra*, occurred in pure stands in this area. The objective of the present study was to determine the relative abundance of *P. glabra* within its range in the southeastern United States.

METHODS

To determine the relative abundance of *P. glabra* within portions of its range in the southeastern United States, vegetation was sampled by the quadrat method at 14 stations. Six areas in Dorchester and Colleton coun-

ties, South Carolina had been sampled and reported previously by the present researchers in an earlier paper (Dial et al. 1976). Eight additional sites in Georgia, Florida, Mississippi, Alabama and Louisiana were selected to sample vegetation in the area of maximum development of *P. glabra*. Site 2 was selected in Seminole County, Georgia; Site 3 in Jackson County, Florida; Site 4 in Gadsden County, Florida; Site 5 in Washington County, Florida; Site 6 in Okaloosa County, Florida; Site 7 in Pearl River County, Mississippi; Site 8 in Geneva County, Alabama; and Site 9 in Washington Parish, Louisiana. In each of the aforementioned areas, twenty 10 x 10 m quadrats were selected to sample the arborescent vegetation. Importance values of the arborescent species were calculated by the following formula: Importance Value = the sum of the relative density, relative frequency and relative dominance (percent basal area). Nomenclature follows that of Radford et al. (1968).

A smaller 2 m by 4 m plot located near the center of the larger plot was used to sample seedlings and saplings. A 1 m² plot located near the center of the 2 m by 4 m plot was used to sample herbs and grasses.

Sample plots were randomly selected within the specific areas sampled; no two plots were ever adjacent to each other. The fact that the sampling was not random must be emphasized; the locations for the 14 sample areas were chosen with discrimination for the purpose of sampling *P. glabra* in areas of high density.

RESULTS & DISCUSSION

Pinus glabra reached its best development in a stand located in Pearl County, Mississippi, just east of the Pearl River. Here *P. glabra* attained an importance value of 157, while *Carpinus caroliniana*, the most important associate attained an importance value of 58 (Table 1). If *Carpinus*, an understory tree, were not included in the importance value calculations, *P. glabra* would have had an even higher importance value. The average importance value of *P. glabra* on the Florida sites was slightly higher (78.5) than the importance values for *P. glabra* on the South Carolina sites where the average importance value was 69. Importance values for *P. glabra* were higher in Mississippi and Georgia, but represent data from single study sites sampled by 20 quadrats. In Florida, *P. glabra* attained an importance value of 127 at the Okaloosa site, which was located west of the Choctawhatchee River.

Pinus glabra was usually associated with *Liquidambar styraciflua* and *Pinus taeda* in South Carolina. *Carpinus caroliniana*, *Quercus virginiana* and *Carya glabra* might also be associated with *P. glabra* in South Carolina but generally were not as common as *Liquidambar* and *P. taeda*. In Florida, *Q.*

TABLE 1. Importance values of tree species associated with *Pinus glabra* at nine study sites in the southeastern United States. Site 1, South Carolina; Site 2, Georgia; Sites 3-6, Florida; Site 7, Mississippi; Site 8, Alabama; Site 9, Louisiana. See the methods section for site location.

SPECIES	IMPORTANCE VALUES FOR 9 STUDY SITES								
	1	2	3	4	5	6	7	8	9
<i>Pinus glabra</i>	69	130	43	53	91	127	157	45	118
<i>Quercus nigra</i>	15	59	5	42	17			21	
<i>Pinus taeda</i>	35				22	11	4		
<i>Liquidambar styraciflua</i>	38	13		31	16	22	26	7	19
<i>Ilex opaca</i>	9			7	4			13	
<i>Acer rubrum</i>	17	7		13			3	6	13
<i>Salix nigra</i>	2					3			
<i>Carya glabra</i>	20					3			
<i>Quercus virginiana</i>	26		22	48	75	25		74	
<i>Fagus grandifolia</i>	6		54	34					55
<i>Carpinus caroliniana</i>	15			13	9	20	58	31	11
<i>Persea palustris</i>	1								
<i>Cornus florida</i>	1								
<i>Nyssa biflora</i>	8			4	5	6	31	29	19
<i>Quercus michauxii</i>	10			3					9
<i>Ulmus alata</i>	8								
<i>Fraxinus americana</i>	3								
<i>Quercus laurifolia</i>	6		17		32	82		51	13
<i>Quercus stellata</i>	3				3				
<i>Ostrya virginiana</i>	3					3			
<i>Quercus alba</i>	4		5						
<i>Pinus elliotii</i>		76	13	15					
<i>Ulmus americana</i>		5	5						5
<i>Carya spp.</i>		3		20					
<i>Magnolia grandiflora</i>			130	23	8			10	
<i>Quercus falcata</i>		14	6						
<i>Carya aquatica</i>				9			6	12	6
<i>Taxodium distichum</i>				4	5		3		7
<i>Fraxinus caroliniana</i>							3		
<i>Betula nigra</i>							3		20
<i>Prunus sp.</i>								5	

virginiana was the usual associate of *P. glabra*, while *Quercus nigra*, *Liquidambar*, *Carpinus*, *Nyssa biflora*, *Magnolia grandiflora* and *Quercus laurifolia* were less frequently associated with the species (Table 1). Generally, the aforementioned trees were commonly found with *Pinus glabra* in the southeastern United States. Additional trees associated with *P. glabra* included *Acer rubrum*, *Pinus elliotii*, *Carya aquatica*, and *Taxodium distichum*, yet none of these trees with the exception of *P. elliotii* attained high importance values in the sites sampled in the present study.

Pinus glabra often forms a part of the understory and occasionally the overstory in mixed hardwood pine forests in the lower coastal plain of the

southeastern United States. *Pinus glabra* has the capacity for survival in deep shade and specimens of all sizes and ages from seedlings to mature seed trees, thrive in deep shade. Green (1938) calls *P. glabra* the most shade tolerant of the eastern pines.

Pinus glabra was conspicuously present in all stages of its life history, and was one of the most commonly encountered seedlings and saplings in the study plots. Other seedlings and saplings associated with *P. glabra*, listed in decreasing order of density include: *Liquidambar styraciflua*, *Quercus nigra*, *Acer rubrum*, *Carya glabra*, *Ilex opaca*, *Persea palustris*, and *Carpinus caroliniana*. Others with lower density were also present.

Shrubs and lianas were represented by *Rubus* spp., *Myrica cerifera*, *Sebastiania ligustrina*, *Sabal minor*, *Vaccinium* spp., *Aralia spinosa*, *Smilax* spp., *Rhus radicans*, *Gelsemium sempervirens*, *Lonicera japonica*, *Vitis rotundifolia*, *Parthenocissus quinquefolia*, *Campsis radicans*, *Bignonia capreolata*, and many others. Common grasses and herbs included *Arundinaria tecta*, *Panicum* spp., *Uniola laxa*, *Elephantopus tomentosus*, *Scleria* spp., and others. *Polypodium polypodioides* was usually present on the limbs of large live oaks, if *Quercus virginiana* occupied the study sites.

Harrar (1964) reported that *Pinus glabra* rarely, if ever, grows in so called pure stands "with the exception of an area in northwest Florida between the Choctawhatchee and Chattahoochee rivers where it reaches its maximum development." Data in the present study indicate that the development of *P. glabra* in northwestern Florida was no more pronounced than in other areas sampled. In fact, development was not as great in northwestern Florida as in Pearl River County, Mississippi or Washington Parish, Louisiana (Table 1). No pure stands of *P. glabra* were observed in this work in northwestern Florida as reported by Harrar (1964) although sand pine, *Pinus clausa* was observed in nearly pure stands on higher drier sites in this area.

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A NEW SPECIES OF *WALLENIA* (MYRSINACEAE) FROM HAITI¹

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ABSTRACT

A new species, *Wallenia formonensis*, is described from a disturbed cloud forest at 1520 m alt. on the southern slope of Morne Formon in the Massif de la Hotte of southern Haiti. The genus, *Wallenia*, of some 25 species, is, itself, endemic to the West Indies. The cloud forests and moist pine forests of the higher elevations of Morne Formon and adjacent M. Macaya are diverse and contain many local endemics. The flora of this area is known mainly through the field work of Erik L. Ekman, but is in need of additional botanical investigation.

The species described in this paper was discovered in the high elevations of Morne Formon in the Massif de la Hotte, southern Haiti. Field work formed part of an inventory of the flora and fauna of the recently established Pic Macaya National Park. The discovery of this species brings to eight the number of species of *Wallenia* recorded for Hispaniola (Barker and Dardeau 1930, Moscoso 1943, Liogier 1971). Two other species of *Wallenia* occur in Pic Macaya National Park: *W. aquifolia* Urb. & Ekm. and *W. ekmanii* Urb. Both species are endemic to the mountains of southern Haiti. Other Myrsinaceae occurring in the park include *Ardisia fuertesii* Urb., *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult., and *Myrsine magnoliifolia* (Urb. & Ekm.) Alain.

Although the high elevation cloud forests and moist pinelands of the Massif de la Hotte were explored by Erik L. Ekman (Ekman 1928, Moscoso 1943, unpublished field notes of E. L. Ekman), the diverse and highly endemic flora of the region is in need of additional botanical exploration, as evidenced by the discovery of several "new" species, one of which is described herein.

WALLENIA formonensis W. Judd, sp. nov. (Figure 1)

Species haec ab *Wallenia jacquinioides* (Griseb.) Mez differt foliis parvioribus, i.e., ca 2.5–4.7 cm vs. 5–9.5 cm longis, et inflorescentiis plerumque brevioribus.

Tree to ca 10 m tall. Indumentum of multicellular, peltate, gland-

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headed hairs. Twigs roughened, glandular-punctate. Leaves alternate and pseudovercillate; petiole 4–13 mm long, adaxially grooved, glandular-punctate; blade obovate, (1.6)2.5–4.7 cm long, (0.5)1–2.2 cm wide, coriaceous with ovoidal, brownish, resin-containing, secretory cavities in mesophyll, especially near margin, the apex truncate to rounded, the base attenuate, the margin entire, plane to revolute, especially along proximal portion of blade, the adaxial surface dull to slightly lustrous and obscurely glandular-punctate, the abaxial surface pale and conspicuously glandular-punctate, the venation brochidodromous, adaxially obscure, abaxially with secondary veins slightly raised and visible, the tertiary veins obscure, not raised-reticulate. Inflorescences axillary racemes or rarely scarcely branched panicles, the primary axis 2–4 cm long, glandular-punctate, bearing ca 13 to 30 flowers. Flowers imperfect (plants dioecious) but appearing perfect, 5-merous, each subtended by a more or less linear caducous bract to 3 mm long; only staminate flowers seen. Pedicels 2–4.5 mm long, glandular-punctate. Sepals 5, imbricate, widely ovate with rounded to obtuse apices and slightly erose, glandular-fimbriate margins, 1.3–1.7 mm long, 1.3–1.5 mm wide, sparsely glandular-punctate and with conspicuous red to brown ovoidal secretory cavities. Corolla broadly campanulate, white with conspicuous brownish ovoidal secretory cavities, the tube ca 1 mm long, the lobes 5, triangular/ovate with rounded apices, 1.3–2 mm long, 1.3–1.9 mm wide. Stamens 5, the filaments narrow, 3–4 mm long, the anthers ca 1 mm long with conspicuous dorsal cluster of reddish ovoidal secretory cavities. Pistillodium ca 1.7 mm long with ovoid, glabrous ovary tapering to short style; secretory cavities present. Pistillate flowers and drupes not seen.

TYPE: HAITI. DEPARTEMENT DU SUD: Massif de la Hotte, Pic Macaya National Park, disturbed cloud forest on southern slope of Morne Formon, ca 1520 m alt., north of community of Formon, occasional, 11 Jun 1984, James D. Skear, Jr. 1524 (HOLOTYPE: FLAS; ISOTYPES: EHH, NY).

Wallenia formonensis is a member of *Wallenia* subgenus *Homowallenia* Mez, a group characterized by scarcely heteromorphic flowers that are borne on axillary racemose inflorescences (Mez 1901, 1902). The species is quite similar to the Oriente/Cuban taxon, *Wallenia jacquinioides* (Griseb.) Mez, and the two species are likely closely related. *Wallenia formonensis* differs from *W. jacquinioides* in its consistently smaller leaves (i.e., (1.6)2.5–4.7 by (0.5)1–2.2 cm vs. (3)5–9.5 by (0.8)1.5–3.2 cm in *W. jacquinioides*), shorter inflorescences (i.e., 2–4 cm vs. 3–6 cm in *W. jacquinioides*), and a tendency toward producing more flowers per inflorescence. The new species is also easily distinguished from the similar Dominican species, *W. apiculata* Urb. and *W. urbaniana* Mez, by its less

coriaceous leaves with obscurely reticulate higher-order venation, i.e., the tertiary and higher-order veins are not raised-reticulate. The calyx and corolla of the latter two species lack prominent red to brown ovoidal secretory cavities. *Wallenia formonensis* differs from the recently described *W. gracilis* Alain (Liogier 1971) in its blunt-tipped and only obscurely reticulate-veined leaves, inflorescences with several to many flowers, and corolla with rounded lobes.

The cloud forests and moist forests of *Pinus occidentalis* Sw. of the higher elevations (i.e., chiefly above 1300 m alt.) of the Massif de la Hotte are

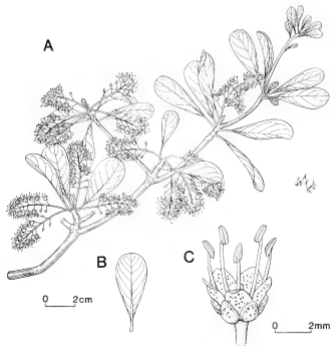


Figure 1. *Wallenia formonensis* W. Judd: A, habit; B, leaf; C, staminate flower. Drawn from the holotype.

floristically diverse and contain numerous endemics, e.g., ca 34% of the flowering plants of Pic Macaya National Park are endemic to Hispaniola (Judd unpublished data). Such forests in the Massif de la Hotte are now essentially limited to the upper slopes of Morne Formon and M. Macaya. Other trees and shrubs endemic to the Massif de la Hotte that recently have been collected by the author (or J. D. Skean) in Macaya National Park include: *Calyptanthus botteana* Urb. & Ekm., *Cestrum filipes* Urb. & Ekm., *Cleyera ternstroemioides* (O. E. Schmidt) Kobuski, *Dendrophthora carnosa* Urb. & Ekm., *Eugenia formonica* Urb. & Ekm., *Eupatorium flavidulum* Urb. & Ekm., *E. urbanii* Ekm., *E. porphyrocladium* Urb. & Ekm., *Haenianthus oblongatus* Urb., *Mecranium microdictyum* Urb. & Ekm., *M. tricoctatum* Urb. & Ekm., *Meliosma abbreviata* Urb., *Meriania squamulosa* Urb. & Ekm., *Miconia apiculata* Urb. & Ekm., *M. barkeri* Urb. & Ekm., *M. hypiodes* Urb. & Ekm., *M. ossaeifolia* Urb. & Ekm., *Myrsine magnoliifolia* (Urb. & Ekm.) Alain, *Pachyanthus blancheanus* (Urb.) Urb., *Psychotria alpestris* Urb. & Ekm., *Rondeletia formonia* Urb. & Ekm., *Sapium haitiense* Urb., *Solanum formonense* O. E. Schulz, *S. botteanum* Urb. & Ekm., *Stevensia botteana* Urb. & Ekm., *Symplocos botteana* Urb. & Ekm., *Ternstroemia barkeri* Ekm. & Schmidt, and *Wallenia aquifolia* Urb. & Ekm. The region also supports many endemics at lower elevations in the moist forest on limestone in the vicinity of Formon. Woody taxa occurring with this newly described species include *Besleria lutea* L., *Branellia comocladifolia* Humb. & Bonpl. subsp. *domingensis* Cuatt., *Didymopanax tremulum* Krug & Urb., *Gomidesia lindeniana* Berg, *Gyrotaenia myriocarpa* Griseb., *Heterotrichum umbellatum* (Mill.) Urb., *Mecranium microdictyum* Urb. & Ekm., *Miconia subcompressa* Urb., *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult., *Turpinia picardae* Urb., and *Vernonia saepium* Ekm. There is hope that the establishment of the Pic Macaya National Park will lead to the preservation of these interesting forests.

ACKNOWLEDGEMENTS

I thank Dr. Charles Woods, Florida State Museum, coordinator and principal investigator of the U.S.A.I.D. sponsored project, *Biogeophysical Inventory of the National Parks of Haiti*, who organized the field trips to the Massif de la Hotte. Thanks are also due to James D. Skean who assisted in the collection of the plants of this region. I am grateful to Dr. Dana G. Griffin, III for his helpful suggestions concerning the manuscript, and to the New York Botanical Garden for the loan of comparative material of *Wallenia*. Finally, I wish to thank Wendy Zomlefer for preparing the illustration.

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SOLIDAGO (ASTERACEAE) OF LIMITED DISTRIBUTION IN THE CENTRAL UNITED STATES

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ABSTRACT

Solidago ouachitensis C. & J. Taylor, a rare endemic of the Ouachita Mountains of Arkansas and Oklahoma is described new to science. The range of *Solidago speciosa* var. *pallida* is extended southward into New Mexico and Oklahoma.

INTRODUCTION

Continuing work on *Solidago* has resulted in the location of two additional taxa of *Solidago* for the south central United States (Taylor & Taylor 1983, 1984). One of these taxa is a new species from the Ouachita Mountains of Arkansas and Oklahoma. The other taxon, *Solidago speciosa* var. *pallida*, is sporadic along the front range of the Rocky Mountains and is being reported new to Oklahoma and New Mexico. Both taxa are examples of schizoendemism, their isolation probably occurring since the glaciers receded.

1. *SOLIDAGO OUACHITENSIS* C. & J. Taylor, sp. nov.

Solidago caulibus simplicibus glabris, e caude ramoso; foliis lanceolatis glabris acutis, usque ad 16 cm longis et 6 cm latis, grosse serratis, in caulibus decurrentibus; inflorescentiis axillaribus; bracteis involuclorum glabris; pedunculis pubescentibus vel glabris; floribus 4-8, ligulatis 1 (0-2) per capitulum, acheniis 18 striis glabris.

Plants 7-12 dm tall, with few to several mostly unbranched glabrous stems from a branched rootstock. Leaves alternate, lanceolate to obovate, acute, largest leaves at midstem up to 16 cm long, 6 cm wide, with prominent midvein and numerous smaller lateral veins, glabrous, edges coarsely toothed, serrations up to 5 mm in size. Base of leaf decurrent on stem causing striations. Leaf internodes mostly 5-7 cm long. Inflorescence axillary, the upper 1/3-1/2 of stem leaves normally with 4-8 heads per axil, pedicels glabrous to puberulent, involuclral bracts 4.5-5 mm by 1 mm, inner obtuse, outer acute, glabrous, margins ciliate, 1-nerved. Total flowers 4-8, ray flowers 1 (0-2) per head, ligule 3 mm x 0.5 mm; disk corollas 4 mm long, (tube 2 mm, lobes 2 mm). Mature achenes 4 mm long, with about 18 striations, glabrous.

TABLE 1. Comparison of selected characters between *Solidago* taxa: *ouachitensis*, *caesia* var. *caesia*, c. var. *curtisii*, and *flaccidifolia*.

Character	OUACHITENSIS	CAESIA	CURTISII	FLACCIDIFOLIA
Longest leaf (cm)	12-16	10-12.5	11.5-17	10-15
Widest leaf (cm)	4-6	1.5-2.5	2-2.8	1.5-3.5
Internode lgth (cm)	5-7	1.5-2.5	1.3-3.5	2.5-3.5
Floral axis	glabrous	glabrous	pubescent	pubescent
Heads/leaf axil	4-8	4-10	5-15	4-10
Phyllary lgth (mm)	4.5-5	3.5-4.5	4-4.5	3.5-4
Phyllary width (mm)	1	0.7	0.7-1	0.7
Phyllary surface	glabrous	glabrous	± pubescent	pubescent
Flower number	4-8	8-9	6-12	5-9
Ray flower number	1(0-2)	3-4	3-4	3-4
Achene size (mm)	4	2.5	2-2.5	3
Achene surface	glabrous	pubescent	pubescent	pubescent

Endemic to very mesic forests on north-facing slopes in the Ouachita Mountains of Arkansas and Oklahoma. (Figs. 1, 2).

TYPE: U.S.A. OKLAHOMA. LeFlore Co.: mesic forest on north-facing slope of Rich Mountain, 5.3 mi N and 7 mi E of Big Cedar, 7 Oct 1984, J. & C. Taylor 32788. (HOLOTYPE: DUR; ISOTYPES: GH, MO, NLU, NY, OCLA, OKL, OKLA, SMU, UARK).

Solidago ouachitensis is a member of the *caesia-flexicaulis* complex of the eastern United States. It was first collected by G. W. Stevens in 1913 from near Page, Oklahoma. Until last year, it had been collected only four times from a total of three locations. The distribution shown for *S. curtisii* in Arkansas (Smith 1978) is based on material of this species as is apparently the report of *S. flaccidifolia* Small for Oklahoma (Urtal 1984). Urtal's report is based on G. W. Stevens, s.n., Oklahoma, LeFlore Co., near Page in open woods on mountain side (US). Our specimen (DUR) with the same collecting data is Stevens 2761 and is in early bud.

Table 1 gives a comparison of selected characters of sympatric *Solidago ouachitensis* and *S. caesia* var. *caesia* as they occur in the Ouachita Mountains of Arkansas and Oklahoma. Also included for comparison are two other closely related allopatric members of the *caesia-flexicaulis* complex. Measurements for *S. flaccidifolia* (*S. caesia* var. *paniculata* Gray) and *S. caesia* var. *curtisii* Wood (*S. curtisii* Gray) are based on the original descriptions and measurements from specimens collected by the authors in the Appalachian Mountains of North Carolina and Tennessee.

Examination of data in Table 1 shows several morphological differences between *S. ouachitensis* and *S. caesia* var. *caesia*: leaf length/width ratio, leaf width, internode length, size of head, ray number, and achene size and surface. In the last seven years since our discovery of *S. ouachitensis*, no in-



Figure 1. Holotype of *Salidago onachitensis* C. & J. Taylor.

intermediates have been found by the authors despite yearly field trips in the area it is growing.

In the Appalachian Mountains, the closest related taxa are *S. caesia* var. *curtisii* and *S. flaccidifolia*. As the *caesia-flexicaulis* complex is variously treated by taxonomists (Cronquist 1980; Gleason 1968; Mackenzie 1933; Small 1903; Radford et al. 1968; Taylor & Taylor 1983; Uttall 1984a, 1984b, and pers. comm.) the measurements of Table 1 are based on the strict sense of the taxa. The disagreement as to number of species to be

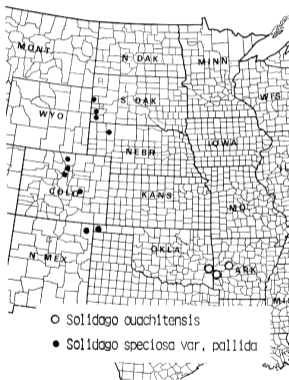


Figure 2. Distribution of *Solidago auachitensis* and *Solidago speciosa* var. *pallida*. (R - additional locations reported by McGregor et al. 1977).

recognized is due to the large number of intermediates which do not clearly key to any single taxon. The characters which separate *S. ouachitensis* from these Appalachian taxa, are the glabrous achene, larger achene size, the single ray flower, greater internode length, and very wide leaf.

The vegetation of the Ouachita Mountains is closely allied with the Appalachian Mountains, and the dominants in the forest are similar or the same. During a cooler moister time, the goldenrod populations of these mountains occupied much larger ranges and were probably sympatric. *Solidago ouachitensis* is now a relict, and appears to be a holoschizoendemic as described by Keener (1983).

Solidago ouachitensis is restricted to very mesic, north-facing slopes, and its limited distribution makes it one of the rarest endemics of the Ouachita Mountains and a candidate for listing as endangered under the Endangered Species Act. Populations located in Mt. Nebo State Park in Arkansas are currently protected under Arkansas State Park regulations. The type location on the north slope of Rich Mountain is de facto wilderness, but the National Forest Service has not recommended this botanically rich area be included in the national wilderness system. The third site is in private ownership. A similar holoschizoendemic, *Solidago spithamea*, is also known from only three locations in the Appalachian Mountains, and is currently being processed for designation as Endangered.

Other specimens examined (Fig. 2) are ARKANSAS: Polk Co.: north-facing slope adjacent to Big Fork Creek, 0.6 mi NW on Hwy 8 then 0.6 mi N of the town of Big Fork Creek, *J. & C. Taylor 32786* (DUR, SMU); and N facing slope and small spring on Big Fork Creek, about 18 mi S of Mena, elev. 1000–1100 ft., *McWilliams, s.n.*, 30 Oct 1954 (UARK); rocky dry area, top of mountain, P.O. Mena, elev. 2600, *Denaree 59493* (SMU). Yell Co.: bench overlook on Mt. Nebo, 8 mi E of Dardanelle, *J. & C. Taylor 32770* (DUR, SMU), and rocky woods, north side of Mt. Nebo, *Palmer 26487* (UARK). OKLAHOMA: LeFlore Co.: open woods on mountain side near Page, *Stevens 2761* (DUR, US?), and top north slope of Rich Mountain, *Taylor 25502* (DUR).

2. *SOLIDAGO SPECIOSA* NUTT. var. *PALLIDA* PORTER. Bull. Torrey Bot. Club 19:130. 1892. *S. pallida* (Porter) Rydb. Bull. Torrey Bot. Club 35:153. 1906.

New to NEW MEXICO: Colfax Co.: Raton Pass, 17 Oct 1932, *A. & R. Nelson s.n.* (RM); and OKLAHOMA: Cimarron Co.: upper slickrock edge of Fern Canyon, 5 mi E of Kenton, *J. & C. Taylor 32592* (DUR, SMU). These populations at the southern end of the range of the variety (Fig. 2) appear to be relict, part of a spotty and limited distribution along the canyons and foothills of the front range of the Rocky Mountains from Oklahoma to South Dakota.

McGregor et al. (1977) shows this variety maintains a thread of contact with *Solidago speciosa* Nutt. proper along the Niobrara River in Nebraska.

However, the morphological affinities of var. *pallida* are not with the var. *rigidiuscula* Torr. & Gray, the common variety in the prairies, but with var. *jejunifolia* (Steele) Cronq. found in sandy areas adjacent to the Great Lakes. Cronquist (1947) indicated the closeness of var. *jejunifolia* with *pallida* and based his description and recognition of *jejunifolia* on its separate geographical distribution.

The affinity of our plants with those of more northern areas indicates again the relict nature of these populations, persisting and surviving a climate changing to warmer and drier conditions.

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THE REDISCOVERY OF *POTAMOGETON FLORIDANUS* SMALL (POTAMOGETONACEAE)

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ABSTRACT

Potamogeton floridanus Small, first collected in Milton, Florida in 1886 and represented by two specimens, was named in 1903. Its taxonomic status has fallen since into ambiguity among students of the genus, owing largely to the fact that its existence has continued to be represented only by the two original collections. It has not been recognized as a distinct species by anyone other than Small since 1935. Recently the plant was rediscovered and is known now from four disparate populations. Specimens from these populations match exactly the type and the type description. Observations in the field suggest strongly that these specimens represent a valid species endemic to the lower Blackwater River drainage in Santa Rosa County, Florida.

In May, 1886, A. H. Curtiss sent to the Torrey Herbarium a pondweed from ". . . the Blackwater River, northwestern Florida." It was regarded simply as a ". . . peculiar form of *Potamogeton natans*" (Morong 1886). Morong, noting this collection, described it as having ". . . small, acute, elliptical leaves, 4–6 cm long by 5–15 mm wide, and erect peduncles about 6 cm long." He noted further that it looked ". . . exactly like specimens in the Torrey Herbarium from India which are labeled *Potamogeton natans* var." Curtiss subsequently sent a specimen collected from the same Blackwater River site in late June of the same year. Neither of these collections included fruiting material.

Small (1903) included in his manual a new pondweed from the "Blackwater River, W. Fla.," and named it *Potamogeton floridanus*. He compared it with and treated it next to *P. natans* L., giving the overall dimensions of *P. floridanus* as smaller than those of *P. natans*, and with narrower floating leaves. In his description of the species, Small did not indicate that he had seen fruiting material, although in his 1913 edition he made an inexplicable reference to the drupelet.

Bennett (1907) expressed little doubt that the specimen upon which Small based *P. floridanus* was one and the same as that upon which Morong commented in 1886; he was, however, of the opinion that the specimen

was actually *P. tepperi* Benn., a species which has much the appearance of a "... small *natans*, and is often so named." Bennett determined that the "*P. natans* var." specimens from India to which Morong referred were indeed *P. tepperi*.

The binomial *Potamogeton floridanus* Small was relegated to synonymy, with equivocations, under *P. tepperi* by Ascherson and Graebner (1907), apparently on the advice of Bennett.

Taylor (1909) included *P. floridanus* under *P. natans* on the basis of the speculation that the former was "... an immature form ..." of the latter. He noted also, however, the "... slender stem and leaves acute at both ends ..." and that mature fruit was unknown. *Potamogeton tepperi* was not mentioned, either as a synonym or even as a species attributed to North America. Small (1913 & 1933), nevertheless, continued to recognize the two Blackwater River specimens as representing an indigenous, albeit rare, Florida species.

Ogden (1943), apparently reluctant to determine this plant as the Asian species *P. tepperi*, acknowledged that it might be "... a pronounced ecological form of *P. oakesianus* or *P. natans* ..." but pointed out that neither species "... has been otherwise found within 600 miles of Florida." He preferred to regard the two Curtiss specimens as representing hybrids between some linear-leaved species and *P. illinoensis* Morong, although his own detailed studies of the stem anatomy caused him to cast considerable doubt upon this hypothesis.

As a result of the passage of the Endangered Species Act of 1973, the Smithsonian Institution was directed to review the status of the nearly 25,000 kinds of plants which are native to the United States. *Potamogeton floridanus* was among the plants that were nominated for additional consideration, but since it had not been seen alive since 1886, it was subsequently listed in the Federal Register as "possibly extinct."

Haynes (1978), nearly one hundred years after Curtiss collected his material, could add nothing more to our understanding of this plant. He retired the problem by noting that "... the exact nature of *P. floridanus* Small, based on two collections made by Curtiss in 1886 (NY), is uncertain."

The absence of additional collections, along with equivocations by the major students of the group, left the floristic botanist with little choice other than to relegate *P. floridanus* to synonymy or to ignore it altogether.

The only recent authors whom one might have expected to treat *P. floridanus* chose not to do so (Ward 1968, 1979; Godfrey and Wooten 1979). In 1980, when an update of the status of United States plants appeared in the Federal Register, *P. floridanus* had been dropped from the list because of its

reputed hybrid origin, since it had been decided by personnel charged to operate the endangered species program that hybrids no longer would be considered.

Three recent collections (*Wilhelm & Blackmon* 9706, 23 November 1981, NY; *Wilhelm & Blackmon* 11522, 10 Jul 1983, USF; and *Burkhalter* 9398, 3 Jun 1984, UWFP), with attendant field observations, have added more information regarding the taxonomic status of *P. floridanus*. Sadly, however, Small's (1913) inexplicable reference to the drupelet notwithstanding, fruits for this species have yet to be collected.

The idea that *P. floridanus* may represent an early introduction is, on the face of it, not altogether spurious. The old port of Pensacola long has been a place of entry into this country for ballast weeds and other species native to areas remote from the central Gulf coast region (Mohr 1878). *Najas ancistrocarpus* Magnus, for example, was collected ". . . in tidal creeks near Milton at the head of Pensacola Bay" and reported under the name *N. conferta* A. Br. (Fernald 1902).

Specimens, however, of the Asian species *Potamogeton tepperi* (Litvinov 3352 MO, determined by Bennett, and Merrill 1723 MO) are coarse broad-leaved plants with rounded leaf bases and stout petioles and peduncles, resembling *P. natans* much more closely than the Florida material. The recent collections of *P. floridanus* match exactly the description of Small's species and the type specimens (Fig. 1). Examination of all the herbarium specimens and plants in the field reveals a degree of uniformity in floating-leaf morphology which is typical of other *Potamogeton* species. The floating leaves are lanceolate, tapering at both ends, and with long slender petioles. The length/width ratio of *P. floridanus* is 5.1 ± 0.8 ; that of *P. tepperi* is 1.8 ± 0.3 .

Taylor's implication that the Curtiss specimens are likely to be nothing more than immature forms of *P. natans* is to us unacceptable. Obvious morphological differences notwithstanding, *P. natans* remains unknown from the southeastern United States (Godfrey and Wooten 1979). *Potamogeton oakesianus* Robb., the other possible species of which Ogden speculated *P. floridanus* might be a "pronounced ecological form," is even more remote from the Gulf coastal plain than *P. natans* (Fernald 1950).

Ogden's equivocal speculation that Curtiss' collections represent hybrids between a broad-leaved and narrow-leaved species is not only inconsistent with his own anatomical studies, but field observations on the habitat and associates of the plant further frustrate the hybrid hypothesis.

There currently are four small disparate populations of *P. floridanus* known, all in the vicinity of Milton. Two are in Pond Creek, a clear-flowing tributary of the Blackwater River; one just south of the U.S. Route

Potamogeton diversifolius Raf. No other species of *Potamogeton* were observed. The narrow-leaved species *P. curtissii* Morong (= *P. foliosus* var. *macellus* Fern.) was described by Morong (1886) based upon material collected by Curtiss from the same location he collected *P. floridanus*. We have been unable to relocate these plants.

The reluctance by students of the genus to recognize *P. floridanus* as a species seems to have originated not so much from a lack of morphological distinctness as from the fact of its very restricted range, and from the fact that it remained unrepresented by additional collections.

Endemism in the central Gulf coast area, however, is not uncommon. There are quite literally dozens of species with very restricted ranges in the region. *Baptisia calycosa* var. *villosa* Canby, *Chrysopsis godfreyi* Semple, *C. gossypina* ssp. *cruiseana* (Dress) Semple, *Conradina glabra* Shinn., *Crataegus lacrimata* Small, *Eriocaulon lineare* var. *gigas* Mold., *Hymenocallis choctawensis* Traub, *H. henryae* Traub, *Hypericum chapmanii* P. Adams, *H. lissophloens* P. Adams, *Lilium iridollae* Henry, and *Verbesina chapmanii* J. R. Colem. are only a few of many examples. It is likely that *Potamogeton floridanus* was somewhat more widespread in the Milton area in the 1880's when Curtiss was able simply to visit reaches of the river in the vicinity of the railroad whistle-stops, but the water in such areas today apparently is no longer suitable for the plant. It is certain, with the chronic degradation of our rivers, streams, and lakes, that the presettlement populations of most of our native aquatic plants have been decimated several times over.

Potamogeton floridanus is clearly not an immature form of *P. natans*, nor is it a "pronounced ecological form" either of *P. natans*, *P. oakesianus*, nor any other *Potamogeton*. It is not the Asian *P. tepperi*. It is our opinion that *P. floridanus* is a valid native North American species, unlikely to be of hybrid origin. It is still extant in at least four locations near Milton, Florida. Be-

Potamogeton natans L. var. ?
 Blackwater riv. in the extreme north
 west of Florida.
 Coll. A. H. Curtiss May 1886.
 (Coll. also in June, but found no fruit)

Figure 2. Label with original handwriting from isotype of *Potamogeton floridanus* Small, collected by A. H. Curtiss, May, 1886.



Figure 3. Specimen of *Potamogeton floridanus* Small, collected by Wilhelm & Blackmon (9706) NY, 23 Nov 1981.

cause of its extreme rareness, narrow distribution, and obvious vulnerability, we feel it would be appropriate to reconsider it as a federally endangered species.

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RECENT COLLECTIONS AND STATUS OF
LESQUERELLA LYRATA ROLLINS
(CRUCIFERAE)

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ABSTRACT

The narrow endemic *Lesquerella lyrata* Rollins (Cruciferae), considered by Department of Interior specialists as possibly extinct, was found in several localities, including the type locality, in April 1984. Ideas as to its sporadic yet abundant occurrence are proposed, and positive management practices suggested.

Lesquerella lyrata Rollins is a narrow endemic reported to be restricted to a few localities (Fig. 1) in the eastern portion of Franklin County, Alabama (Rollins 1955, Rollins and Shaw 1973). It is a component of the glade flora and is generally found in association with limestone outcroppings. The rarity and restricted distribution of *L. lyrata* have resulted in its listing as an endangered species in Alabama (Freeman et al. 1979a, 1979b). *Lesquerella lyrata* also is currently under review by the U. S. Department of the Interior (1980) as an endangered or threatened species and is included in the rare plant inventory prepared by Kral (1983) for the USDA Forest Service. Recent collections of *L. lyrata* reported in this paper are of significance since the Department of the Interior lists *L. lyrata* as possibly extinct.

HABITAT AND POPULATION SIZE

During early April of 1984, *L. lyrata* was rediscovered near the type locality described by Rollins (1955) as 7 miles east of Russellville near Richardson's Crossing. Even earlier that month a large population of *L. lyrata* was found on limestone outcroppings and in adjacent fields in the vicinity of Spring Valley in Colbert County, Alabama (Fig. 1). The population at Richardson's Crossing consisted of several hundred plants scattered in a field that was plowed during the fall of 1983. An adjacent field that was not plowed in the fall of 1983 but apparently cropped during 1983 was found to harbor more than a thousand plants of bladderpod. An additional

population of a few dozen individuals (Fig. 1) was observed along the roadside of County 83 approximately 0.8 mile north of Richardson's Crossing.

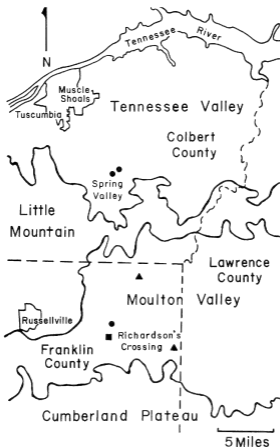
The population of *L. lyrata* just north of Spring Valley consisted of several thousand plants scattered along the roadside, in adjacent fields, and around small limestone outcroppings. Hundreds of plants occurred in unplanted cotton fields that were plowed and disked in the fall of 1983. An additional population of a couple of hundred plants was observed in the same glade system in a pasture approximately one-half mile west of the large population.

The presence of large populations numbering in the thousands was confirmed again in late March and early April of 1985 just north of Spring Valley and at Richardson's Crossing. A large population of *L. lyrata* also was present at Richardson's Crossing in the early spring of 1983 (Reed C. Rollins pers. comm.). A population of several thousand plants was found in 1985 in a pasture 0.8 mile north of Richardson's Crossing where only a few dozen plants were observed in April 1984. Although the two other localities cited in the original description by Rollins (1955) were visited during April 1985 as well as other suitable habitat in the eastern portion of Franklin County, no additional populations of *L. lyrata* were located.

The populations of *L. lyrata* from Franklin and Colbert counties represent two separate and distinct glade systems. While both are in the Interior Low Plateau described by Fenneman (1958), the Spring Valley populations are in the Tennessee Valley and those at Richardson's Crossing in the Moulton Valley. These two subdivisions of the Interior Low Plateau are separated by Little Mountain which is characterized by sandstone outcroppings described by Harper (1942). The collection sites in the Tennessee Valley and Moulton Valley vary by about 200 ft. elevation.

RECOMMENDED MANAGEMENT PRACTICES

Lesquerella lyrata likely evolved on the glade systems that are now highly disturbed and occur as isolated pockets surrounded by agricultural lands. Acquisition and protection of the glade systems containing *L. lyrata* are paramount in protecting the species. The glade system near Richardson's Crossing also has other rare plant species listed at the State and Federal level such as *Leavenworthia alabamica* Rollins var. *alabamica*, *Delphinium alabamicum* Kral, *Psoralea subcaulis* T. & G., *Isoetes butleri* Engelm., *Talinum calcaricum* Ware, *Petalostemum gattingeri* Heller, and *P. foliosum* Gray. The latter species was reported by Baskin and Baskin (1973) just south of Richardson's Crossing but has not been relocated by the authors.



- ▲ Collections cited by Rollins (1955)
- Type locality (Rollins 1955)
- 1984 and 1985 collections

Figure 1. Distribution of *Leisparrella lyrata* in northwestern Alabama.

The large numbers of *L. lyrata* in cultivated fields is a phenomenon that also has been observed for *Leavenworthia alabamica* var. *alabamica*, *L. crassa* Rollins, and *Lesquerella densipila* Rollins at scattered localities in Colbert, Franklin, Morgan, and Lawrence counties, Alabama. These taxa apparently move from the thin soil of glades into fields that are planted in cotton or soybeans on an annual basis. The typical mid-May to June planting of soybeans allows these early flowering annuals to set seed prior to soil tillage and planting. The presence of *Lesquerella* and *Leavenworthia* in unplanted cotton fields may be sporadic since the mid-April to May planting and the earlier spring application of pre-emergent herbicides may prevent or preclude the establishment of large populations. However, wet springs such as that in 1984 that delay soil tillage may allow germination and completion of the life cycle of *Lesquerella* and *Leavenworthia*. The importance of seed banks in cultivated fields in relation to survival of these species should not be ignored. Conservation easements with private land owners should be pursued. As evidenced by the populations numbering in the thousands, agricultural use and survival of these species are not incompatible. Preservation of selected glade systems along with easements that harmonize tillage patterns and herbicide applications with the life history of these rare annuals should insure their survival. Further research is required relating to the use of herbicides and germination of species of *Lesquerella* and *Leavenworthia*.

CITATION OF RECENT COLLECTIONS

ALABAMA. Colbert Co.: sandy silty clay of plowed field by Co. 77 just N (0.5 mi) of Spring Valley, 2.2 mi S of jct AL 157 and Co. 77, 2 Apr 1984, *Kral & Webb 71171* (VDB); thin dark soils over limestone and in small limestone glade, horse pasture by schoolhouse, Spring Valley School, W side of Spring Valley, 2 Apr 1984, *Kral & Webb 71175* (VDB). Franklin Co.: fallow field on N side of AL 24, 6.0 mi E of jct AL 24 and US 43 (in Russellville) along AL 24 near jct with Co. 83, 7 Apr 1984, *Webb & Pardus 4943* (TENN, VDB); same locality, 22 Mar 1985, *Rollins & Rollins 8317* (GH); pasture on E side of Co. 83, 0.8 mi N of jct with AL 24 (Richardson's Crossing), ca 6 mi E of Russellville, 6 Apr 1985, *Webb 5077* (TENN, VDB).

ACKNOWLEDGEMENTS

We thank Professor Reed C. Rollins for permission to cite his recent collection of *L. lyrata*.

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NOTES

A RECOMBINATION IN *HYDRANGEA* L. (SAXIFRAGACEAE)—*HYDRANGEA ARBORESCENS* L. f. *carnea* (Raf.) L. J. Uttal comb. et stat. nov. *Hydrangea vulgaris* Michx. var. *carnea* Raf. New Fl. 3:77. 1838. Flowers incarnate. No type having been designated, the description stands as the type.

This is an apparently very rare color form of the common white-flowered *Hydrangea arborescens* L. of the eastern United States in which the outer surface of the petals and calyx lobes are the color of raw beef. The cyme is very conspicuous and attractive. Anthocyanic coloration of flowers in *Hydrangea* L. is common in Asiatic species in shades of pink, blue, violet, or purple. The deep-flesh color of the present taxon is the only deviation from white flower color known from North American *Hydrangea*. One specimen: TENNESSEE. Unicoi Co: Unaka Mountain, elev. ca 1500 m, Cherokee National Forest Service Road 132, 1 m shrub with normal white-flowered shrubs among rocks near summit, 8 Jul 1985, Uttal 13881 (VPI). It and the white-flowered shrubs belong to *H. arborescens* subsp. *arborescens* sensu McClintock (Proc. Calif. Acad. Sci. 29:147–256. 1957), and lack marginal sterile flowers with dilated sepals. No reports of other specimens or literature references have been found by the author except for synonymy under *H. arborescens* in Rehder (Bibliography Cultivated Trees and Shrubs. 199. 1949).—L. J. Uttal, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, U.S.A.

MONERMA CYLINDRICA (POACEAE: MONERMEAE) NEW TO TEXAS.—A recent collection from Northeastern Louisiana University (R. Dale Thomas 88432 & B. E. Dutton 1665) was received by the S. M. Tracy Herbarium (TAES) for identification and identified as *Monerma cylindrica* (Willd.) Coss. & Dur., an adventive species native to the Old World. Previously, this species was reported from San Francisco Bay south to Baja California Norte (Gould & Moran 1981, Gould & Shaw 1983) and recently from southwest Louisiana (Thomas & Dutton 1985).

While examining specimens at TAES, an additional collection of *M. cylindrica* from Texas was located which had previously been misidentified as *Parapholis incurva* (L.) C. E. Hubb., a closely related taxon of the same tribe. *Parapholis* is reported growing in saline coastal sites along the Atlantic and Pacific Coasts and in Texas along the Gulf of Mexico (Gould & Shaw 1983). *Monerma* is characterized by having only a single glume per spikelet with the exception of the terminal spikelet where two glumes are present

and alternate on the rachilla. *Parapholis* can be easily distinguished from *Monerma* by the presence of two glumes for each spikelet, these adjacent to one another (Chase 1951). Our identifications were corroborated by Stephan L. Hatch, curator of the S. M. Tracy Herbarium. After a review of literature and herbarium specimens deposited at TAES and the University of Texas Herbarium (TEX and LL), we concluded *M. cylindrica* to be a new record for Texas. This species is not included in Correll and Johnston (1970) or Gould (1975).

Collection data of *M. cylindrica*: UNITED STATES. TEXAS. Galveston Co.: Occasional, clay loam banks at intake canal of P. H. Robinson Generating Station near Bacliff, 8 May 1974, Waller and McAden 2661 (SMU, TAES, TEX).

This is Technical Bulletin TA No. 20687, Texas Agricultural Experiment Station.—Chuck R., Coffey and Jesus Valdes R., Department of Range Science, Texas A&M University, College Station, TX 77843, U.S.A.

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REVIEWS

PLANT DISEASES: Infection, Damage and Loss. 1984. Edited by: Wood, R.K.S. and G.J. Jellis. Blackwell Scientific Publications, Ltd., Oxford, London, Edinburgh, Boston, Palo Alto, Melbourne. 327 pp. + viii. Cloth, \$44.00.

The book is based on a symposium held at the University of Surrey in December 1982 by the British Society for Plant Pathology. The objective was to publish the review papers of the symposium, whose theme was to survey the effects of pathogens on plants, for use by senior undergraduates, postgraduates, and scientists in general.

The Chapters (review articles) are grouped into four sections: 1) How pathogens cause disease (four Chapters), 2) Physiological responses of

plants to pathogens (five Chapters), 3) Infection and host damage (seven Chapters), and 4) Damage and loss (ten Chapters). Each Chapter presents a review of that topic along with a rather extensive bibliography on the subject. The wide variety of topics concern cultivated crops such as cotton, potatoes, cereal grains, and ornamentals as well as forest crops. An Index to the book occurs at the end.

The 26 Chapters were authored by thirty-three plant pathologists from Britain (26), Denmark (1), France (1), Italy (2), Australia (1), and the United States (2). On page 285, a permanent correction has been affixed over the original printed material concerning the authors of the article. Otherwise, the printing and layout exude quality throughout.—WFM

THE VASCULAR PLANTS OF SOUTH DAKOTA. 1985. Theodore Van Bruggen. 2nd ed. Iowa State University Press, Ames, Iowa, 50010. 476 pp. + xxv. Paperback, \$28.95.

This manual is an updated version of the 1976 edition. It was printed by The Iowa State University Press from camera-ready pages provided by the author. The Introduction contains information on the geology, physiography, and climate with supporting maps. Photographs aid in illustrating the vegetation. This section is an excellent treatment of the past and present geological and botanical history of the state.

In the Statistical Summary, the number of vascular plant species totals 1608 for South Dakota. This number includes the native and introduced taxa with no distinction between them. There are three principal vegetation regions represented: Eastern Deciduous Flora, Plains and Prairie Flora, and the Rocky Mountain Flora. The following statement addresses the endemic flora: "If one assumes a less than conservative taxonomic interpretation of the species present, and their ranges, it is doubtful that any endemics are present in the state."

The systematic treatment has keys to the major groups and their subcategories down to the generic level that are typical dichotomous keys with one to three characters per unit. However, keys to the species include brief diagnostic characters or descriptions, frequency, distribution, synonymy, flowering or fruiting (months) terminating in the binomial with the author citation. A glossary, general references, and an index to common and scientific names follow the systematic treatment.

Even though its odd size may be more common than I realize (15 cm wide by 19.4 cm tall—paperback), it will lie flat when it is open if it is opened near the middle of the text. This is extremely helpful when one is keying out a plant. *Strophostyles* (p. 275) is not in the Index although its common name is listed. The specific epithet of *Desmanthus illinoensis* is mis-

spelled and the full author citation should read (Michx.) MacM. ex Robins. & Fern.

This manual is well worth possessing, not only for the identification of the flora of South Dakota, but for the past and present history associated with the state from a botanical viewpoint.—WFM

ACTA BOTANICA HUNGARICA. Volume 29, numbers 1–4, 1983, pp. 1–399. Twenty-one papers. Studies in Rondeletieae (Rubiaceae), IV. A new genus: *Javorkaea*. A. Borhidi, Magda Járjai-Komlódi.—Studies in Rondeletieae (Rubiaceae), V. Los límites del género *Suberanthus*. A. Borhidi, Mayra Fernandez Zequeira.—Studies in Rondeletieae (Rubiaceae), VI. Estudio taxonómico de la *Rondeletia odorata* Jacq. Mayra Fernandez Zequeira, P. Herrera Oliver.—Studies in Rondeletieae (Rubiaceae), VII. The significance of leaf epidermis for taxonomy in *Neomazaea* sensu lato. M. A. Vales.—Morfología del polen de las especies cubanas de Gymnospermas. L. Stuchlick, Milagros Moncada.—New names and new species in the flora of Cuba and Antilles, III. A. Borhidi.—Xylotomic examination of some Venezuelan *Capparis* species, III. K. Babos, I. R. Bermudez, I. J. C. Cumana.—Contribución al estudio anatómico del xilema de la familia Simarubaceae en Cuba, I. *Alvaradoa* Liebm. y *Simaruba* Aubl. M. A. Vales, Cándida Martínez.—Plant communities of Cuba, I. Fresh and salt water, swamp and coastal vegetation. A. Borhidi, O. Muñiz, E. Del Risco.

Volume 30, numbers 1–2, 1984, pp. 1–247. Eighteen papers. Revisión del género *Machaonia* H. et B. (Rubiaceae) en Cuba. Mayra Fernandez, A. Borhidi.—Cytological investigation of *Scilla bifolia* populations in Hungary I. Z. Kereszty, L. Szilagyí.—Comparative anatomy of the androecium of male sterile and fertile sunflowers (*Helianthus*). M. Szabó, S. Gulyás, J. Frank.—Plant communities of Cuba, II. The riverside scrub vegetation. A. Borhidi, R. Capote.—Reproductive allocation in the stages of sandy succession, II. *Erigeron canadensis* L., *Polygonum arenarium* W. et K. Erika Melkó.

Volume 30, numbers 3–4, 1984, pp. 249–480. Fifteen papers. Morfología de granos de los polen de las Chloranthaceae y Canellaceae cubanas. L. Stuchlick.—Xylotomic examination of some Venezuelan species of the Capparidaceae, I. K. Babos, I. R. Bermudez, I. J. C. Cumana.—Estudio taxonómico del género *Ariadne* Urb. (Rubiaceae). Mayra Fernandez, A. Borhidi.—A preliminary numerical taxonomic study of the *Scilla bifolia* agg. (Liliaceae, Scilloideae) in Hungary. Z. Kereszty, J. Podani.—BLL

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A NEW SPECIES AND TAXONOMIC NOTES ON
GENTIANELLA (GENTIANACEAE)
IN SOUTH AMERICA¹

JAMES S. PRINGLE

Royal Botanical Gardens

Box 399, Hamilton, Ontario, CANADA L8N 3H8

A NEW SPECIES FROM NORTHERN PERÚ

GENTIANELLA chlorantha Pringle, sp. nov. Figs. 1, 2.

Suffrutex caulibus usque ad 2.5 dm altis, erectis, ramosis. Folia numerosa, ascendencia, elliptica, 6–8 mm longa, 1.5–2.5 mm lata, trinervia nervo medio infra anguste carinato, obtusa. Flores solitarii, subsessiles. Calyx 7.5–9.5 mm longus. Lobi calycis oblongi vel ovato-oblongi, 2.5–3.5plo longiores quam tubus, acuti vel subacuti. Corolla 14–18 mm longa, viridis, lobis obovatis circa 2.25plo longioribus quam tubo et circa 1.6plo longioribus quam latioribus, apicem versus rotundatis et eroso-undulatis. Corolla intus glabra vel sub sinibus trichomariibus paucis minutisque. Filamenta circa 5.5 mm longa. Antherae caesiae. Ovarium stipitatum.

Subshrub with several erect or suberect stems 0.7–2.5 dm tall; most stems dividing into 2–several strongly ascending branches, with flowering and vegetative branches present simultaneously. Leaves densely spaced throughout, the older portions of the stems ringed with old leaf bases, the distal 0.5–1.5 dm densely leafy at flowering time. Leaves mostly 6–8 mm long and 1.5–2.5 mm wide, consisting of an erect, pseudopetiole portion 1–2 mm long and an ascending, elliptic to ovate-elliptic blade, prominently 3-nerved (sometimes with an additional pair of lesser nerves) with the midrib narrowly carinate below, the apex obtuse, thickened. Flowers solitary (sometimes appearing grouped when terminating 2 or 3 short branches), erect, subsessile or on peduncles less than 2 mm long. Calyx 7.5–9.5 mm long, with erect, oblong to ovate-oblong lobes 2.5–3.5 × as long as the tube, subacute to acute. Corolla 14–18 mm long, green throughout, with the lobes obovate, ca 2.25 × as long as the tube and ca 1.6 × as long as wide, distally rounded, erose-undulate. Interior corolla surface glabrous or with a very few inconspicuous trichomes below the sinuses. Stamens inserted at ca 0.67 × the length of the corolla tube; filaments ca 5.5 mm long; anthers bluish. Ovary stipitate.

¹Contribution No 58 from the Royal Botanical Gardens, Hamilton, Ontario, Canada.

TYPE COLLECTION: PERÚ. AMAZONAS. Bagua: Cordillera Colán NE of La Peca, ca 10,400 ft, humid pájonal, *Barbour 3439* (HOLOTYPE: MO; ISOTYPE: HAM). Known only from the type collection.

Previous authors have recognized an excessive number of species of *Gentianella* (formerly treated as a subgenus of *Gentiana*) from much of Perú. Macbride in 1959 reduced many specific names to synonymy, and further reduction has occurred subsequently (Pringle 1981). However, when Gilg's (1916) and Macbride's (1959) publications were written, few specimens from the Departamento de Amazonas were available. In view of the relatively restricted ranges of many of the Andean species of *Gentianella*, newly discovered species from this part of Perú are hardly surprising. *Gentianella chlorantha* appears to be relatively closely related to *G. radicata* (Griseb.) Pringle, which was described from specimens collected in the mountains above Lima. *Gentianella chlorantha* differs from *G. radicata* in its fewer and larger flowers; in its green corollas (white or pale

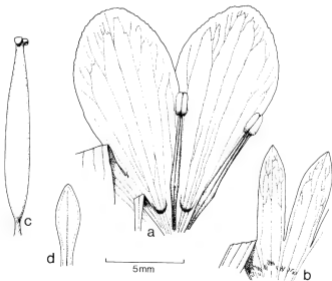


Fig. 1. *Gentianella chlorantha*. a, portion of corolla, interior surface, and stamens; b, portion of calyx, exterior surface; c, pistil; d, leaf.



Fig. 2. *Gentianella chlorantha*, portion of holotype (MO). Figs. 3–6. Small plants of *Gentianella* spp. from Antisana, Ecuador. Figs. 4 and 6 pressed with corollas spread out to show lobe shape. Figs. 3–4. *G. cerastioides*, *Asplund 17330* (S). Figs. 5–6. *G. rapisola*, *Asplund 17333* (S). Figs. 2–6 to same scale.

violet with deep purple veins in *G. radicata*, according to Macbride and various label data, although not well preserved in Grisebach's material ["flavae? . . . striatae"]); and in its broader, elliptic rather than linear leaves.

GENTIANELLA CERASTIOIDES and *G. RUPICOLA*

The distinctness of *Gentianella rupicola* (H.B.K.) Holub from *G. cerastioides* (H.B.K.) Fabris has been a long-persistent question. In 1916, Gilg commented that it was often difficult and sometimes impossible to determine to which of these species a specimen should be assigned. Gilg, however, felt that evidence to support the uniting of these taxa was inadequate at the time, and that the differences between the extreme (and nomenclaturally typical) forms of the respective species were much greater than would normally be acceptable within a single species. Fabris (1960) did reduce *G. rupicola* to synonymy under *G. cerastioides*, but his wording likewise indicated uncertainty.

Much of what passed as *Gentiana rupicola* in Gilg's time actually was *Gentianella cerastioides*, as indicated by his descriptions of *G. rupicola* and his citations of specimens. Very little material of true *G. rupicola* was available for study by Gilg (1896, 1916) or later by Macbride (1959) and Fabris (1960), and most of the few specimens of *G. rupicola* that they did see were of poor quality. Consequently, Macbride's description of *Gentiana rupicola*, and Fabris's concept of this species as possibly merely a high-altitude form of *G. cerastioides*, appear to have been based largely on misidentified material of *G. cerastioides*. The extensive collecting for the Flora of Ecuador project has increased by severalfold the specimens of this complex available for study, making possible a new approach to this problem. Descriptions of these species will appear in the Flora of Ecuador, but, in view of the statements made by Fabris (1960) and the wide use of his monograph, my acceptance of *G. rupicola* as a distinct species requires a more thorough discussion than would be appropriate in the Flora.

Gilg (1896, 1916), Macbride (1959), and earlier authors differentiated these species primarily on the basis of height, erectness of stems, length of internodes and pedicels, and number of flowers per stem. Their descriptions of the flowers indicated virtually no differences. In the present study, however, I found that all specimens in this group could readily be sorted into two taxa on the basis of floral characters. I also noted that those persons who collected both of these taxa in the same area consistently kept them separate, under different numbers.

A summary of the more conspicuous differences between these species is presented in Table 1. A more detailed discussion, emphasizing recognition of these species in the herbarium, appears below.

TABLE 1. Summary comparison of the more conspicuous differences between *Gentianella cerastioides* and *G. rupicola*.

CHARACTER	<i>G. CERASTIODES</i>	<i>G. RUPICOLA</i>
Length of flowering stem	0.5–17 (-25) cm	0.5–3 (-11) cm
Number of flowers per stem	Usually 1 or 2, occasionally up to 6	Usually 1, occasionally 2 or 3
Pedicle length	0.3–5 cm	0.1–2.5 (-4) cm
Corolla length (closed)	(14-) 17–40 mm	(14-) 17–28 mm
Position of corolla lobes	Spreading, the corolla opening widely	Incurved, the corolla scarcely opening
Shape of corolla lobes	Narrowly cuneate-obovate, not ventricose	Elliptic, somewhat ventricose
Corolla color	Usually violet or blue-violet, occasionally pink or white	Usually red (crimson to scarlet), occasionally orange, rarely yellow

Corolla color, when retained, sharply differentiates *G. rupicola* from *G. cerastioides*. In *G. rupicola*, it is usually red, often described as "crimson," "bright red," or "scarlet," occasionally orange-red, rarely yellow. In contrast, corollas of *G. cerastioides* range from pink through various shades of violet to violet-blue or white. Most corollas are medium to pale violet, although a few specimens have fairly deep blue-violet corollas. (Corollas may sometimes appear bluer when dried than when fresh, but the contrast between those of *G. rupicola* and those of *G. cerastioides* remains.) In some specimens of *G. cerastioides*, the corollas are minutely spotted. Even in ancient specimens in which corolla color is not well preserved, the corollas of *G. rupicola* appear darker and more reddish than those of *G. cerastioides*.

Corolla color is correlated with the shape of the intact corolla and with the shape of the corolla lobes (Figs. 3–6). Balls (*in sched.*) described the corollas of his *B.7281* (E, K), representing true *G. rupicola*, as "long-globular in shape. The petals do not appear to open, so that the flower has always the appearance of being in rather full bud." Pressing tends to push the petals apart, but they remain incurved toward the summit. The corollas of *G. cerastioides*, in marked contrast, open widely, ranging from funnellform to nearly rotate, with outwardly flaring lobes. This characteristic is particularly well shown in photographs taken in the field (e.g., photo attached to *Raub-Hirsch E310* [F]), but is likewise indicated in the aspect of herbarium specimens.

The corolla lobes of *G. rupicola* are more or less elliptic, widest near the middle, with the margins convex nearly their full length. They are evidently almost ventricose in the fresh corolla, with the margins often being folded under when pressed. Those of *G. cerastioides* are cuneate to

spatulate-obovate, widest well above the middle. Below the widest point, they taper with straight or slightly concave margins to the base. They are not at all ventricose, and generally press flat.

Differences in habit are of limited use in distinguishing these species. *Gentianella cerastioides* does exhibit a greater range in stem length than does *G. rupicola*, and the longer stems of *G. cerastioides* are usually erect, whereas even the longest stems of *G. rupicola* are decumbent. In both species, however, specimens with very short stems (presumably from exposed habitats) are frequent. On the longer stems of *G. cerastioides*, the upper internodes are often 1–6 cm long, occasionally up to 8 cm, whereas even on the longest stems of *G. rupicola* the internodes seldom exceed 1 cm (*Sparre 15694* [S], with internodes up to 3 cm long, is an exception). On short-stemmed plants of *G. cerastioides*, all the leaves are closely spaced. Nevertheless, even on acaulescent extremes of *G. cerastioides*, such as *Mulroy 1097* (HAM) and *Sparre 15869* (S), the narrow, cuneate-obovate, flaring, pale violet corolla lobes readily identify such specimens as being *G. cerastioides*; and long-stemmed extremes of *G. rupicola*, such as *Sparre 15694*, are likewise readily identified by the broad, elliptic-obovate, incurved, red corolla lobes. In both species, the majority of the flowering stems bear but one flower; in *G. cerastioides*, stems bearing up to five flowers are not unusual, but in *G. rupicola*, even three-flowered stems are rare. Pedicel length is highly variable in both species, but ranges to a greater maximum in *G. cerastioides*.

The altitudinal ranges of the two species overlap considerably, ca 3150–4500 m for *G. cerastioides*, and ca 3650–4600 m for *G. rupicola*. *Gentianella cerastioides* has the greater geographic range, from the Departamento de Nariño in southern Colombia to the Departamento de Azuay in southern Ecuador. *Gentianella rupicola* is known only from Ecuador, from Pichincha to Chimborazo.

My count (Pringle 1981) of $2n = 18$ for *G. cerastioides* was obtained from a specimen of *G. cerastioides* s. str., as delimited in the present study.

HYBRIDIZATION IN ECUADOREAN GENTIANELLA

Twenty-five species of *Gentianella* are native to Ecuador (Pringle, ms. for Flora of Ecuador). Most grow in páramo habitats ca 2800 to ca 4500 m altitude in the Andes, and several have large, open, blue-violet to rose-violet corollas that presumably attract similar pollinators. To date, no interspecific hybrids have been reported. Botanical exploration for the Flora of Ecuador with detailed locality data has for the first time clearly indicated the existence of hybridization in *Gentianella* in South America. Two

hybrids are described below. Descriptions of the parental species have been published by Fabris (1960) and will appear, with further details, in the Flora of Ecuador.

GENTIANELLA CERASTIOIDES (H.B.K.) Fabris \times *G. FOLIOSA* (H.B.K.) Fabris. Figs. 7–11. *Gentianella foliosa*, like *G. cerastioides* (above), is widely distributed at high altitudes in Ecuador and is well represented in herbaria. Both species have corollas similar in size and color.

A series of specimens at AAU, all from "Volcán Iliniza, NE slope below the refugio, lee side of loma with bunchgrass and shrubs, alt. 4300 m," Prov. Pichincha, Ecuador, evidently represents hybridization between these two species. *Holm-Nielsen et al.* 24956 and 24971 are, respectively typical specimens of *G. cerastioides* and *G. foliosa*. *Holm-Nielsen et al.* 24957 (Fig. 10) is similar in habit to *G. cerastioides*, but has 5 flowers per stem, on stems ca 6 cm tall, more flowers than is usual on plants of *G. cerastioides* of that size, and has relatively short, stout pedicels like those of *G. foliosa*. The flowers are similar in aspect to those of *G. foliosa*, having the relatively abruptly rounded corolla lobes of that species, and the leaves are somewhat wider and more lanceolate than is usual in *G. cerastioides*. Intermediacy is even more evident in *Holm-Nielsen et al.* 24964 (Fig. 9), which is similar in habit to 24957 but has stems 8–11 cm tall, bearing up to 6 flowers. The upper leaves are distinctly lanceolate, representative dimensions being 22 mm long, 5 mm wide, i.e., similar in shape to those of *G. foliosa* but in the size range characteristic of *G. cerastioides*. Some show a tendency toward arcuate spreading, as in *G. foliosa*. The corollas are similar to those of 24957.

GENTIANELLA FOLIOSA \times *G. SULPHUREA* (Gilg) Fabris. Figs. 11–13, Table 2. *Gentianella sulphurea* has a much more restricted distribution than the other two species discussed here. Only 5 collections besides those mentioned below, all from the central part of the Ecuadorean Andes, have been encountered in my studies. Although *G. sulphurea* differs strikingly from *G. foliosa* in its leaf shape, corolla color, and lack of corolla trichomes, and usually also in its stature and pedicel length, the close relationship between these species was noted by Gilg (1896) and Fabris (1960). The two species are similar in habit, inflorescence type, and size and shape of the corolla, except that the corolla lobes of *G. sulphurea* are proportionately wider than those of *G. foliosa*.

A series of 16 specimens at AAU, all from páramo habitats in the Cordillera de los Llanganates, from points 3 km SW to 13 km NW of Cerro Hermoso, Prov. Tungurahua, clearly represents a large hybrid swarm. Included are specimens representative of *G. foliosa* and *G. sulphurea*, intermediate specimens closer to each of the parental species, and specimens about



Figs. 7-11. *Gentianella* from Volcán Iliniza, Ecuador, all to same scale. Figs. 7-8. *G. crasioides*, Weylandt 323 (S). Figs. 9-10. *G. crasioides* × *G. foliosa*, Holm-Nielsen *et al.* 24964 (AAU) and 24957 (AAU), respectively. Fig. 11. *G. foliosa*, Holm-Nielsen *et al.* 24971 (AAU).

midway between the parental species in morphology. Several intermediate specimens are compared with the parental species in Table 2. One of the most clearly intermediate plants, as indicated by its description in the table, is illustrated in Fig. 12. Descriptions of the parental species are based on all specimens examined for the Flora of Ecuador, exclusive of a few anomalous individuals assigned to *G. foliosa*. Collection numbers are those of Holm-Nielsen & Jaramillo.

Detached flowers in packets were examined for internal corolla pubescence in two intermediate specimens, nos. 28168 and 28189, in both of which the corollas were yellow with red suffusions. The former bore tufts of trichomes below the corolla sinuses, more restricted and shorter than those of *G. foliosa*, but thus differed from *G. sulphurea*, in which corolla trichomes are absent or occasionally few and minute. In 28189, the corolla trichomes were more numerous and longer, the plant in this respect being more like *G. foliosa* although otherwise bearing a greater resemblance to *G. sulphurea*.

Hybridization may also account for some of the anomalous specimens obviously allied to *G. foliosa* that have been grouped as *G. stellarioides* (Griseb.) Fabris. Fabris (1960) described this "species" as "bastante polimorfa" even though he thus identified only 9 specimens representing perhaps as few as 5 collections. In particular, a specimen collected by Jameson on the "snowy summit of the Andes," Ecuador (S), differs from typical *G. foliosa* in having much longer pedicels (2.5–9 cm), more deeply lobed corollas, and narrower, less abruptly tapering corolla lobes, suggesting that its origin might be *G. foliosa* × *G. rapunculoides* (Willd. ex Schultes) Pringle. Jameson's labels, however, do not provide precise locality data or otherwise indicate which specimens were found in proximity to one another.

NOMENCLATURAL TRANSFERS

Although most students of the Gentianaceae now accept generic status for *Gentianella* Moench, they have wisely refrained from making "automatic transfers" for all of the South American taxa accepted as *Gentiana* spp. by Gilg (1916) or Macbride (1959). The following species, however, appear from my own studies and from a monograph of the Argentine Gentianaceae by Fabris (1953) to be taxonomically acceptable, and the combinations published here are required for specimens sent to me for identification, for discussion in the present paper, or for use in works by other authors.

Combinations herein attributed to "Fabris ex Pringle" were proposed by H. A. Fabris, as seen *in sched.* on specimens in AAU, E, and WIS.

HYBRIDS

CHARACTER	<i>G. SOLIOSA</i>	28676 (closer to <i>G.</i> <i>FORIOSA</i>)	28115	28120	28168	28189 (closer to <i>G.</i> <i>SULPHUREA</i>)	<i>G. SULPHUREA</i>
length 3rd internode below terminal in- florescence on longest stem	15-40 mm	40 mm	22 mm	19 mm	9 mm	15 mm	3-10 mm
length this internode/ length subtending leaves	0.6-1.5	1.1	0.77	0.79	0.34	0.56	0.1-0.7
shape of lower leaves	oblong-oblanccolate	oblong	elliptic-obovate	elliptic	elliptic	elliptic-obovate	elliptic-obovate
shape of upper leaves	ovate-lanceolate	elliptic-oblong	elliptic	elliptic	elliptic	elliptic	elliptic
length largest leaf	20-80 mm	43 mm	30 mm	27 mm	23 mm	23 mm	8-23 mm
length/width largest leaf	5-12	6.1	2.8	3.3	3.3	3.3	2-4
number of flowers in terminal inflorescences	3-21	6-9	5-7	2-6	4-7	2-6	1-2 (-6)
pedicel lengths	8-40 mm	14-21 mm	9-15 mm	15-21 mm	7-14 mm	10-17 mm	5-12 mm
corolla color (from labels)	rose-violet to blue-violet	violet	light violet	pink to red	yellow with red veins and margins	yellow at base pale red above red above	yellowish-green to yellow, rarely with red suffusion
length/width repre- sentative corolla lobe	1.6-2.4	1.7	1.5	1.7	1.4	1.4	1.2-1.5

TABLE 2. Comparison of selected specimens of *Gentiana foliosa* × *G. sulphurea* with the parental species.



Fig. 12. *Gentiana fulvica* × *G. sulphurea*, Cordillera de los Llanganates, Ecuador, *Halen-Nielsen & Jaramillo* 28115 (AAU). Fig. 13. Representative *G. sulphurea*, Atlixo, Ecuador, *Harling et al.* 6663 (HAM).

GENTIANELLA cuspidata (Griseb.) Pringle, comb. nov. *Gentiana cuspidata* Griseb., Gen. Sp. Gent. 224. 1838 ["1839"], basionym, non *Gentiana cuspidata* Wallich ex C. B. Clarke, J. Linn. Soc. Bot. 14:45. 1875.

According to Macbride (1959), *Gentiana cuspidata* Griseb. "Seems to be the same as *G. multicaulis* (G. Don) Gilg, non Griseb., i.e. *G. Pavonii* Griseb., and then the earlier name" [authors' names added]. Examination of the respective type collections, however, indicates that *G. cuspidata* differs from *G. pavonii* in the greater size of the plants, more diffuse inflorescences, larger flowers, and widely opening corollas, and presents a very different general aspect. Type collection, *G. cuspidata*: PERU (not more precisely located): *Dombey s.n.*, holotype: P, and isotypes: NY(2)! On *G. pavonii*, see Pringle (1981).

GENTIANELLA dianthoides (H.B.K.) Fabris ex Pringle, comb. nov. *Gentiana dianthoides* H.B.K., Nov. Gen. Sp. 3:170 (quarto ed.). 1819, basionym.

GENTIANELLA dielsiana (Gilg) Pringle, comb. nov. *Gentiana dielsiana* Gilg, Bot. Jahrb. Syst. 22:316. 1896, basionym.

GENTIANELLA dolichopoda (Gilg) Pringle, comb. nov. *Gentiana dolichopoda* Gilg, Bot. Jahrb. Syst. 54(Beibl. 118):36. 1916, basionym.

GENTIANELLA gilgiana (Reimers) Fabris ex Pringle, comb. nov. *Gentiana gilgiana* Reimers, Bot. Jahrb. Syst. 62:326. 1928 ["1929"], basionym.

GENTIANELLA helianthemoides (Gilg) Pringle, comb. nov. *Gentiana helianthemoides* Gilg, Bot. Jahrb. Syst. 22:321. 1896, basionym.

This species was described from the Provincia de Salta, Argentina. A recent collection from the adjacent Departamento de Tarija, Bolivia, is the first for that country. Voucher specimen: BOLIVIA. Mendez: Tarija 25 kms hacia Camargo, 2765 m, 35° degrees E, *Beck* 843 (LPB).

GENTIANELLA mendocina (Gilg) Pringle, comb. nov. *Gentiana mendocina* Gilg, Bot. Jahrb. Syst. 54(Beibl. 118):36. 1916, basionym.

GENTIANELLA persquarrosa (Reimers) Pringle, comb. nov. *Gentiana persquarrosa* Reimers, Bot. Jahrb. Syst. 62:332. 1929, basionym.

GENTIANELLA radicata (Griseb.) Pringle, comb. nov. *Gentiana radicata* Griseb., Gen. Sp. Gent. p. 29. 1838 ["1839"], basionym.

GENTIANELLA riojae (Gilg) Fabris ex Pringle, comb. nov. *Gentiana riojae* Gilg, Bot. Jahrb. Syst. 22:319. 1896, basionym.

GENTIANELLA vaginalis (Griseb.) Pringle, comb. nov. *Gentiana vaginalis* Griseb., Gen. Sp. Gent. p. 215. 1838 ["1839"], basionym.

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A NEW COMBINATION IN *CHIMAPHILA* (ERICACEAE)

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Preparation of floristic treatments of the Pyroloideae (Ericaceae) that occur in the West Indies, Mexico, and Central America necessitates a new combination in *Chimaphila* from Hispaniola. Collections of *Chimaphila* from Hispaniola were first reported by Urban (1908) as *C. umbellata* (L.) W.P.G. Barton (cited as *Chimophila umbellata* Nutt.), a wide-ranging and variable species that is found throughout temperate Europe and Asia, Japan, and North America from Canada to Central America. Blake (1914, 1917), emphasizing the smaller leaves, fewer teeth on the leaf margins, glabrous peduncles and pedicels, and glabrous filaments of the material from Hispaniola, described *C. domingensis* S.F. Blake. Comparing this taxon with the species of *Chimaphila* that occur in North America, *C. maculata* (L.) Pursh, *C. menziesii* (R. Br. ex G. Don) Sprengel, and *C. umbellata*, it is evident that *C. domingensis* is closely related to *C. umbellata*. Both taxa have oblanceolate or spatulate to elliptic leaves, teeth confined to the upper margins of the leaves, cuneate leaf bases, linear-subulate bracts, and 2-6-flowered, corymbose inflorescences. The relatively minor size and pubescence differences of *Chimaphila* in Hispaniola could easily have arisen as a consequence of isolation. In order to reflect what is assumed to be the shared evolutionary origin of *C. domingensis* and *C. umbellata* the following new combination is proposed.

CHIMAPHILA UMBELLATA (L.) W.P.G. Barton subsp. **domingensis** (S.F. Blake) Dorr, comb. et stat. nov. *Chimaphila domingensis* S.F. Blake, J. Bot. 52:169. 1914. TYPE: DOMINICAN REPUBLIC. Prope Constanza in Valle Nuevo, 2200 m alt., in pineto, Aug. 1910, H. von Tuschheim 3434 (ISOTYPES: BM!, GH-photograph!; ISOTYPES: B†, G-2 sheets!, GH!, K!, MO!, NY!, US-microfiche!).

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RENOVATION OF *DYSSODIA* (COMPOSITAE: TAGETEAE)

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ABSTRACT

Reconsideration of circumscription of *Dyssodia* s.l. has led to resurrection of *Adenophyllum*, *Boeberastrum*, *Cosmoclinium*, *Dysodispis*, and *Thymophylla* and to change to generic rank for one section: *Boeberoides* (DC.) Strother with one species, *B. grandiflora*. New combinations in *Adenophyllum* are: *A. anomalum*, *A. appendiculatum*, *A. aurantium*, *A. cooperi*, *A. glandulosum*, *A. porophylloides*, *A. porophyllum* var. *cancellatum*, *A. porophyllum* var. *radiatum*, *A. speciosum*, *A. squamosum*, and *A. wrightii* var. *pulcherrimum*; in *Cosmoclinium*: *C. montanum*; and in *Thymophylla*: *T. acerosa*, *T. aurea* var. *polychaeta*, *T. concinna*, *T. gentryi*, *T. gypsophila*, *T. micropoides*, *T. mutica*, *T. pentachaeta* var. *belenidium*, *T. pentachaeta* var. *hartwegii*, *T. pentachaeta* var. *puberula*, *T. setifolia* var. *radiata*, *T. tenuiloba* var. *texana*, *T. tenuiloba* var. *traculii*, *T. tenuiloba* var. *wrightii*, and *T. tephroleuca*.

In a review of Tageteae (Strother 1977), I acknowledged that my earlier (Strother 1969) circumscription of *Dyssodia* was too broadly drawn and that the subgenera and some sections would be better treated as distinct genera, because some of the subdivisions are more closely allied with other Tageteae than with each other. Those conclusions were drawn from integration of new and re-evaluated, old observations of morphology and chromosome numbers both within *Dyssodia* s.l. and across Tageteae. The desirability of such a reinterpretation of *Dyssodia* (sensu Strother 1969) has been indicated, at least implicitly, by Robinson (1981) and Downum et al. (1985).

The resulting realignments require several nomenclatural changes, which are set forth here. The format is intended to coordinate with my 1969 treatment and to account for the one name added to *Dyssodia* in the interval. Circumscriptions of species and varieties are unchanged except that of *D. decipiens*, which is expanded to include *D. sanguinea*. In the following synopses of genera and in the nomenclator for *Dyssodia*, accepted names are in capitals (for previously published) or boldface (new combinations); for all, basionyms are indicated.

Review of revised phyletic postulates for relationships among genera of Tageteae is beyond the scope of this paper. Nevertheless, some of the more

salient differences that form the bases for recognition of the retained, resurrected, and newly recognized genera may be summarized in the following key:

- a. Phyllaries free quite to base or nearly so.
- b. Erect annuals and perennial herbs; leaves not fleshy; calyx of 3–5(1–12) bracteoles.
- c. Leaves pinnatifid with 3–17 linear to lance-cuneate or oblanceolate lobes, glands scattered in lamina and/or submarginal; receptacles fimbriate or finely setose; lobes of disc corollas short, deltate to lance-deltate. *Dysodia*
- c. Leaves simple or trifoliolate, glands mostly in rows between lateral nerves; receptacles minutely paleate; lobes of disc corollas lance-linear to subulate. *Comastium*
- b. Sprawling or decumbent annuals; leaves fleshy; calyx none or a single bracteole. *Boeberastrum*
- a. Phyllaries weakly to strongly connate.
- d. Leaves mostly pinnate or pinnatifid, if simple, then lanceolate, linear, or filiform; calyx of deltate, linear, subulate, or pectinate bracteoles; some or all phyllaries gland-bearing.
- e. Plants less than 3 dm high; leaves linear-filiform or pinnatifid with linear-filiform lobes; phyllaries strongly connate $2/3+$ their length, margins of the outer seldom free more than $1/2$ their length; receptacles naked or nearly so. *Thysophyllum*
- e. Plants (2–)4–20+ dm high; leaves or lobes linear or broader; phyllaries weakly connate $1/3$ – $2/3$ their length (somewhat more in *Dysodiopsis*), often separating in age, margins of the outer usually free to base; receptacles fimbriate or setose.
- f. Leaves mostly pinnate or pinnatifid, if simple, then lanceolate, glands marginal and subterminal; lobes of disc corollas lance-linear to subulate; style-branch tips papillate and conic or hispidulous and subulate. *Adenophyllum*
- f. Leaves linear, glands scattered along either side of midvein; lobes of disc corollas lance-deltate; style-branch tips papillate, abruptly truncate and with a fine, setaceous appendage. *Dysodiopsis*
- d. Leaves simple, oblong to lance-ovate; calyx of broadly lanceolate bracteoles; phyllaries glandless. *Baobersides*

SYNOPSIS OF GENERA

ADENOPHYLLUM Pers., Synop. Pl. 458. 1807. = *Dysodia* Cav. sect. *Adenophyllum* (Pers.) O. Hoffm. in Engl. & Prantl, Naturl. Pflanz. 4(5):266. 1894.—TYPE: *Adenophyllum coccineum* Pers. = *Willdenowia glandulosa* Cav. = **ADENOPHYLLUM GLANDULOSUM** (Cav.) Strother.

Willdenowia Cav., Icon. Pl. 1:61, t. 89. 1791, non *Willdenowia* Thunb. 1788, nec *Willdenowia* Cothenius 1790.—TYPE: *Willdenowia glandulosa* Cav. = **ADENOPHYLLUM GLANDULOSUM** (Cav.) Strother.

Schlechtendalia Willd., Sp. Pl. 3:2125. 1804, nom. rej. vs. *Schlechtendalia* Less., 1830.—TYPE: *Willdenowia glandulosa* Cav. = **ADENOPHYLLUM GLANDULOSUM** (Cav.) Strother.

- Clomencoma* Cass., Dict. Sci. Nat. 9:416. 1817. = *Dyssodia* Cav. subg. *Clomencoma* (Cass.) Strother, Univ. Calif. Publ. Bot. 48:37. 1969. = *Dyssodia* Cav. sect. *Clomencoma* (Cass.) Strother, Univ. Calif. Publ. Bot. 48:49. 1969.—TYPE: *Aster aurantium* L. = *Clomencoma aurantium* (L.) Cass. = *ADENOPHYLLUM AURANTIUM* (L.) Strother.
- Lebetina* Cass., Dict. Sci. Nat. 25:395. 1822. = *Dyssodia* Cav. sect. *Lebetina* (Cass.) O. Hoffm. in Engl. & Prantl, Naturl. Pflanz. 4(5):266. 1894.—TYPE: *Lebetina camellata* Cass. = *ADENOPHYLLUM POROPHYLLUM* (Cav.) Hemsley var. *CANCELLATUM* (Cass.) Strother.
- Trichostolepis* Rydb., N. Amer. Fl. 34:170. 1915.—TYPE: *Trichostolepis wrightii* (A. Gray) Rydb. = *ADENOPHYLLUM WRIGHTII* A. Gray.

Annual or perennial herbs and shrubs, most robust or coarse, (2-) 10–20+ dm high; leaves opposite or alternate, pinnate with lanceolate or ovate leaflets or pinnatifid with obovate, linear, or filiform lobes, bases, rachises, and teeth usually setose or bristly, glands marginal, often associated with bases of lobes, and subterminal in lobe tips; calyx of 12–16(1–22, sometimes wanting in *A. anomalum*), subulate, lance-linear, or pectinate, often seta-tipped bracteoles, often equalling or surpassing the phyllaries; involucre 8–20(3.5–25) mm high; phyllaries 8–20(–30), weakly connate 1/3–2/3 their length, often separating with age, margins of the outer usually free to base or nearly so, glands round to elliptic or elongate; receptacles fimbriate or setose; ray corollas golden yellow, orange, or scarlet; lobes of disc corollas lance-linear to subulate; style-branch tips papillate and conic or hispidulous and subulate; achenes stoutly to narrowly obpyramidal; pappus of (8–)15–20 squamellae, variously mucicous, aristate, or dissected into 4–11 bristles; $x = 7, 13$.

- BOEBERASTRUM** (A. Gray) Rydb., N. Amer. Fl. 34:161. 1916. = *Dyssodia* Cav. sect. *Boeberastrum* A. Gray, Proc. Amer. Acad. Arts 19:39. 1883.—TYPE: *Dyssodia anthemidifolia* Benth. = *BOEBERASTRUM ANTHEMIDIFOLIUM* (Benth.) Rydb.

Sprawling annuals with stems to 3 dm long; leaves at first opposite, soon alternate, the blades fleshy, spatulate or pinnatifid with linear lobes, not setaceous at base, on lobes, or at tips, glands submarginal or scattered in lamina; calyx none or a single bracteole; involucre 5–8 mm high; phyllaries 8, free to base, glands mostly round; receptacles fimbriate; ray corollas bright yellow; lobes of disc corollas narrowly lance-linear to subulate; style-branch tips papillate, rounded-truncate; achenes stoutly obconical or obscurely obpyramidal; pappus of 16–20 squamellae, each scale dissected into 5–10 bristles; $x = 7$.

- Boeberoides** (DC.) Strother, stat. nov. = *Dyssodia* Cav. sect. *Boeberoides* DC., Prodr. 5:640. 1836.—TYPE: *Dyssodia grandiflora* DC. = *BOEBERODES GRANDIFLORA* (DC.) Strother.

Coarse herbs (annual?) to 25 dm high; leaves all opposite or subopposite, blades oblong to lance-ovate, often with 2–6 inconspicuous subulate lobules at base, glands scattered in lamina; calyculus of 10–20 broadly lanceolate bractlets; involucre ca 20 mm high; phyllaries 18–20, strongly connate ca $2/3+$ their length, glandless; receptacles foveolate; ray corollas yellow-orange; lobes of disc corollas lance-linear; style-branch tips hispidulous, long-subulate; achenes obpyramidal; pappus of ca 20 squamellae, each scale dissected into 7–10 bristles; $x = ?$

COMACLINIUM Scheidw. & Planchon, Fl. Ser. Jard. l'Europe 8:19, t. 756. 1852.—TYPE: *Comaclinium aurantiacum* Scheidw. & Planchon. =COMACLINIUM MONTANUM (Benth.) Strother.

Perennial herbs to 10 dm high; leaves opposite, becoming alternate, the blades simple (–trifoliolate), lanceolate, usually with 1–3 pairs of subulate-setose lobules at base, glands mostly in rows between lateral nerves; calyculus of 3–12 linear bracteoles; involucre 12–15 mm high; phyllaries 10–16, free to base or nearly so, streaked with linear to elliptic glands; receptacles minutely paleate; ray corollas orange; lobes of disc corollas lance-linear to subulate; style-branch tips papillate, conic; achenes stoutly obpyramidal; pappus of ca 20 squamellae, the outer shorter, all dissected into 5–10 bristles; $x = ?$

DYSODIOPSIS (A. Gray) Rydb., N. Amer. Fl. 34:171. 1915. =*Hywnatheraw* Cass. sect. *Dysodiopsis* A. Gray, Smithsonian Contr. Knowl. 3(5):116 (Pl. Wright. D). 1852.—TYPE: *Dysodia tagetoides* Torrey & A. Gray. =DYSODIOPSIS TAGETOIDES (Torrey & A. Gray) Rydb.

Annuals or short-lived perennials, 4–8+ dm high; leaves opposite at base, alternate above, blades linear, coarsely toothed, obscurely setaceous at base, glands scattered along either side of midvein; calyculus of 5–8, conspicuous, subulate or pinnatisect bracteoles nearly as long as phyllaries; involucre 9–12 mm high; phyllaries 10–12, strongly connate but with outer margins free to base, glands round to elliptic; receptacles minutely fimbriate; ray corollas lemon to greenish yellow; lobes of disc corollas lance-deltate (not short-deltate); style-branch tips papillate, truncate, and with a fine, fragile, setaceous appendage; achenes narrowly obpyramidal; pappus 10–12 unequal, lanceolate scales ending in 1(–3) aristae; $x = 13$.

DYSSODIA Cav., Descr. Pl. 202. 1802.—TYPE: *Tagetes papposa* Vahl. =DYSSODIA PAPPOSA (Vahl.) Hitchc.

Boebera Willd., Sp. Pl. 2125. 1804.—TYPE: *Boebera chrysanthemoides* Willd. =*Tagetes papposa* Vahl. =DYSSODIA PAPPOSA (Vahl.) Hitchc.

Rovilla Less., Synop. Gen. Comp. 245. 1832.—TYPE: *Rovilla lutea* Less. =DYSSODIA PINNATA (Cav.) Robinson.

Syncephalantha Bartling, Ind. Sem. Hort. Goett. 6, 1836 [ex Linnaea 12:80, 1838].
 = *Dysodia* Cav. sect. *Syncephalantha* (Bartling) Strother.—TYPE: *Syncephalantha*
decipiens Bartling. = *DYSSODIA DECIPENS* (Bartling) M. Johnston in M. Johnston &
 B. Turner.

Annuals or perennial herbs 1–3(–9) dm high; leaves opposite, often becoming alternate distally, the blades pinnatisect with linear to linear-cuneate or oblanceolate lobes, little, if at all, sericeous at base, on teeth, or at tips of lobes, glands scattered in lamina and/or submarginal; calyculus of 3–5(1–9) deltate to linear bracteoles 1/2–1 times as long as phyllaries; involucre 5–8(–10) mm high; phyllaries 4–8(–16), free to base or nearly so, glands round to elliptic; receptacles fimbriate to finely setose; ray corollas yellow to yellow-orange; lobes of disc corollas short, deltate to lance-deltate; style-branch tips papillate, rounded-truncate to shortly deltate; achenes stoutly obpyramidal to obconic; pappus of 15–20 unequal to subequal squamellae, each scale dissected into 5–10 bristles; $x = 13$.

THYMOPHYLLA Lagasca, Gen. Sp. Nov. 25, 1816. = *Dysodia* Cav. sect. *Thymophylla* (Lagasca) O. Hoffm. in Engl. & Prantl, Nat. Pflanz. 4(5):266, 1894.—TYPE: *THYMOPHYLLA SETIFOLIA* Lagasca.

Hymenatherum Cass., Bull. Soc. Philom. Paris 1818:183, 1818. = *Dysodia* Cav. subg. *Hymenatherum* (Cass.) Strother, Univ. Calif. Publ. Bot. 48:57, 1969. = *Dysodia* Cav. sect. *Hymenatherum* (Cass.) Strother, Univ. Calif. Publ. Bot. 48:78, 1969.—TYPE: *Hymenatherum tenuifolium* Cass. = *THYMOPHYLLA TENUIFOLIA* (Cass.) Rydb.

Dysodia Cav. sect. *Aciphyllaea* DC., Prodr. 5:641, 1836. = *Aciphyllaea* (DC.) A. Gray, Mem. Amer. Acad. Arts, ser. 2, 4:9, 1849. = *Hymenatherum* Cass. sect. *Aciphyllaea* (DC.) A. Gray, Smithsonian Contr. Knowl. 3(5):115 (Pl. Wright. 1), 1852.—TYPE: *Dysodia acerosa* DC. = *THYMOPHYLLA ACEROSA* (DC.) Strother.

Gnaphalopsis DC., Prodr. 7:258, 1838. = *Hymenatherum* Cass. sect. *Gnaphalopsis* (DC.) A. Gray, Smithsonian Contr. Knowl. 3(5):116 (Pl. Wright. 1), 1852. = *Dysodia* Cav. sect. *Gnaphalopsis* (DC.) Strother, Univ. Calif. Publ. Bot. 48:57, 1969.—TYPE: *Gnaphalopsis micropoides* DC. = *THYMOPHYLLA MICROPOIDES* (DC.) Strother.

Louellia A. Gray, Mem. Amer. Acad. Arts, ser. 2, 4:89, 1849.—TYPE: *Louellia aurea* A. Gray. = *THYMOPHYLLA AUREA* (A. Gray) E. Greene in Britton & A. Brown.

Hymenatherum Cass. sect. *Heterochroma* A. Gray, Synop. Fl. N. Amer. 1(2):453, 1884.—TYPE: *Hymenatherum concinna* A. Gray. = *THYMOPHYLLA CONCINNA* (A. Gray) Strother.

Dysodia Cav. sect. *Aurantiacae* Strother, Univ. Calif. Publ. Bot. 48:64, 1969.—TYPE: *Hymenatherum aurantiacum* Brandegec. = *THYMOPHYLLA AURANTIACA* (Brandegec) Rydb.

Annual or perennial herbs or shrublets less than 3 dm high; leaves opposite or alternate, the blades linear-filiform (narrowly spatulate in *T. micropo-*

ides) or pinnatisect with linear-filiform lobes, little, if at all, setaceous at base, on teeth, or at tips of lobes, glands scattered along rachis and lobes (submarginal and scattered in lamina of *T. micropoides*); calyculus of 1-3(0-8), deltate to subulate bracteoles, usually much shorter than the phyllaries; involucre 3-7 mm high; phyllaries 8-13(-22), strongly connate 2/3 + their length, seldom with outer margins free more than 1/2 their length, glands mostly round; receptacles naked or nearly so; ray corollas golden to pale yellow (white in *T. concinnum*); lobes of disc corollas short, deltate to lance-deltate; style-branch tips papillate, deltate or conic; achenes stoutly to narrowly obconic, obpyramidal, or cylindrical; pappus of 10(-20) squamellae, variously mucous, aristate, or dissected into 5-7 bristles; $x = 8$ [reports of $n =$ ca 13, 15, ca 26 in species of *Thymophylla* (as *Dyssodia*, e.g., in Strother, 1969) probably represent misinterpretations of triploid ($2n = 24$) and hexaploid ($2n = 48$) individuals].

NOMENCLATOR FOR DYSSODIA S.L.

- D. acerosa* DC., Prodr. 5:641. 1836. = *Thymophylla acerosa* (DC.) Strother, comb. nov.
D. anomala (Canby & Rose) Robinson. = *Hymenatherum anomalum* Canby & Rose, Contr. U.S. Natl. Herb. 1:105. 1891. = *Adenophyllum anomalum* (Canby & Rose) Strother, comb. nov.
D. anthemidifolia Benth., Bot. Voy. Sulphur 29. 1844. = *BOEBERASTRUM ANTHEMIDI-FOLIUM* (Benth.) Rydb., N. Amer. Fl. 34:162. 1915.
D. appendiculata Lagasca, Gen. Sp. Nov. 28. 1816. = *Adenophyllum appendiculatum* (Lagasca) Strother, comb. nov.
D. aurantia (L.) Robinson. = *Aster aurantius* L., Sp. Pl. 877. 1753. = *Adenophyllum aurantium* (L.) Strother, comb. nov.
D. aurantiaca (Brandegee) Robinson. = *Hymenatherum aurantiacum* Brandegee, Zoe 5:258. 1908. = *THYMOPHYLLA AURANTIACA* (Brandegee) Rydb., N. Amer. Fl. 34:175. 1915.
D. aurea (A. Gray) Nelson. = *Lowellia aurea* A. Gray, Mem. Amer. Acad. Arts, ser. 2. 4:91. 1849. = *THYMOPHYLLA AUREA* (A. Gray) E. Greene in Britton & A. Brown, Illust. Fl. 3:435. 1898.
D. aurea (A. Gray) Nelson var. *polychaeta* (A. Gray) M. Johnston. = *Hymenatherum polychaetum* A. Gray, Smithsonian Contr. Knowl. 3(5):116 (Pl. Wright. D). 1852. = *Thymophylla aurea* (A. Gray) E. Greene var. *polychaeta* (A. Gray) Strother, comb. nov.
D. concinna (A. Gray) Robinson. = *Hymenatherum concinnum* A. Gray, Synop. Fl. N. Amer. 1(2):453. 1886. = *Thymophylla concinna* (A. Gray) Strother, comb. nov.
D. cooperi A. Gray, Proc. Amer. Acad. Arts 9:201. 1874. = *Adenophyllum cooperi* (A. Gray) Strother, comb. nov.
D. DECIPiens (Bartling) M. Johnston in M. Johnston & B. Turner, Rhodora 64:13. 1962. = *Syncephalausta decipiens* Bartling, Index Sem. Hort. Goett. 6. 1836. [ex Linnaea 12:80. 1838].
D. gentryi M. Johnston, Southw. Naturalist 3:219. 1959. = *Thymophylla gentryi* (M. Johnston) Strother, comb. nov.
D. glandulosa (Cav.) O. Hoffm. in Engl. & Prantl, 1894 (non *Dyssodia glandulosa* Cav.,

- 1802). = *Willdenowia glandulosa* Cav., Icon. Pl. 1:61, t. 89. 1791. = *Adenophyllum glandulosum* (Cav.) Strother, comb. nov.
- D. grandiflora* DC., Prodr. 5:640. 1836. = *Boeberoides grandiflora* (DC.) Strother, comb. nov.
- D. gypsophila* B. Turner, Madroño 21:421. 1972. = *Thymophylla gypsophila* (B. Turner) Strother, comb. nov.
- D. littoralis* Brandegee, Zoe 5:163. 1903. = *BOEHERASTRUM LITTORALIS* (Brandegee) Rydb., N. Amer. Fl. 34:162. 1915.
- D. micropoides* (DC.) Loes. = *Gnaphalopsis micropoides* DC., Prodr. 7:258. 1838. = *Thymophylla micropoides* (DC.) Strother, comb. nov.
- D. montana* (Benth.) A. Gray. = *Clomenocoma montana* Benth., Pl. Hartweg, 86. 1841. = *Comaclinium montanum* (Benth.) Strother, comb. nov.
- D. mutica* M. Johnston, Southw. Naturalist 5:225. 1960. = *Thymophylla mutica* (M. Johnston) Strother, comb. nov.
- D. neomexicana* (A. Gray) Robinson. = *Hymenatherum neomexicanum* A. Gray. = *ADENOPHYLLUM WRIGHTII* A. Gray, Smithsonian Contr. Knowl. 5(6):92. (Pl. Wright. II). 1853, non *Dystodia* (*Hymenatherum*) *wrightii* (A. Gray) Robinson, 1913.
- D. neomexicana* (A. Gray) Robinson var. *pulcherrima* Strother, Univ. Calif. Publ. Bot. 48:43. 1969. = *Adenophyllum wrightii* A. Gray var. *pulcherrimum* (Strother) Strother, comb. nov.
- D. PAPPOSA* (Vent.) A. Hitchc., Trans. Acad. Sci. St. Louis 5:503. 1891. = *Tagetes papposa* Vent., Descr. Pl. Nouv. Cels. 4th livr. 36. 1801.
- D. pentachaeta* (DC.) Robinson. = *Hymenatherum pentachaetum* DC., Prodr. 5:642. 1836. = *THYMOPHYLLA PENTACHAETA* (DC.) Small, Fl. Southeast. U.S. 1295. 1903.
- D. pentachaeta* (DC.) Robinson var. *belemidium* (DC.) Strother. = *Hymenatherum belemidium* DC., Prodr. 7:292. 1838. = *Thymophylla pentachaeta* (DC.) Small var. *belemidium* (DC.) Strother, comb. nov.
- D. pentachaeta* (DC.) Robinson var. *hartwegii* (A. Gray) Strother. = *Hymenatherum hartwegii* A. Gray, Smithsonian Contr. Knowl. 3(5):117 (Pl. Wright. D). 1852. = *Thymophylla pentachaeta* (DC.) Small var. *hartwegii* (A. Gray) Strother, comb. nov.
- D. pentachaeta* (DC.) Robinson var. *puberula* (Rydb.) Strother. = *Thymophylla puberula* Rydb., N. Amer. Fl. 34:177. 1915. = *Thymophylla pentachaeta* (DC.) Small var. *puberula* (Rydb.) Strother, comb. nov.
- D. PINNATA* (Cav.) Robinson, Proc. Amer. Acad. Arts 49:501. 1913. = *Aster pinnatus* Cav., Icon. Pl. 3:6. 1794.
- D. PINNATA* (Cav.) Robinson var. *GLABRESCENS* Strother, Univ. Calif. Publ. Bot. 48:33. 1969.
- D. porophylla* (sic) (Cav.) Cav. = *Pteronia porophyllum* Cav., Icon. Pl. 3:13., t. 225. 1794. = *ADENOPHYLLUM POROPHYLLUM* (Cav.) Hemsley, Biol. Cen. Amer. Bot. 2:218. 1881.
- D. porophylla* (Cav.) Cav. var. *cancellata* (Cass.) Strother. = *Lebetina cancellata* Cass., Dict. Sci. Nat. 25:395. 1822. = *Adenophyllum porophyllum* (Cav.) Hemsley var. *cancellatum* (Cass.) Strother, comb. nov.
- D. porophylla* (Cav.) Cav. var. *radiata* DC., Prodr. 5:639. 1836. = *Adenophyllum porophyllum* (Cav.) Hemsley var. *radiatum* (DC.) Strother, comb. nov.
- D. porophylloides* A. Gray, Mem. Amer. Acad. Arts, ser. 2. 5:322. 1854. = *Adenophyllum porophylloides* (A. Gray) Strother, comb. nov.
- D. sanguinea* (Klatt) Strother. = *Synophalanthus sanguineus* Klatt, Leopoldina 25:106. 1889.

- = *DYSSODIA DECIPIENS* (Bartling) M. Johnston in M. Johnston & B. Turner.
- D. setifolia* (Lagasca) Robinson. = *THYMOPHYLLA SETIFOLIA* Lagasca, Gen. Sp. Nov. 25. 1816.
- D. setifolia* (Lagasca) Robinson var. *radiata* (A. Gray) Strother. = *Thymophylla greggii* A. Gray var. *radiata* A. Gray, Smithsonian Contr. Knowl. 3(5):119 (Pl. Wright. 1). 1852. = *Thymophylla setifolia* Lagasca var. *radiata* (A. Gray) Strother, comb. nov.
- D. speciosa* A. Gray, Proc. Amer. Acad. Arts 5:163. 1861. = *Adenophyllum speciosum* (A. Gray) Strother, comb. nov.
- D. squamosa* A. Gray, Proc. Amer. Acad. Arts 19:38. 1883. = *Adenophyllum squamosum* (A. Gray) Strother, comb. nov.
- D. TAGETIFLORA* Lagasca, Gen. Sp. Nov. 29. 1816.
- D. tagetoides* Torrey & A. Gray, Fl. N. Amer. 2:361. 1842. = *DYSODIOPSIS TAGETOIDES* (Torrey & A. Gray) Rydb., N. Amer. Fl. 34:171. 1915.
- D. tenuifolia* (Cass.) Loes. = *Hymenatherum tenuifolium* Cass., Bull. Soc. Phil. 1818:183. 1818. = *THYMOPHYLLA TENUIFOLIA* (Cass.) Rydb., N. Amer. Fl. 34:173. 1915.
- D. tenuiloba* (DC.) Robinson. = *Hymenatherum tenuilobum* DC., Prodr. 5:462. 1836. = *THYMOPHYLLA TENUILOBA* (DC.) Small, Fl. Southeast. U.S. 1295. 1903.
- D. tenuiloba* (DC.) Robinson var. *texana* (Cory) Strother. = *Dyssodia texana* Cory, Rhodora 49:162. 1947. = *Thymophylla tenuiloba* (DC.) Small var. *texana* (Cory) Strother, comb. nov.
- D. tenuiloba* (DC.) Robinson var. *treculii* (A. Gray) Strother. = *Hymenatherum treculii* A. Gray, Proc. Amer. Acad. Arts 19:42. 1883. = *Thymophylla tenuiloba* (DC.) Small var. *treculii* (A. Gray) Strother, comb. nov.
- D. tenuiloba* (DC.) Robinson var. *wrightii* (A. Gray) Strother. = *Hymenatherum wrightii* A. Gray, Mem. Amer. Acad. Arts, ser. 2. 4:89. 1849. = *Thymophylla tenuiloba* (DC.) Small var. *wrightii* (A. Gray) Strother, comb. nov.
- D. tephroleuca* S. E. Blake, J. Wash. Acad. Sci. 25:320. 1935. = *Thymophylla tephroleuca* (S. E. Blake) Strother, comb. nov.

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- . 1977 [1978]. Tageteae — systematic review. Pp. 769-783 in *The biology and chemistry of the Compositae*, eds. V. H. Heywood et al. London: Academic Press.

NOTEWORTHY PLANTS FROM NORTH FLORIDA. II.

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ABSTRACT

The following appear to be first reports for the state of Florida: *Agrostis elliottiana*, *Aster bemisphericus*, *Plantago rugelii*, *Ratibida columnifera*, *Salix ericophala*, *Stachys tenuifolia*, *Veronica agrastis*, and *Vicia hageri*. Over 30 additions to the flora of the Florida panhandle are documented here.

This is the second installment of an anticipated series (Anderson 1984) to update our knowledge of the flora of the Florida panhandle and Clewell's guide (1985) to the flora. The area of coverage is from Madison, Lafayette, and Dixie counties west to the Alabama state line. New discoveries and significant range extensions are given; a few collections appear to be first reports for the entire state. Exotics that appear to be adventive or naturalized are also listed. Voucher specimens are at FSU unless noted otherwise.

Some adjustments or clarifications in nomenclature are reported to reflect current understanding. Additional nomenclatural changes that affect our flora are recorded by Wunderlin et al. (1985).

AGROSTIS ELLIOTTIANA Schult. Gadsden Co.: Chattahoochee, A. K. Gholson 10845 (FLAS), R. K. Godfrey 81222; native, new to Florida.

ALSTROEMERIA PSITTACINA Lehm. Gadsden Co.: large colony naturalized over 10 years (A. K. Gholson, pers. comm.), Chattahoochee, L. C. Anderson 8211; new to Florida panhandle.

ALYSICARPUS OVALIFOLIUS (Schum. & Thonn.) J. Leonard. This is the common species in the southeastern United States rather than *A. vaginalis* (L.) DC. The latter is found in Florida in Dade and Monroe Counties and is the common species in the Caribbean region. Our species can be distinguished by its lax inflorescences and larger leaves; *A. vaginalis* has dense short spikes and smaller leaves (R. Wunderlin, pers. comm.).

AMARANTHUS LIVIDUS L. Franklin Co.: Apalachicola, L. C. Anderson 7359; new to Florida panhandle.

ARISTIDA RAMOSISSIMA Engelm. ex Gray var. *CHASEANA* Hent. Bay Co.: Westbay, R. K. Godfrey 73951 (det. K. Alfred); new to Florida panhandle.

ASCLEPIAS VIRIDULA Chapm. Washington Co.: Rock Hill, 3.5 air mi SE

of Chipley, *L. C. Anderson* 8464; range extension to the northwest for this Florida endemic.

ASTER HEMISPHERICUS Alex. Washington Co.: Rock Hill, 3.5 air mi SE of Chipley, *R. K. Godfrey* 81896, *R. Kral* 3521 (det. J. Semple); native, new to Florida. Clewell (1985) said "reportedly from the western panhandle." These collections confirm its presence in the state.

ASTER LONGIFOLIUS Lam. Jefferson Co.: 5.3 mi S of Wacissa, *R. K. Godfrey* 80175; Wakulla Co.: vic. Newport, *R. K. Godfrey* 80177 (det. A. G. Jones); new to Florida panhandle.

ASTER SIMMONDSII Small. Franklin Co.: Bloody Bluff, 10 air mi N of Apalachicola, *L. C. Anderson* 7776, 3 air mi SW of Sumatra, *L. C. Anderson* 7816, 7817; Wakulla Co.: McBride Slough, *L. C. Anderson* 7765, St. Marks, *R. K. Godfrey* 67760 (det. A. G. Jones); new to Florida panhandle.

CAMPANULA FLORIDANA S. Wats. ex Gray. Franklin Co.: 5 air mi S of Sopchoppy, *L. C. Anderson* 8250. This is a range extension westward from Taylor County.

CERATOPHYLLUM MURICATUM Cham. Franklin Co.: Cape St. George Island, *L. C. Anderson* 9064. The species was listed from neighboring St. Vincent Island by Chapman (1897); he listed it tentatively (under its synonym) as follows: "*Ceratophyllum echinatum* Gray?". Clewell (1985) did not list the species under either name.

CRATAEGUS PHAENOPYRUM (L. f.) Medic. Washington Co.: 5.5 air mi SW of Chipley, *L. C. Anderson* 8206; *R. K. Godfrey* 81202. Coker and Totten (1934) reported the species (as *C. youngii* Sarg.) from Wakulla County, but the Wakulla station has not been rediscovered, and the taxon is not listed by Clewell (1985).

ELEOCHARIS TORTILIS (Link) Schultes in R. & S. Franklin Co.: Shell Hammock, 5.5 air mi SW of Panacea, *L. C. Anderson* 8275; Gulf Co.: M & K tract, 8.5 air mi NW of Apalachicola, *L. C. Anderson* 8833. Clewell (1985) reported this species was known in the panhandle only from one specimen collected by Chapman in Gadsden County.

HYDROCOTYLE SIBTHORPIOIDES Lam. Jackson Co.: Neal's Landing, Lake Seminole, *L. C. Anderson* 8449, *A. K. Gbolson* 11290; new to Florida panhandle.

IMPATIENS BALSAMINA L. Bay Co.: Callaway, *W. S. Judd* 2307 (FLAS); Leon Co.: Lake Ella, Tallahassee, *L. C. Anderson* 8082; adventive, new to Florida panhandle.

ISOTRIA VERTICILLATA (Muhl. ex Willd.) Raf. Washington Co.: ca. 6 air mi SE of Vernon, *L. C. Anderson* 8194. Correll (1950) reported this orchid from Gadsden County, but its occurrence there has not been rediscovered.

LINDERNIA GRANDIFLORA Nutt. Franklin Co.: 4.7 air mi S of Sopchoppy, *L. C. Anderson* 6995, 7105; Jefferson Co.: E of Newport, 2 mi W of Aucilla River, *R. K. Godfrey* 81768; new to Florida panhandle.

LUDWIGIA CURTISSII Chapm. Franklin Co.: St George Island, *R. K. Godfrey* 71148 (det. Ching I-Peng); new to Florida panhandle.

LUDWIGIA ERECTA (L.) Hara. Franklin Co.: sandbar at milepost 7.1 on Apalachicola River, *L. C. Anderson* 8528, 8677; Gulf Co.: Brothers River, 13 air mi N of Apalachicola, *L. C. Anderson* 8932; new to Florida panhandle.

LUDWIGIA LANCEOLATA Ell. Jefferson Co.: Lloyd, *R. K. Godfrey* 61411; Madison Co.: 8 mi W of Greenville, *R. Kral* 3741; Taylor Co.: 1.2 mi SE of Salem, *R. K. Godfrey* 64738; Wakulla Co.: NW of Crawfordville, *R. K. Godfrey* 64876 (det. Ching I-Peng); new to Florida panhandle. This species is listed under *L. alata* Ell. by Clewell (1985). Both species occur in our area; *L. lanceolata* has sepals about half as long as the capsule and pollen shed in tetrads, whereas *L. alata* has sepals nearly as long as the capsule and pollen shed singly.

MANISURIS CYLINDRICA (Michx.) Kuntze. Jackson Co.: Apalachee Game Management Area, N of Sneeds, *J. B. Nelson & G. R. Knight* 2615; new to Florida panhandle.

MARSILEA UNCINATA A. Br. Franklin Co.: N. Market Street, Apalachicola, *L. C. Anderson* 7625, 8009, *A. K. Gbolson* 11212. A second population of *Marsilea* from Avenue K in Apalachicola (*L. C. Anderson* 7356) has not produced sporocarps during the past year, so its identity as *M. vestita* or *M. uncinata* has not been resolved.

A collection of *M. vestita*, so annotated by D. S. Correll, from Apalachicola (*Chapman* in 1860) was cited by Ward and Hall (1976). They suggested the label data may be in error because Chapman (1897) did not list the species for Florida. Johnson (1986) has determined *M. uncinata* to be synonymous with *M. vestita* ssp. *vestita*, so all Franklin Country collections are *M. vestita*.

MENTHA PIPERITA L. Franklin Co.: Apalachicola, *L. C. Anderson* 7357, 7535; Wakulla Co.: St. Marks, *R. K. Godfrey* 64407.

MENTHA ROTUNDIFOLIA (L.) Juds. Franklin Co.: Avenue F, Apalachicola, *L. C. Anderson* 7352, Avenue M, Apalachicola, *L. C. Anderson* 8312; naturalized, new to Florida panhandle.

OENOTHERA NUTANS Atkins. Jackson Co.: Caverns State Park, *R. S. Mitchell* 824; Leon Co.: Tallahassee, *W. D. D'Arcy* 1299 (FLAS); Liberty Co.: rte 20 near Ochlockonee River, *R. R. Smith* 1936 (FLAS) (det. W. Dietrich); new to Florida panhandle.

PHYSALIS CORDATA Miller. Dixie Co.: Suwannee River, E of Old Town, R. K. Godfrey 65885; Gadsden Co.: Quincy, R. K. Godfrey 67548 (det. J. R. Sullivan); new to Florida panhandle.

PHYSALIS WALTERI Nutt. is the correct name for Florida plants previously referred to as *P. viscosa* L. (det. J. R. Sullivan).

PLANTAGO HETEROPHYLLA Nutt. Calhoun Co.: Chipola River, H. Kurz in 1943 (FLAS); Gadsden Co.: Chattahoochee, R. K. Godfrey 81234, Quincy, E. West in 1933 (FLAS); Jackson Co.: Paramore Landing, Lake Seminole, A. K. Gholson 10309; Leon Co.: Tallahassee, L. C. Anderson 8004; new to Florida panhandle.

PLANTAGO RUGELII DCNE. Leon Co.: Lakeshore Drive, Tallahassee, L. C. Anderson 5952 (det. J. Bassett), 8442; ruderal native, new to Florida.

POLYGALA VERTICILLATA L. Wakulla Co.: Hwy 98, N of St. Marks, L. C. Anderson 8290; new to Florida panhandle.

POLYGONUM AVICULARE L. Franklin Co.: Apalachicola, R. K. Godfrey 81441; new to Florida panhandle.

RATIBIDA COLUMNIFERA (Nutt.) Woot. & Standl. f. *PULCHERRIMA* (DC.) Fern. Leon Co.: Madiera Circle, Tallahassee, L. C. Anderson 8064, 8078; adventive, new to Florida (possibly escaped from cultivation but not seen in local gardens).

SALIX ERIOCEPHALA Michx. Gadsden Co.: E of Little River on I-10, A. K. Gholson 11533; Jackson Co.: 7 mi W of Malone, R. K. Godfrey 79125, 79360, 79419, 80348, 80757 (det. G. Argus); native, new to Florida as far as the name is concerned. Listed as *S. rigida* Muhl. in Clewell (1985); the latter does not occur in north Florida.

SCOPARIA MONTEVIDENSIS (Spreng.) R. E. Fries. Santa Rosa Co.: Milton, J. R. Burkhalter 9199; Wakulla Co.: NE of Medart near junction hiways 98 and 319, L. C. Anderson 7263. This South American species was first collected in Florida at Port St. Joe, Gulf Co., M. F. Baker in 1939 (FLAS) and at Carrabelle, Franklin Co., M. F. Baker in 1940 (FLAS). It has not been re-collected at Port St. Joe, but it is represented by many collections from Franklin County. The species is now spreading.

STACHYS TENUIFOLIA Willd. var. *PERLONGA* Fern. Gadsden Co.: 3 air mi SE of Havana, L. C. Anderson 7378, 8448; native, new to Florida. These plants are atypically bristly with branching inflorescences and are tentatively placed as var. *perlonga* (J. B. Nelson, pers. comm.). Small (1933) listed the species for Florida, but Nelson (1981) found no extant specimens for the state. Closest known populations of the variety are in northern Georgia and southern Mississippi.

STELLARIA PROSTRATA Baldw. Franklin Co.: St. Vincent Island, L. C. Anderson 7024; new to Florida panhandle.

THELYPTERIS INTERRUPTA (Willd.) Iwatsuki. Franklin Co.: 1.5 mi S of Bald Point, 7.8 air mi SE of Panacea, *L. C. Anderson* 7753, 9073. This tropical fern was first reported for north Florida from Dog Island, Franklin Co., by Anderson and Alexander (1985). The Dog Island population was severely damaged by hurricane Elena in September, 1985; the mainland population may have the only extant plants in the area.

VERONICA AGRESTIS L. Franklin Co.: Commerce Street, Apalachicola, flowers white, capsule 4-5 mm long with short, stout style, *L. C. Anderson* 7919; adventive, new to Florida.

VERONICA POLITA Fries. Pensacola, *J. R. Burkbalter* 3482; new to Florida panhandle. This species is sometimes included as part of *V. agrestis*; the two are distinguished by Pennell (1921).

VICIA FLORIDANA S. Wats. Franklin Co.: McIntyre on Ochlockonee River, *L. C. Anderson* 7005; range extension westward from Taylor County.

VICIA HUGERI Small. Jackson Co.: Three Rivers State Rec. Area, N of Sneads, *G. R. Knight* 414; native, new to Florida.

VIOLA SORORIA Willd. Nearly glabrous plants from Florida with light-colored flowers that have been assigned to this species have been problematic. Cooperrider's treatment (1884) is followed here. *Viola sororia* f. *beckwithae* House. Franklin Co.: cemetery, Apalachicola, *R. K. Godfrey* 76266; Jefferson Co.: 3.2 mi N of Waukeenah, *L. C. Anderson* 7846; Leon Co.: Tallahassee, *L. C. Anderson* 7834, 7848; new to Florida panhandle. *Viola sororia* f. *priceana* (Poll.) Cooperrider. Dixie Co.: Suwanee, SE of rte 249, *S. W. Leonard* 8087; new to Florida panhandle.

YUCCA GLORIOSA L. Franklin Co.: Bald Point, facing Ochlockonee Bay, *L. C. Anderson* 7747; new to Florida panhandle. The collection was from a sandy, rear-dune setting far from habitation, but the plants are probably adventive rather than relictual.

ZEPHYRANTHES CANDIDA (Lindl.) Herbert. Franklin Co.: naturalized along Avenue K (also on Avenue F) in Apalachicola, *L. C. Anderson* 7537; new to Florida panhandle.

ZEPHYRANTHES GRANDIFLORA Lindl. Franklin Co.: naturalized at Brickyard Landing, Apalachicola River, *L. C. Anderson* 7326; new to Florida panhandle.

ACKNOWLEDGMENTS

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SYNOPSIS OF THE FLORIDA SPECIES OF *PECTIS* (ASTERACEAE)

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ABSTRACT

A key, descriptions, revised nomenclature, range statements and maps are presented for the species of *Pectis* known to occur in Florida. A new combination, *Pectis glaucescens*, is published for the plant formerly known as *P. leptcephala*. A naturally occurring triploid interspecific hybrid, *Pectis* × *floridana* (*P. glaucescens* × *P. prostrata*), is described and illustrated.

Four species of *Pectis* (Asteraceae) have been reported to occur in Florida: *P. humifusa*, *P. leptcephala*, *P. linearifolia*, and *P. prostrata* (Fernald 1897; Rydberg 1916; Small 1933; Keil 1975; Long and Lakela 1976; Cronquist 1980; Wunderlin 1982). Systematic investigations of *Pectis* necessitate some taxonomic changes for the species occurring in Florida. An examination of type specimens deposited in the herbarium of the Museum National d'Histoire Naturelle (P) revealed that the basionym of *P. leptcephala* is predated by an earlier available epithet and that a nomenclatural change is required. Recent field studies have revealed the presence of a heretofore unrecognized natural interspecific hybrid that closely resembles *Pectis linearifolia*. The range of several species is greater than indicated in local and regional manuals (e.g., Anderson 1984).

PECTIS L., Syst. Nat. Ed. 10. 1221. 1759. Type: *P. linearifolia* L.

Tap-rooted or fibrous-rooted annual or perennial herbs. Stems prostrate to erect, often several arising together from the base, straw-colored to deep purplish brown, often diffusely branched, glabrous to puberulent. Leaves opposite, linear to oblanceolate, connected at the base by a narrow connate rim, proximally ciliate with slender bristles, dotted on the undersurface with pellucid glands containing scented oils or unscented compounds, glabrous or minutely puberulent on the margin and midvein. Heads radiate, solitary or in open to condensed cymose clusters, the peduncles bearing one to several alternate scale-like bractlets. Involucres cylindrical to fusiform or campanulate; phyllaries in a single series, of equal length, distinct or cohering in the proximal 1 mm, linear to obovate, the margins narrowly

hyaline, often overlapping, acute to rounded, the abaxial surface with a prominent, proximally gibbous keel, dotted or streaked with glands, usually ciliolate distally, glabrous or puberulent. Receptacle flat or hemispherical, naked, shallowly pitted. Ray florets pistillate and fertile, equal in number to the phyllaries and individually inserted on the phyllary bases rather than the receptacle; corollas yellow, often suffused with red in age, the tube slender, the ligule elliptical, entire or shallowly 2-3-lobed. Disk florets perfect; corollas yellow, the tube slender, gradually expanded to the throat, the limb (in Florida species) bilabiate with a 1-lobed anterior lip and a 4-lobed posterior lip; stamens (in Florida species) 5, included, the apical anther appendages very short, rounded or emarginate; style included or exerted, the branches very short, papillose. Achenes cylindrical, black or dark brown, variously puberulent with 2-celled trichomes. Pappus of lanceolate to setiform scales, awns or bristles, sometimes reduced to a low crown. Chromosome base number: $x = 12$.

About 85 species ranging from California, Nebraska and Florida south through much of Latin America to the Galapagos Islands, northern Argentina and the West Indies. In Florida, more frequent from mid-peninsular regions southward, uncommon in the panhandle region (Fig. 1).

KEY TO THE SPECIES OF *PECTIS* IN FLORIDA

1. Heads borne on slender peduncles mostly 5-35 mm long.
 2. Foliar glands all or mostly in marginal row; phyllaries falling individually, not coherent at base; achenes seed-bearing. 1. *P. glaucescens*
 2. Foliar glands submarginal and scattered over the undersurface of the blade; phyllaries coherent at base, falling together with the enclosed achenes; achenes with abortive ovules. 3. *P. × floridana*
1. Heads sessile or borne on peduncles mostly less than 3 mm long.
 3. Involucres campanulate; phyllaries obovate, 2-4 mm wide; disk florets 12-21. 5. *P. hamifusa*
 3. Involucres cylindrical to fusiform; phyllaries linear to oblong, 1-2.5 mm wide; disk florets 4-10.
 4. Leaves mostly more than 2 mm wide; heads fusiform; foliar glands very numerous, scattered on the undersurface of the leaves; herbage not scented. 4. *P. prostrata*
 4. Leaves mostly 1-1.5 mm wide; heads cylindrical; herbage scented.
 5. Phyllaries prominently keeled, cohering at base and falling together with the enclosed achenes; achenes with abortive ovules; herbage spicy-scented. 3. *P. × floridana*
 5. Phyllaries not prominently keeled, falling individually; achenes seed-bearing; herbage lemon-scented. 2. *P. limarifolia*

1. ***PECTIS glaucescens* (Cassini) Keil, comb. nov.** *Chthonia glaucescens* Cassini, Dict. Sci. Nat. 9:174. 1817. TYPE: of unknown origin (HOLOTYPE: P-JU!).

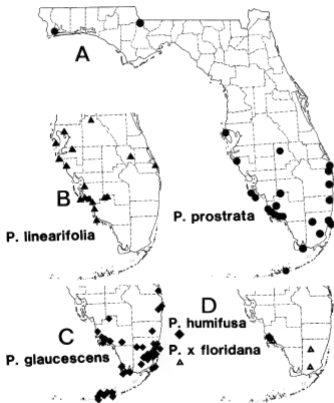


Figure 1. Distribution of *Petris* species in Florida. A. *P. prostrata* Cav. B. *P. linearifolia* Urban. C. *P. glaucescens* (Cass.) Keil. D. *P. humifusa* Swartz and *P. x floridana* Keil.

Cithonia leptocphala Cassini, Dict. Sci. Nat. 27:206. 1823. TYPE: of unknown origin (HOLOTYPE: [according to Cassini] in the Desfontaines herbarium at P, but not located during my visit in 1985). *Pectis leptocphala* (Cassini) Urban, Symb. Antil. 5:280. 1907.

Pectis lesingii Fernald, Proc. Amer. Acad. Arts 33:67. 1897. TYPE: UNITED STATES: FLORIDA: Dade Co.: between the Everglades and Biscayne Bay, *Curtis 1162* (LECTO-TYPE: GH[!]; ISOLECTOTYPES: BMI, CM[!], F[!], K[!], M[!], MICH[!], NY (2)[!], P[!], US[!]). The lectotype is here chosen from seven syntypes.

Spicy-scented annuals (sometimes persisting and becoming subligneous at base), simple to much-branched from the base, sometimes mat-forming but not radicate. Stems slender, erect to prostrate, 2–50 cm long, cymosely much-branched, sparsely to densely puberulent, sometimes glabrate. Leaves narrowly linear, 1–3.5 cm long, 0.2–1.8 mm wide, mucronulate or setose-tipped, often revolute, proximally ciliate with 1–5 pairs of bristles 1–2 mm long, submarginally punctate on the abaxial surface with broadly elliptic to circular glands 0.2–0.3 mm diameter, sometimes with additional scattered glands, minutely scaberulous on the margins, otherwise glabrous. Heads solitary or in diffuse few- to many-headed cymose clusters; peduncles filiform (3–)7–35 (–54) mm long, with 2–5 slender, scale-like bractlets 0.5–1.5 mm long. Involucres cylindrical; phyllaries 5, distinct, falling individually from the receptacle at maturity, linear-oblancoate, 4–5 mm long, obtuse to acute, slender-keeled to near the apex, often bowed-out near the middle, sparsely punctate with elliptical glands 0.1–0.2 mm long, distally ciliolate, otherwise glabrous. Ray florets 5; corollas 3–5 mm long, the narrow ligule 2–3.5 mm long, often involute when dry. Disk florets 3–7; corollas 2–3 mm long; anthers 1 mm long. Ray and disk achenes similar, 2.5–3 mm long, antrorsely strigillose. Pappus variable, composed of 0–5 antrorsely scabrid bristles or slender scales 1–2 mm long, and 0–5 entire to irregularly lacerate scales 0.2–0.7 mm long. Chromosome number: $n = 24$.

Common and widespread in southern Florida and the Bahamas; also in Hispaniola and Jamaica. In Florida it occurs from Glades and Martin counties south to Key West (Fig. 1-C). Flowering specimens have been collected throughout the year. *Pectis glaucescens* is most common on limestone soils in open grassy sites. Various types of human disturbance, particularly road construction, have created habitats suitable for these plants, and in places this species is an abundant roadside weed. It also occurs as a lawn weed in the Miami area and probably elsewhere.

2. *PECTIS LINEARIFOLIA* Urban, Symb. Antil. 5:276. 1907. TYPE: UNITED STATES: FLORIDA: Hillsborough Co.: Tampa, *Nash 2479* (LECTOTYPE: US[!]; ISOLECTOTYPES: E[!], GH[!], K[!], LE[!], MO (2)[!], MSC[!], NY[!], P (2)[!], PR[!], UC[!], WU[!]). The lectotype is here designated from isosyntypes. Urban designated two syntypes,

one from Florida and the second from Jamaica. Both specimens were apparently destroyed when the Berlin herbarium burned during World War II. I am excluding the Jamaican collection (JAMAICA: without locality, *MacFarlane s. n.* (GOET! [fragment], K!), which is actually *P. glaucescens*.

Lemon-scented annuals, simple or much-branched from the base. Stems slender, erect to decumbent, 4–40 cm long, puberulent, the upper branches mostly short. Leaves linear, 1–5 cm long, 1–3 mm wide, mucronate or setose-tipped, often revolute, proximally ciliate with 2–6 pairs of bristles 1–2.5 mm long, submarginally punctate on the abaxial surface with round glands 0.2–0.4 mm diameter, scaberulous on the margins, otherwise glabrous. Heads solitary or in congested terminal and axillary leafy-bracted cymose clusters, sessile or on peduncles up to 1 mm long. Involucre cylindric to narrowly campanulate; phyllaries 5, distinct, falling individually from the receptacle at maturity, linear or linear-oblongate, 5–6 mm long, 1–1.5 mm wide, acute, indurate-keeled in the proximal half, punctate with scattered elliptical glands 1–2 mm long, apically ciliate, otherwise glabrous. Ray florets 5; corollas 4.5–5.5 mm long, the narrow ligules 3–4 mm long, often involute when dry. Disk florets 4–10; corollas 2.5–3 mm long; anthers 0.6–1 mm long. Ray and disk achenes similar, 2.25–3.25 mm long, antrorsely strigillose. Pappus of ray and disk achenes similar, composed of 2–5 antrorsely barbed bristles or slender scales 1.5–2.5 mm long and several shorter barb-margined scales. Chromosome number: $n = 24$.

Endemic to mid-peninsular Florida from Pinellas Co. and northern Polk Co. east to Martin Co. and south to northern Collier Co. (Fig. 1-B). The main flowering period is from August to December, but this species sometimes flowers in the spring months as well. The distribution of *P. linearifolia* is mostly to the north of that of *P. glaucescens*. Both species occur in open sandy or gravelly soils with grasses and other low herbs. I have seen the two together at only one site (along a railroad and roadside in Martin Co.) and observed no hybrids. It is likely that the two taxa grow together at other sites as well. *Pectis linearifolia* is represented by fewer and more widely scattered collections than is *P. glaucescens* and is apparently less common.

3. *PECTIS* × *floridana* Keil, nothosp. nov. (Fig. 2).

E ceteris speciebus Floridae numero triploideo chromosomatum et acheniis sterilibus differt. E *P. prostrata* foliis angustioribus, capitulis gracilioribus et oleis essentialibus graveolentibus et E *P. glaucescens* glandibus foliorum dispersis, pedunculis brevioribus et phyllariis proximale coherentibus distinguitur. E *P. linearifolia* phyllariis proximale coherentibus et valde carinatis, pedunculis longioribus et odoris oleorum essentialium separari potest.

Spicy-scented annuals, simple or much-branched from the base, often mat-forming and sometimes radicate. Stems slender, erect to decumbent, 5–30 cm long, puberulent. Leaves linear, 1.5–3.5 cm long, 1–2 mm wide, punctate on the abaxial surface with numerous scattered glands ca 0.2 mm diameter, scaberulous on the margins, otherwise glabrous. Heads solitary or in condensed axillary and terminal cymose clusters; peduncles filiform, 5–25 mm long, bearing 1–4 scale-like bractlets. Involucre cylindrical to narrowly fusiform; phyllaries 5, coherent at base and falling as a group together with the enclosed achenes, linear or linear-oblancoelate, 5–7 mm long, 1–2 mm wide, subacute, strongly indurate-keeled to near the apex, punctate with scattered oval glands 0.2–0.3 mm long, ciliate apically, otherwise glabrous. Ray florets 5; corollas 3.5–4.2 mm long, the narrow ligule 2–2.7 mm long, often involute when dry. Disk florets 4–6; corollas 2.5 mm long, the anthers ca 1 mm long. Ray and disk achenes similar, 3–3.5 mm long, strigillose to short pilose, the pericarp darkening but not swelling, the ovule abortive and shrunken. Pappus of 2 (ray) or 5 (disk) slender, antrorsely scabrid, setose-tipped scales 2–2.5 mm long, sometimes with one or more additional shorter scales or bristles. Chromosome number: $3n = 36$.

TYPE: UNITED STATES: FLORIDA: Collier Co.: 6 mi SE of Royal Palm Hammock along US 41, 18 Nov 1982, Keil 16488 (HOLOTYPE: FTG; ISOTYPES: to be distributed).

Known at present from Collier and Dade counties (Fig. 1-D). The individuals collected at these sites were in flower in November and had evidently been flowering for at least two months.

Additional specimens examined: FLORIDA: Dade Co.: along US 41, 18 mi W of Florida Turnpike, Keil 16476 (OBI); Everglades National Park at Pa Hay Okee Overlook, Gillis 7121 [mixed with *P. glaucescens*] (I).

Pectis × *floridana* is apparently a first generation hybrid between *Pectis glaucescens* and *P. prostrata*. Second generation hybrids and backcrosses have not been discovered. In south peninsular Florida, the two parental taxa are known to grow together at several locations. At two sites where I encountered mixed populations of these species, I observed morphologically intermediate individuals that I at first mistook for *P. linearifolia*. However, chromosome counts of the two species and the intermediates plus the characters of these plants demonstrate that the intermediates are hybrids. *Pectis prostrata* is a diploid and *P. glaucescens* is a tetraploid. The resemblance to *P. linearifolia* is apparently coincidental (Keil 1983). The hybrids are triploids and apparently are completely sterile. Meiosis is very irregular. Pollen grains are malformed and variable in size, and have 0 percent stainability in cotton blue in lactophenol (400 grains counted).

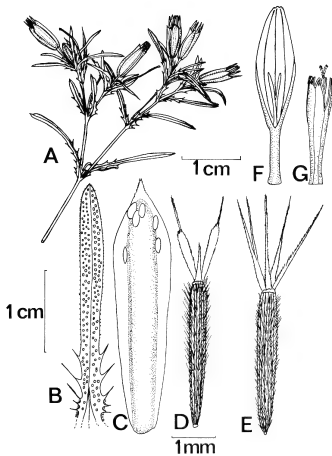


Figure 2. *Pectis* × *floridana* Keil. A. Branchlet with heads. B. Principal foliage leaf. C. Phyllary. D. Ray achene. E. Disk achene. F. Ray corolla. G. Disk corolla. C-G, same scale.

Regeneration of the hybrids from season to season apparently requires new hybridization events. There is apparently no barrier to hybridization between *P. prostrata* and *P. glaucescens*. At the type locality the hybrids were almost as common as the parental taxa. At this site the plants formed a dense mixed roadside population, and the branches of individuals of the two parental species and the hybrids frequently were intertangled. Hybrid individuals were apparently as healthy and vigorous as the parents. *Pectis* × *floridana* can be expected in other areas where the two parents occur together.

The triploid hybrids are the potential progenitors of a new hexaploid species. Polyploidy is common in the species of *Pectis* of the Caribbean region. Both parental taxa are facultatively autogamous, and a fertile hexaploid, if formed, would very likely retain this capacity, thus enabling it to establish a population even if it were surrounded by individuals of the parental taxa.

4. *PECTIS PROSTRATA* Cavanilles, *Icon. Descr. Pl.* 4:12. 1797. TYPE: grown at the Madrid Botanical Garden from seed collected by Née in Querretaro, Mexico (HOLOTYPE: MA, photo OBI!). *Cibtonia prostrata* (Cavanilles) Cassini ex Steudel, *Nom. Bot.* 598. 1821, pro syn.

Lorentia prostrata Lagasca, *Gen. Sp.* Pl. 28. 1816. TYPE: CUBA: without location, *Bolbo J.N.* (HOLOTYPE: MA, photo OBI!).

Pectis costata Ser. & Merc. ex DC., *Prodr.* 5:100. 1836. TYPE: CUBA: without location, *Sagra J.N.* (HOLOTYPE: G-DC!; ISOTYPE: P!).

Pectis prostrata Cavanilles var. *arcolata* Fernald, *Proc. Amer. Acad. arts* 33:68. 1897. TYPE: MEXICO: CHIHUAHUA: Hacienda San Jose, *Palmer 53* (HOLOTYPE: GH!; ISOTYPES: BM!, K!, LE!, NY!). *Pectis arcolata* (Fernald) Rydberg, *N. Amer. Fl.* 34:197. 1916.

Pectis multisetosa Rydb., *N. Amer. Fl.* 34:198. 1916. TYPE: GUATEMALA: SANTA ROSA: Chupadero, *Heyde and Lux 4232* (HOLOTYPE: NY!; ISOTYPES: F!, UC! [fragment]).

Unscented annuals, simple or much-branched from the base, often mat-forming and sometimes radican. Stems slender, erect to prostrate, 1–30 cm long, often much-branched, sparsely to densely puberulent. Leaves linear to oblong or narrowly oblanceolate, 1–3 cm long, 1.5–5 mm wide, obtuse to subacute, mucronate, proximally ciliate with 4–12 pairs of bristles 1–3 mm long, densely punctate on the undersurface with scattered round glands 0.1–0.2 mm diameter, scaberulous on the margins, proximally villous-ciliolate, otherwise glabrous. Heads solitary, sessile or subsessile in dense terminal or axillary cymose clusters; peduncles up to 2 mm long, bearing 1-several scale-like bractlets. Involucres cylindrical or fusiform; phyllaries 5, coherent at base and falling as a group together with the enclosed achenes, oblong to narrowly obovate, 5–6.5

mm long, 1.5–2.5 mm wide, obtuse to subacute, strongly indurate-keeled to near the apex, punctate with scattered oval glands 0.1–0.2 mm long, ciliate apically, otherwise glabrous. Ray florets 5; corollas 2.5–3.5 mm long, the narrow ligule 1.5–2 mm long, often involute when dry. Disk florets 3–6; corollas 2–2.5 mm long, the anthers ca 1 mm long. Ray and disk achenes similar, 2.5–3.5 mm long, strigillose to short pilose. Pappus of 2 (ray) or 5 (disk) lanceolate scales 1.5–2 mm long. Chromosome number: $n = 12$.

Widespread from the southwestern United States south throughout much of Mexico and Central America and from Florida to the Bahamas, Cuba, Hispaniola and Puerto Rico. In Florida, known from the panhandle region in Escambia and Gadsden counties and in the peninsula in scattered locations from Pinellas and Highlands counties south into the Keys (Fig. 1-A). Flowering mostly from August to December. This species is probably more widespread than present records indicate. It is often overlooked or ignored because it is a rather unattractive roadside weed. In my field studies in southern Florida I found it to be common in disturbed habitats.

Pectis prostrata is a variable species represented in Florida by comparatively small-headed plants. Larger headed plants occur in some areas of Mexico and Central America. It is not certain whether this species is indigenous in Florida or introduced from some other region. The first collections from the state were made in the 1840's but by that time Florida had been a part of Spain's commercial shipping network for several hundred years. *Pectis prostrata* is rather weedy and its occurrence on the islands of Hispaniola and Puerto Rico are probably a result of human introduction. It is facultatively autogamous and readily pioneers roadsides and other disturbed open habitats. It is apparently spreading along roadsides and can be expected to become even more common in Florida in the future. This species may spread to Georgia or Alabama if the population sampled in Gadsden County (Anderson 4573) persists. This collection site is approximately 10 miles from the Florida-Georgia state line.

5. *PECTIS HUMIFUSA* SWARTZ, Prodr. 114. 1788. TYPE: VIRGIN ISLANDS: St. CROIX [Santa Cruz]: without location, Swartz s.n. (LECTOTYPE: BM!; ISOLECTOTYPE: G-DC!). The lectotype is here chosen from syntypes. *Cibtonia humifusa* (Swartz) Cassini ex Steudel, Nom. Bot. 598. 1821, pro syn. *Lorentia humifusa* (Swartz) Lessing, Linnaea 6:719. 1831.

Cibtonia repens Cassini, Dict. Sci. Nat. 27:204. 1823. TYPE: PUERTO RICO: without location, Sagro s.n. (HOLOTYPE: P-JU!; ISOTYPES: P!, P-LA!).

Pectis sieberi Lessing, Linnaea 6:717. 1831. TYPE: FRENCH WEST INDIES: Martinique, Sieber 24 (HOLOTYPE: CW?; ISOTYPES: HAL!, JE!, K!, L!, M!, MO!, NY?, P (?), PR!, WU!).

Pectis serpyllifolia Lessing, *Linnaea* 6:715. 1831. TYPE: PUERTO RICO: without location, *Wydler 208* (LECTOTYPE: G-DC!; ISOLECTOTYPES: E!, K!, L!, OXF!, S!, TCD!). The lectotype is here chosen from four syntypes.

Non-scented mat-forming annuals or often perennials, the base often more or less woody. Stems several to many from the base, 2–25 cm long, prostrate, much-branched, densely leafy, often strongly radicate, puberulent. Leaves oblong-ob lanceolate to obovate, 3–17 mm long, 1.5–4 mm wide, obtuse, mucronulate, proximally ciliate with 2–6 pairs of bristles 1–2 mm long, the bases sheathing, on both surfaces punctate with numerous scattered round glands 0.1–0.2 mm diameter, scaberulous on the margins, proximally villous-ciliate, otherwise glabrous. Heads terminal and axillary, solitary or in few-headed cymes, sessile or on slender peduncles 1–12 mm long with 2–3 scale-like bractlets. Involucres campanulate; phyllaries 5, obovate, 4.5–6 mm long, 2–4 mm wide, broadly overlapping, broadly obtuse, indurate-keeled in the proximal 1/2 or 2/3, densely punctate with numerous scattered tiny glands, apically ciliate, otherwise glabrous. Ray florets 5; corollas 3.5–5 mm long, the tube 1–2 mm long and the narrow ligules 2.5–3 mm long. Disk florets 12–21; corollas 2.5–3 mm long; anthers ca 1 mm long. Achenes 2.5–4 mm long, puberulent with trichomes 0.2–0.5 mm long, the ray achenes abaxially glabrous. Ray pappus of 2–3 slender, antrorsely scabrid, bristle-tipped scales 1.5–2.5 mm long and 2–10 shorter lacerate-margined scales or slender bristles. Disk pappus of 4–15 antrorsely scabrid bristles or slender scales 2–3 mm long and up to 15 shorter bristles or scales. Chromosome number: $n = 36$.

From Puerto Rico eastward and southward throughout the Lesser Antilles to the coast of Surinam. Known in Florida from a single collection in 1956 from Collier County (Fig. 1-D) where it is probably adventive (Keil 1975). Efforts in 1982 to relocate the collection site were unsuccessful and it is not known whether this species has persisted in Florida.

SPECIES LIKELY TO DISPERSE TO FLORIDA

Several other species of *Pectis* are common in the West Indies and may eventually disperse to Florida. *Pectis linifolia* var. *linifolia* is a very common and widespread taxon found on most of the islands of the West Indies including the Bahamas. It is a tall, slender, unscented plant with a pappus of stout awns. *Pectis elongata* var. *floribunda* is an erect, bushy-branching, lemon-scented herb found in both the Greater and Lesser Antilles. *Pectis tenuicaulis*, ranging from Venezuela and Colombia to the Dominican Republic, Puerto Rico and several islands of the Lesser Antilles, is similar to *Pectis prostrata* but has 3-rayed instead of 5-rayed heads. *Pectis ciliaris* occurs

in northern South America and the Greater Antilles. It resembles *P. prostrata* but it is a tetraploid. In *P. ciliaris* the phyllaries are less-prominently keeled than in *P. prostrata* and fall separately.

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BUMELIA DOMINICANA (SAPOTACEAE),
A NEW NAME FOR AN OLD SAPOTE

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In his treatment of the Jamaican *Bumelia* (Sapotaceae), W.T. Stearn (1968) combined the genera *Bumelia* and *Dipholis* due to the lack of significant characters to consistently separate them. Under this interpretation, *Dipholis ferruginea* Ekman & O.C. Schmidt became *Bumelia ferruginea* (Ekman & O.C. Schmidt) W.T. Stearn. This is a later homonym of *B. ferruginea* Nuttall, a name applied to a segregate of *B. lanuginosa* (Michaux) Persoon which occurs in the eastern United States and northern Mexico. Since this new combination is in direct contravention to Article 64 of the International Code of Botanical Nomenclature (Voss et al. 1983), the name is illegitimate.

BUMELIA dominicana Whetstone & Atkinson, nom. nov. *Dipholis ferruginea* Ekman & O.C. Schmidt, Feddes Repert. Spec. Nov. Regni. Veg. 32:94. 1933. *Bumelia ferruginea* (Ekman & O.C. Schmidt) W.T. Stearn, J. Arnold Arbor. 49:287. 1968. ~~non~~ Nuttall (1849).

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TAXONOMIC AND NOMENCLATURAL
NOTES ON *VACCINIUM* L.
SECTION *CYANOCOCCUS* (ERICACEAE)

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ABSTRACT

Vaccinium simulatum Small is lectotypified, author citation for *V. atrococcum* Heller is corrected, and the type locality of *V. corymbosum* is restricted.

In studying the genus *Vaccinium* L. (Ericaceae) in Virginia and West Virginia, the following taxonomic and nomenclatural details were discovered which seem expedient to publish in advance of the regional treatments.

1. *VACCINIUM SIMULATUM* Small, Fl. Southeastern U.S. 896, 1336, 1903. SYNTYPES: KENTUCKY. Harlan Co.: Big Black Mountain, Aug 1893, Kearney s.n. (LECTOTYPE, here designated, NY, photo neg. no. 11894 NY!). VIRGINIA. Grayson Co.: slopes of White Top Mountain, alt. 4500 ft., 20 May 1892, Britton, Britton, and Vail s.n., (NY, photo neg. no. 11892 NY!).

The lectotype is a fruiting specimen, the paratype is a specimen just past anthesis. The corollas of sect. *Cyanococcus* A. Gray are of limited taxonomic usefulness, whereas the berry of this species is distinctive: shining purple-black, spherical, very juicy, tart. For this reason, the fruiting specimen was selected for the lectotype.

In describing *Vaccinium simulatum* from two dried specimens collected by others, Small gave flawed measurements for corolla (3.5–4.5 mm long) and berry (5–7 mm in diameter). In life, the cylindro-campanulate corolla is 5–6 mm long, and the berry 6–10 mm in diameter. Small also said the berry is "somewhat glaucous." I have visited the type locality where the species is still abundant and observed the berries are shining purple-black. A topotype specimen (*L.J. Uttal 13848*) in fruit is deposited in VPI, and it is planned for duplicates to be sent to NY, FLAS, GH, and NCU. On drying, the berries took on a bluish cast, as black berries of other *Vaccinium* species (i.e., *Vaccinium fuscatum* Ait.) sometimes do, which presumably caused Small to misinterpret the berry color. In case of a flawed description, the name is based upon the type specimen, bolstered in this case by topotypes. Occasional glaucous-berried specimens attributed to *Vaccinium*

simulatum may be attributed to introgression with *Vaccinium corymbosum* L. and *Vaccinium pallidum* Ait. In hybrid populations, fruit color may vary from purple-black to glaucous. *Vaccinium simulatum* is indigenous to the Cumberland Plateau, Cumberland Mountains, and middle elevations in the southern Appalachian, from southwest Virginia, eastern Kentucky, eastern Tennessee, western North Carolina and northern Georgia, at elevations from 250 to 1200 meters. It is a forest shrub of loamy soils of ridges and slopes, apparently more mesophytic than most highbush crown-forming species of sect. *Cyanococcus*. It is usually associated with maple forests (*Acer rubrum* L. or *A. saccharum* Marsh.), often with yellow birch, *Betula allegheniensis* Britt., *Hydrangia arborescens* L., and *Kalmia latifolia* L. The forb *Asclepias exaltata* L. is a very frequent edaphic partner of this species. For more detailed discussion of this species see Camp (1945).

2. *VACCINIUM ATROCOCCUM* Heller—correct author citation. *Vaccinium atrococcum* Heller, Bull. Torrey Bot. Club 21:24. 1894.

Vaccinium corymbosum var. *atrocarpum* Gray, Man. ed. 2. 250. 1856.

Vaccinium corymbosum var. *atrocoecum* Gray, Man. rev. ed. 250. 1857.

Correctly cited by Camp (1945), but ignored, the citation usually being *Vaccinium atrococcum* (Gray) Heller for almost a century. Even if Heller intended a recombination, he made an inadvertent species designation by not using the basionym, var. *atrocarpum*.

This name is considered synonymous with *Vaccinium fuscatum* Ait. *vide* Ward (1974).

3. *VACCINIUM CORYMBOSUM* L.—type locality.

Vaccinium corymbosum L., Sp. Pl. 1:350. 1753 (LECTOTYPE: *Kalm s.n.*, "North America," LINN, microfiche no. 497.6!). The type sheet of *Vaccinium corymbosum* bears two elements: (1) a leafy summer branch and (2) a spring branch in anthesis, just leafing out. Vander Kloet (1980) lectotypified the name by the second element, which he described.

Pehr Kalm resided in Raccoon (now Swedesboro), Gloucester County, New Jersey, in the springs of 1749 and 1750 (Benson, 1937). The lectotypified specimen is in the condition one would expect in May in New Jersey. The summer specimen was obtained either in Canada in 1749 or in western Pennsylvania or western New York in 1750. It thus seems safe to restrict the type locality of *V. corymbosum* to the vicinity of Swedesboro, Gloucester County, New Jersey, May 1749 or 1750. This restriction of type locality is considered important because the lectotype is of a morphology common in the northeastern United States and adjacent Canada, not found in the southern states except in the mountains, a point to be considered by

students of the taxonomy of the highbush species of *Cyanococcus* of the southeastern United States.

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Thanks are due P. K. Holmgren, of the New York Botanical Garden, for furnishing me photographs of the type material of *Vaccinium simulatum*, and to the library staff of the Harvard University herbaria for furnishing copies of relevant literature.

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A NEW COMBINATION IN *HEDYOTIS* L. (RUBIACEAE)

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As a result of his continuing studies of *Houstonia*, Terrell (1985) proposed two new varietal combinations under *Houstonia nigricans*. These combinations are warranted if *Houstonia* is accepted as a distinct genus as Terrell contends (cf. Terrell 1959, 1975). Whether *Houstonia* should be recognized as a distinct genus or combined under *Hedyotis* is debatable. I feel that Fosberg (1941, 1941a, 1954), Shinnars (1949), and Lewis (1961, 1962) argue favorably for reducing *Houstonia* under *Hedyotis*. This is the position I have taken for the vascular flora of central Florida (Wunderlin 1982) and, unless convincing evidence is presented to the contrary, intend to maintain for the flora of Florida (in prep.). Thus, the following new combination in *Hedyotis* is required.

HEDYOTIS NIGRICANS var. **floridana** (Standley) Wunderlin, comb. nov.

Basionym: *Houstonia floridana* Standley, N. Amer. Fl. 32(1):36. 1918. *Hedyotis purpurea* var. *floridana* (Standley) Fosberg, Castanea 19:36. 1954. *Houstonia nigricans* var. *floridana* (Standley) Terrell, Phytologia 59:79. 1985.

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SHINNARS, L. H. 1949. Transfer of Texas species of *Houstonia* to *Hedyotis* (Rubiaceae). Field & Lab. 17:166-169.
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MILLEROCAULIS, A NEW GENUS WITH SPECIES
FORMERLY IN OSMUNDACAULIS
MILLER (FOSSILS: OSMUNDACEAE)

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ABSTRACT

Millerocaulis first used by Erasmus and mentioned by Herbst for Miller's previously proposed "*Osmundacaulis herbstii* group" is discussed and validated. *Osmundacaulis*, as now restricted, includes only members of Miller's "*O. skidegatensis* group." A new informal group "*O. boskingii*" is proposed for *Osmundacaulis* (sensu stricto) containing an adaxial crenate-shaped sclerenchyma mass in their leaf and/or petiole traces. New nomenclatural combinations include: *Millerocaulis amajolensis* (Sharma) Tidwell, *Millerocaulis beardmorensis* (Schopf) Tidwell, *Millerocaulis dunlopianii* (Kidston & Gwynne-Vaughn) Tidwell, *Millerocaulis estipularis* (Sharma, Bohra & Singh) Tidwell, *Millerocaulis gibbiana* (Kidston & Gwynne-Vaughn) Tidwell, *Millerocaulis guptai* (Sharma) Tidwell, *Millerocaulis hebeiensis* (Wang) Tidwell, *Millerocaulis herbstii* (Archangelsky & de la Sota) Tidwell, *Millerocaulis indica* (Sharma) Tidwell, *Millerocaulis kidstonii* (Stokes) Tidwell, *Millerocaulis kolbei* (Seward) Tidwell, *Millerocaulis patagonica* (Archangelsky & de la Sota) Tidwell, *Millerocaulis rajmahalensis* (Gupta) Tidwell, *Millerocaulis sahnii* (Mittre) Tidwell, and *Millerocaulis wadei* (Tidwell & Rushforth) Tidwell.

INTRODUCTION

The organ genus *Osmundacaulis* was established by Miller (1967) as the name of a new taxon, that he thought was a new name for the illegitimate later homonym *Osmundites* Unger (1854), non Jaeger (1827), but technically was not. In order to have been a new name for *Osmundites*, *Osmundacaulis* would have required the same type as *Osmundites*. However, Miller (1967, 1971) explicitly excluded Unger's type *O. schemnicensis* (von Petrko) Unger (treated in *Osmunda*), established a different type for *Osmundacaulis* [*O. skidegatensis* (Penhallow) Miller], and gave a validating description.

Osmundacaulis was instituted and named for petrified axes exhibiting general anatomical features of living members of the Osmundaceae, but because they differ anatomically from these members, they cannot be assigned to an extant genus of this family. Miller (1967, 1971) proposed three informal groups within *Osmundacaulis*: the "*Osmundacaulis herbstii* group," the "*O. brazilensis* group" and the "*O. skidegatensis* group." These groups were based upon distinctive anatomical features. These features in-

cluded the thickness of the xylem cylinder, the number of clusters of protoxylem cells in each trace as they departed from the xylem strands and the degree of differentiation of the inner and outer cortices.

The "*O. braziliensis* group," in which the axis lacks a definite sclerotic outer cortex and stipular wings, was proposed as the new genus *Guairea* Herbst. It was removed from the Osmundaceae and placed in the new family Guaireaceae (Herbst 1981).

The "*Osmundacaulis herbstii* group" was proposed as the new genus *Millerocaulis* by Erasmus in his unpublished doctoral dissertation (1978). Because this does not constitute effective publication, the generic name was not effectively published (Art. 29). Herbst (1981:37) accepted Erasmus' *Millerocaulis* but failed to validate it with a description (Art. 32.1). Therefore, *Millerocaulis* is validated here for the first time.

TAXONOMY

Millerocaulis Erasmus ex Tidwell

Fossil osmundaceous rhizomes, rarely arborescent axes, containing stem or stems surrounded by a mantle of leaf bases and roots. Stele ectophloic-dictyoxylic-siphonostele (Miller 1971) with a xylem cylinder approximately 15 tracheids thick. Leaf trace separates from the xylem cylinder with only one protoxylem cluster and often, but not always, lacks axillary sclerenchyma. Petiole bases stipulate and adventitious roots arise either singly or in pairs.

TYPE: *M. dunlopii* (Kidston & Gwynne-Vaughn) Tidwell (*Osmundites dunlopii* Kidston & Gwynne-Vaughn "*dunlopi*").

The generic name honors Dr. Charles N. Miller, Jr. of the University of Montana at Missoula for his contribution to our knowledge of the phylogeny of the Osmundaceae. The list of species assigned to *Millerocaulis* and their synonyms are as follows:

MILLEROCAULIS amajolensis (Sharma) Tidwell, comb. nov. *Osmundacaulis amajolensis* Sharma, Palaeontographica 140B:156. 1973.

MILLEROCAULIS beardmorensis (Schopf) Tidwell, comb. nov. *Osmundacaulis beardmorensis* Schopf, Can. J. Bot. 56:3034. 1978.

MILLEROCAULIS dunlopii (Kidston & Gwynne-Vaughn) Tidwell, comb. nov. *Osmundites dunlopii* Kidston & Gwynne-Vaughn, Trans. Roy. Soc. Edinb. 45(1):759. 1907 ("*dunlopi*"). *Osmundacaulis dunlopii* (Kidston & Gwynne-Vaughn) Miller, Contr. Mus. Paleo. Univ. Mich. [21:146. 1967 ("*dunlopi*"), nom. invalid. under Art. 33.2 - no page reference to basionym] 23:135. 1971.

Osmundites aucklandicus Marshall, Trans. and Proc. N.Z. Inst. 56:210. 1924.

- MILLEROCAULIS estipularis** (Sharma et al.) Tidwell, comb. nov. *Osmundacaulis estipularis* Sharma, Bohra & Singh, Phytomorphology 8:61. 1979 ("estipularis").
- MILLEROCAULIS gibbiana** (Kidston & Gwynne-Vaughn) Tidwell, comb. nov. *Osmundites gibbiana* Kidston & Gwynne-Vaughn, Trans. Roy. Soc. Edinb. 45(1):763. 1907 *Osmundacaulis gibbiana* (Kidston & Gwynne-Vaughn) Miller, Contr. Mus. Paleo. Univ. Mich. [21:146. 1967, nom. invalid. under Art. 33.2 - no page reference to basionym] 23:136. 1971.
- MILLEROCAULIS guptai** (Sharma) Tidwell, comb. nov. *Osmundacaulis guptai* Sharma, Palaeontographica 140B:154. 1973.
- MILLEROCAULIS hebeiensis** (Wang) Tidwell, comb. nov. *Osmundacaulis hebeiensis* Wang, Rev. Palaeobot. Palyn. 39:93. 1983.
- MILLEROCAULIS herbstii** (Archangelsky & de la Sota) Tidwell, comb. nov. *Osmundites herbstii* Archangelsky & de la Sota, Ameghiniana 3:135. 1963. *Osmundacaulis herbstii* (Archangelsky & de la Sota) Miller, Contr. Mus. Paleo. Univ. Mich. [21:146. 1967, nom. invalid. under Art. 33.2 - no page reference to basionym] 23:134. 1971.
- MILLEROCAULIS indica** (Sharma) Tidwell, comb. nov. *Osmundacaulis indica* Sharma, Palaeontographica 140B:157. 1973.
- MILLEROCAULIS kidstonii** (Stopes) Tidwell, comb. nov. *Osmundites kidstonii* Stopes, Ann. Bot. 35:55. 1921 ("kidstoni"). *Osmundacaulis kidstonii* (Stopes) Miller, Contr. Mus. Paleo. Univ. Mich. [21:146. 1967 ("kidstoni"), nom. invalid. under Art. 33.2 - no page reference to basionym] 23:136. 1971.
- MILLEROCAULIS kolbei** (Seward) Tidwell, comb. nov. *Osmundites kolbei* Seward, Geol. Mag., N.S.V. 4:482. 1907. *Osmundacaulis kolbei* (Seward) Miller, Contr. Mus. Paleo. Univ. Mich. [21:146. 1967, nom. invalid. under Art. 33.2 - no page reference to basionym] 23:136. 1971.
- MILLEROCAULIS patagonica** (Archangelsky & de la Sota) Tidwell, comb. nov. *Osmundites patagonica* Archangelsky & de la Sota, Ameghiniana 2(9):153. 1962. *Osmundacaulis patagonica* (Archangelsky & de la Sota) Miller, Contr. Mus. Paleo. Univ. Mich. [21:146. 1967, nom. invalid. under Art. 33.2 - no page reference to basionym] 23:136. 1971.
- MILLEROCAULIS rajmahalensis** (Gupta) Tidwell, comb. nov. *Osmundites rajmahalensis* Gupta, Proc. Ind. Sci. Congr. Varanasi, 55:428. 1968. *Osmundites rajmahalensis* Gupta, Palaeontographica 130B:174. 1970. *Osmundacaulis rajmahalensis* (Gupta) Sharma, Palaeontographica 140B:152. 1973.
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- MILLEROCAULIS wadei** (Tidwell & Rushforth) Tidwell, comb. nov. *Osmundacaulis wadei* Tidwell & Rushforth, Bull. Torrey Bot. Club 97:137. 1970.

OSMUNDACAULIS Miller emend. gen.

Emended diagnosis: Fossil osmundaceous axes, usually arborescent or erect, rarely rhizomatous; a xylem cylinder 25 or more tracheids thick dis-

sected into relatively high number of xylem strands; leaf trace strongly curved, protoxylem divides before leaving the stele; sclerenchyma usually in adaxial concavity of the trace; petioles stipulate, wings may or may not contain sclerenchyma strands; inner and outer cortical tissue well differentiated.

TYPE: *O. skidegatensis* (Penhallow) Miller (*Osmundites skidegatensis* Penhallow).

The "*Osmundacaulis skidegatensis* group" comprises a different taxon among the other members of the Osmundoideae. Thus with the formation of *Millerocaulis* and *Guaikea*, *Osmundacaulis* is reserved exclusively for members of the "*O. skidegatensis* group" (Herbst 1981). Therefore, *Osmundacaulis*, in a strict sense, consists of the species *Osmundacaulis skidegatensis* (Penhallow 1902) Miller, *O. atberstonei* (Schelpe 1956) Miller, *O. natalensis* (Schelpe 1955) Miller and *O. boskingii* Gould (1973).

The inner cortex of *Osmundacaulis* (sensu stricto) is wider than the outer. Among other members of the Osmundoideae, with the exception of *Millerocaulis wadei* (Tidwell & Rushforth 1970) Tidwell, the opposite condition is the case. The outer cortex of these other members of the Osmundoideae is very wide and the inner is thinner. In *M. wadei*, they are about equal in width. According to Miller (1971), cortical cylinders of nearly equal dimensions represent a primitive state, whereas, thicker outer and thinner inner cortices would be more advanced.

Further, two groups in *Osmundacaulis* (sensu stricto) are proposed. One of these groups would contain only *O. skidegatensis* (Penhallow 1902) Miller and the other, designated the "*Osmundacaulis boskingii* group," is represented by arborescent and rhizomatous taxa having crenate-shaped adaxial sclerenchyma mass in their leaf traces and/or petiole vascular strands. At present, these forms have been reported exclusively from the Southern Hemisphere and include *O. atberstonei* (Schelpe 1956) Miller, *O. natalensis* (Schelpe 1955) Miller and *O. boskingii* Gould. The crenate-shaped adaxial sclerenchyma in the trace is not present in *O. skidegatensis*. In this species, the sclerenchyma of the trace and petiolar vascular strand is a single mass connecting downward with similar cells in the pith (Miller 1971).

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REVIEW

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This paper back manual (9 3/8" × 12 1/2") was designed to aid woody plant identification in the east Texas forest region which takes in some 40 counties. It is profusely illustrated with line drawings of all 340 species as well as an illustrated glossary. The table of contents includes: Preface; Map of east Texas counties; Introduction; East Texas; Key to groups; Key to genera; Families, genera, and keys to species; Illustrated glossary; Literature cited; Index of common names and scientific names; Metric system of measurement. BLL.

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WOLFFIA PAPULIFERA THOMPSON (LEMNACEAE), NEW TO MICHIGAN

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ABSTRACT

Wolffia papulifera Thompson is reported for the first time from Michigan and LaPorte County, Indiana. An illustration of *W. papulifera* in flower and electron photomicrographs of its echinate pollen surface are included.

Two recent collections to the Morton Arboretum (MOR) herbarium of *Wolffia papulifera* Thomps. were new records for Michigan and LaPorte County, Indiana. Deam (1940) had reported it from Ohio, Indiana, Illinois, Kentucky, Tennessee, Missouri, Arkansas, and Kansas. Daubs (1965) monographed Lemnaceae and cited collections from Maryland, Florida, Louisiana, Illinois, Missouri, Kansas, Mexico, and Argentina. Other reports include it from Texas (Blake 1952) and Oklahoma (Correll & Correll 1975). In the most recent monograph of Lemnaceae (Landolt 1980), *W. papulifera* and *W. punctata* Grisebach (in part) are reduced to synonymy under *W. brasiliensis* Weddell. Now included in its distribution in North America also are Alabama, Massachusetts, North Carolina, Pennsylvania, and South Carolina.

Voss (1972) did not record it from Michigan nor did Swink and Wilhelm (1979) record it from the seven Indiana counties and one Michigan county of the Chicago region flora. Deam's Indiana record of *Wolffia papulifera* was from Posey County in the extreme southwest corner of the state. Lake County, Illinois (Mohlenbrock & Ladd 1978) was the nearest known locality to Michigan and northwestern Indiana until the Morton Arboretum accessioned its first record from Cook County, Illinois (J. Higgins, s.n. 1983). Under *W. papulifera* or *W. brasiliensis*, the state and county records are still valid. The collection data are:

MICHIGAN: Berrien Co.: Buttonbush swamp in NW quadrant of Bridgman interchange of I-94, 7 Sep 85, K. Drizt s.n. (MOR).

INDIANA: LaPorte Co.: Hudson Lake, ca 2 mi W of New Carlisle, 5 Sep 85, G. Wilhelm & K. Drizt 13082 (MOR).

Wolffia papulifera (sensu Daubs) and *W. brasiliensis* (sensu Landolt) is distinguished from the other species of *Wolffia* on the basis of its central conical papilla on the upper surface of the frond.

Both collections from Indiana and Michigan had plants that were in prime flower and here presented are illustrations of the relatively unknown flowers of *Wolffia*. The smallest known flowering plants are in this genus (Daubs 1965) and its flowers are equally as small. The plants are monoecious with a single stamen in the staminate flower and one pistil in the pistillate flower. Both flowers lack a perianth and are housed in a large central cavity. Six stages are shown (Fig. 1). The central papilla is evident in the vegetative and incipient flowering condition (A & B). In C, on top of the frond, is a round opening where the papilla was and through which the style with its slightly impressed, terminal stigma emerges. Often the anther sacs can be seen within the central chamber. In all cases examined, the style was exposed prior to the emergence of the stamen and always on the side toward the vegetative reproductive pouch or bud. The stamen emerged (D - F) after the stigma appeared to dry up slightly. Anthesis occurred by the breakdown of a line of cells across the top and between the two anther sacs, after which the sacs spread out laterally upon dehiscence (F). The fruit remains within the flower chamber, however, mature fruit was not evident in our material.

Anthers were dissected out of the plants and their anther sacs opened so as to examine pollen grains. They were measured with an ocular micrometer using a Zeiss Photomicroscope II. They varied in size from 26 - 28 μ , somewhat larger than the 18 - 22 μ reported by Daubs (1965). The surface of the pollen grains were examined with an ISI SX-40 electron microscope after they had been coated with gold-paladium in a Polaron Sputter Coater. Although the pollen are distorted due to their collapse in the vacuum, they are, as reported by Daubs (1965), echinate (Fig. 2).

An effort was made to obtain chromosome counts of *Wolffia papulifera*, however all the squashes of the anthers resulted in either microspores beyond the spore tetrad stage or fully developed pollen grains. It is not clear when microsporogenesis occurs but it must be very early in the development of the staminate flower. Chromosome counts are available for *Wolffia* (Landolt, 1980) based on somatic cells. For *W. brasiliensis*, the variation is extreme with $2n = 20, 40, 50, 60,$ and 80 .

ACKNOWLEDGMENTS

I would like to thank Gerould Wilhelm and Ken Dritz for making their collections of *Wolffia* available for study. The beautiful drawing of *Wolffia papulifera* was done by Nancy Bartels.

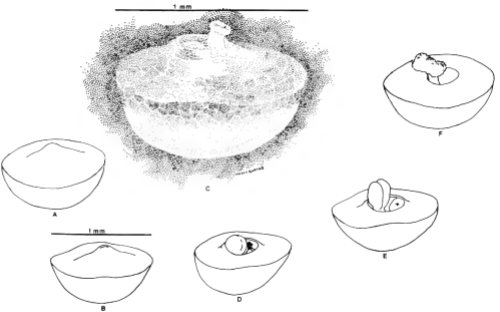


Fig. 1. A—E: *Ustilax papayifera* stages of flowering (Walden & Davis 1968). A: Vegetative plant. B: Incipient flowering. C: Receptive pistillate flower. D—E: Maturation of staminate flower. F: Anthesis.

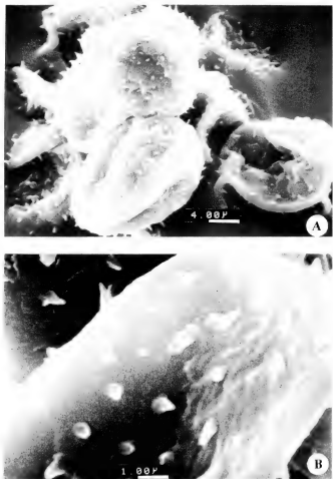


Fig. 2. SEM photomicrographs of pollen grain surface of *Walfia papulifera* (Dritz s.n.). A. Slightly collapsed echinate pollen grains (250 ×). B. Echinate surface of pollen grain (1000 ×).

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REVIEW

A NEW FERN MANUAL

LELLINGER, DAVID B. 1985. A field manual of the ferns and fern-allies of the United States and Canada. 389 pp., 26 figs., 402 color illustrations. Smithsonian Press, Washington, D.C. ISBN 0-87474-603-5 (pbk) and ISBN 0-87474-602-7.

This handsome book is a welcome addition to the popular fern-literature of North America, and will be useful in other parts of the North Temperate Zone. It is particularly valuable as a book written for an amateur audience, in popular and understandable language. However, it also seems critically attentive to accuracy in a field noted for its complexity, wide differences of opinion, and for much superficial popular writing.

The stated purpose of the work is to aid in identifying all of the species of ferns and fern allies that are native to or naturalized in Canada and the United States, excluding Hawaii. In carrying out this purpose it is eminently successful. Descriptions of taxa at the three principal levels, family, genus, and species, are clear and accompanied by discussion and explanation where necessary. Keys are of the "bracket" type, to save space, and they work, so far as I have tried them. Line drawings are provided to illustrate some technical terms in the excellent glossary. A map and diagrams clarify ideas that are unfamiliar to many. And 402 magnificent color photos mostly by A. Murray Evans are provided for visual recognition, as well as to display the beauty of ferns. The photos are small, to keep the cost of the book down, but beautifully reproduced, nine to a page, in three columns, the numbering, curiously, from right to left on the page.

The classification adopted, selected from a number of relatively recent ones available, is not the most conservative in number of families accepted, but neither is it the most extreme. Twenty families of ferns proper are admitted for the United States and Canada, about half of which are readily recognized. The others may require more experience than most amateurs possess. The family key is not easy to follow, but so far as I can see, it will, if carefully used, lead to the correct family. Some of the families are so technical that they are hard to recognize by aspect.

An outstanding feature of the book is its recognition and explanation of hybridity in ferns. The prevalence of hybridization in these plants has led to much confusion and description of questionable species. A careful study of the chapter on hybrid complexes will alert the user to this phenomenon.

The ample introduction should provide the beginner with an idea of the range and fascination of the study of these plants. The more advanced student will find many of his questions answered, too.

The only major suggestion for a second edition would be to include familiar synonyms. The almost total lack of synonyms in a work where much new nomenclature is used is frustrating. One cannot locate a plant that one knows by a former commonly used name except by guessing from its position in the book, unless one already knows the many recent changes in fern classification and nomenclature. In my own case, the only way I could locate what I grew up knowing as *Cheilanthes californica* was to look in the vicinity of the treatment of *Cheilanthes*, where I found *Aspidotis californica*.

All in all, one can recommend this book as the best available popular treatment of American ferns, and it is also useful to the more botanically trained non-pteridologists.

F.R. Fosberg

A NEW VARIETY OF *HEDEOMA HYSSOPIFOLIUM* GRAY (LAMIACEAE)

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ABSTRACT

Disjunct populations of *Hedeoma byssopifolium* from northeastern Chihuahua and western Coahuila differ from Arizona and southwestern New Mexico populations in their more erect, nonrhizomatous stature, more angular stems with vestiture restricted to decurrent lines, larger inflorescences, shorter, nonciliate lower calyx lobes and are recognized as *Hedeoma byssopifolium* var. *chihuahuensis* Henrickson.

During preparation of the treatment of Lamiaceae for the Chihuahuan Desert Flora it became apparent that the disjunct populations of *Hedeoma byssopifolium* from northeastern Chihuahua and adjacent Coahuila differ in a number of substantial characters from populations of central and southeastern Arizona and adjacent New Mexico, and Sonora. The Chihuahuan Desert populations are described below as a distinct variety.

HEDEOMA HYSSOPIFOLIUM Gray var. *chihuahuensis* Henrickson var. nov.

A. H. byssopifolis var. *byssopifolis* caudice bene evoluta superficiali (non subterraneo, non polyrhizomifero), internodiis mediacaulinis folia longioribus (non brevioribus), caulibus quadrangularibus (non rotundato-quadrangularibus), dichasio axillari (1-3-7(-13)-floro (non 1(-3)-floro), calycis lobis superis acicularibus, rectis vel debile sursum arcuatis (non angustideltoideis et valde recurvatis) lobis inferis 1-2.2 mm longis debile ciliatis (non (1.4-)2.2-3.3 mm valde ciliatis) differt.

Erect-ascending suffrutescent herbs 2.5-4(-6) dm tall developing from a woody crown; stems several from base, unbranched or rarely branched in inflorescence; lower internodes 5-10 mm long, mid-stem internodes (12-) 17-26 mm long, 0.7-1.3 mm wide, upper stem internodes 3-10 mm long; stems glabrous or hirtellous with erect hairs 0.05-0.15 mm long in decurrent lines below nodes, quadrangular, shallowly sulcate on surfaces alternate to leaves. Leaves linear-lanceolate, (8-)15-26 mm long, 1-2 mm wide, acute at tip, cuncate at sessile base, entire, glabrous, firm, erect-ascending, shorter than nodes, smooth above, with medial and lateral veins slightly raised, straight and with sunken glands beneath; leaf margins not forming an interpetiolar rim across nodes. Flowers borne in upper fourth of plant in paired, axillary, (1-3-7)-flowered dichasia,

with lateral branches sometimes proliferating monochasially producing up to 13 flowers per inflorescence; bracts and bracteoles leaf-like in shape and texture; bracteoles 1–2.5 mm long, usually longer than peduncles; peduncles 0.5–1(-3); pedicels 1.5–2.5(-7) mm long, both short hirtellous; calyx tubes cylindrical, slightly tapered at base, slightly ampliate, 4.5–6.8 mm long, strongly ribbed, glabrous to short hirtellous; upper 3 calyx lobes acicular, 0.5–1.2 mm long, mostly straight or very slightly curved upward, lower calyx lobes acicular, 0.9–2.2 mm long, weakly ciliate with hairs to 0.1 mm long; calyx annulus at orifice of throat, hairs 0.5–0.7 mm long; corollas lavender to pink, 10–13 mm long, tube straight, slightly ampliate above, upper lobe erect, emarginate, lower 3 lobes spreading, middle lobe longest, emarginate; filaments 3–4 mm long, anthers 1.0–1.1 mm wide (fig. 1a–e).

TYPE: MEXICO. CHIHUAHUA: road from Castillon to Mula, via S. Salvador and Piramide, basaltic cliffs near Virulento, crevices of cliffs, 8–24 inches tall, corollas pinkish, 21–22 Sep 1940, I. M. Johnston & C. H. Muller 1432 (HOLOTYPE: LL; ISOTYPE: GH).

Additional collections: MEXICO. COAHUILA: Cañon del Indio Felipe, a deep wooded canyon with running water in the igneous Sierra Hechiceros, close to the Chihuahuan bountry; crevices in cliffs, abundant, fls. lavender, 27–29 Sep 1940, R. M. Stewart 80 (GH, LL); same area; crevices of cliffs, not abundant, flowers lavender, 27–29 Sep 1940, R. M. Stewart 153 (GH, LL); Sierra de Hechiceros: Canyon del Indio Felipe, (beyond Puerto del Aire) from Rancho El Tule; crevices of cliffs in deep canyon, corolla lavender, 18 Sep 1940, I. M. Johnston & C. H. Muller 1352 (LL).

Hedeoma byssopifolium var. *chihuahuensis* appears restricted to rocky crevices of cliffs in margins of mesic canyons in igneous mountains (Sierra de Hechiceros, Sierra del Virulento) in the Northern Chihuahuan Desert. These populations lie some 550 km southeast of the nearest populations of *H. b.* var. *byssopifolium* in the Animas Mountains in southwestern New Mexico (A. Zimmerman pers. comm.). Irving (1980) notes *Hedeoma b.* var. *byssopifolium* is common in mountains of central and southeastern Arizona and adjacent southwestern New Mexico and Sonora from 1800 to 3100 m where it is most frequent in recently burned areas.

Hedeoma byssopifolium var. *byssopifolium* differs from the above in a wide series of characteristics involving habit, stems, inflorescence development and calyces. While the new variety is an erect-ascending plant 2.5–4(-6) dm tall that grows from crevices in cliffs from a distinct woody crown (fig. 1a), the type variety is a shorter (15–25 cm tall), more delicate, widely spreading plant with stems developing from a system of slender, rhizomes that grow in the forest detritus layer (fig. 1f). Stems are decumbent, often rooting at the nodes, more slender (0.5–0.8 mm in diameter), more even-

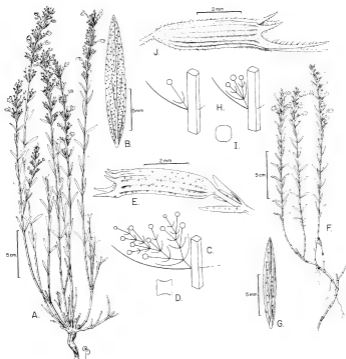


Fig. 1. *Hedone hysopifolia*. a-c.—*H. b.* var. *chibuabensis*. a. Habit of type specimen showing woody, basal rootstock, erect-ascending leaves shorter than internodes, and dense cymes of flowers in upper stems. b.—Leaf, abaxial surface showing venation and punctate glands. c.—Diagram of well branched inflorescence showing bracts and monochasial lateral proliferation. d.—Stem cross section, ca 1.0 mm in diameter, showing quadrangular outline and trichomes limited to decurrent lines below nodes. e.—Calyx with bracts showing short, straight upper and lower lobes. All from J. M. Johnston and C. H. Muller 1432 (LL). f-j.—*H. b.* var. *hysopifolia* T.—Habit, note slender rhizomatous rootstocks, slender stems with internodes shorter than leaves and paired flowers at upper nodes. Plants are more extensive, with more stems than shown. D. A. Young 529, (RSA). g.—Leaf, abaxial view showing venation and punctate glands. h.—Diagram of inflorescences showing solitary vs. 3-flowered structure. i.—Cross section of stem ca 0.6 mm in diameter showing rounded-quadrangular nature and trichomes on all surfaces. j.—Diagram of calyx showing longer, distinctly ciliate lower lobes. g-h from M. E. Joss 4330 (TEX). Magnifications as indicated. Delineation by Bobbi Angell.

ly hirtellous to puberulent with straight or recurved hairs 0.06–0.15 mm long, more rounded-quadrangular (fig. 1i) rather than abruptly quadrangular and petiolar margins continue as a distinct shallow rim across the nodes. Mid stem internodes in the type variety are only (3-)6–11 mm long, shorter than the subtending, (7-)11–18 mm long leaves. Flowers in the type variety are borne in 1(-3)-flowered, axillary, secund dichasia (fig. 1h) while in the new variety dichasia more often contain 1(-3)–7 flowers, and when lateral dichasial shoots proliferate in a monochasial pattern as many as 13 flowers may form per inflorescence (fig. 1c). Several conspicuous differences occur in the calyces. In the type variety the upper 3-calyx lobes are broad at the base and taper to slender tips, the lobes are distinctly recurved, and 0.8–1.2(-1.4) mm long (fig. 1j). In the new variety the lobes are more slender at the base, straight or only slightly upcurved, and only 0.5–0.9(-1.2) mm long (fig. 1e). Lower calyx lobes of the type variety are straight, mostly 2.2–3.2 mm long, and rather conspicuously ciliate with hairs 0.1–0.5 mm long (fig. 1j) while in the new variety they are only 1–2.2 mm long and obscurely ciliate (fig. 1e). Calyx annulus is slightly better developed in the type variety with the hairs measuring 0.6–0.9 mm long but in both the hairs are exserted. Other minor differences occur in vestiture, with the new variety tending to be more glabrous.

Irving (1980) in his excellent monograph of *Hedeoma* noted that populations of eastern Chihuahua differed from western populations in their glabrous stems, subulate-filiform calyx teeth, and sparse calyx annulus and was perhaps deserving of varietal status. In describing the taxon for a monograph the few disjunct eastern Chihuahuan specimens, while different, can be generally fitted within *Hedeoma byssopifolium* with which they are most closely related. But when preparing a treatment for the Chihuahuan Desert flora the consistency of the many differences become very apparent thus necessitating the nomenclatural recognition of these populations.

ACKNOWLEDGEMENTS

I thank M. C. Johnston (TEX) for the Latin diagnosis, Bobbi Angell (NY) for the illustration, Robert S. Irving for comments on the manuscript, and the University of Texas Plant Resources Center (TEX) for use of facilities.

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SABAL ETONIA (PALMAE): SYSTEMATICS,
DISTRIBUTION, ECOLOGY,
AND COMPARISONS TO OTHER
FLORIDA SCRUB ENDEMIC¹

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A taxonomic study of *Sabal etonia* Swingle ex Nash and related taxa (involving field work throughout Florida along with the study of more than 800 herbarium specimens) has shown that this palm is morphologically and ecologically distinctive and most closely related to *S. palmetto* (Walt.) Lodd. ex J. A. & J. H. Schultes and *S. miamiensis* Zona (see Zona 1983). *Sabal etonia* differs from the more widespread *S. palmetto* in its usually subterranean trunk (vs. erect and aerial), crown of usually only 3–5 leaves (vs. 14–40), narrower petioles (ca 0.6–2 vs. 2–4 cm), blades with fewer segments [20–46(-56) vs. 44–80(-90)], shorter median leaf segments [32–66(-69) vs. (55-)60–110(-120) cm], shorter hastulas [1–2.7 vs. (2.8-)3–13.3 cm], inflorescence structure (2 orders vs. 3 orders of branching), larger fruits (diameter usually 12–15 vs 9–12 mm), and larger seeds (diameter of usually 8–10 vs. 6–8 mm). *Sabal miamiensis* is intermediate between *S. etonia* and *S. palmetto* in most vegetative characters, but has a subterranean trunk like the former and three branch orders in its inflorescences like the latter; its fruits and seeds are typically larger than either species (see Zona 1985, for a detailed discussion of *S. miamiensis*).

The morphological character most obviously distinguishing *Sabal etonia* from *S. palmetto* is acaulescence. Authors of recent treatments of the flora of Florida (Long & Lakela 1976, Wunderlin 1982) have placed great emphasis on the above-ground trunk of *S. palmetto* versus the subterranean trunk of *S. etonia*. Usually, the trunk of *S. palmetto* is emergent and erect, but that of *S. etonia* is subterranean and sigmoid. An excellent illustration of the

¹This paper is Florida Agricultural Experiment Station Journal Series No. 7060.

peculiar trunk of *S. etonia* may be found in Bailey (1944). While these character states are typical for the species, they are by no means consistent. Occasionally, one encounters individuals of *S. etonia* with well developed emergent trunks. Bailey (1944) mentioned *S. etonia* in Marion County with six foot (ca 2 m) trunks; however, such individuals are encountered very infrequently in dry habitats (such as sand pine scrub). Individuals of *S. etonia* growing in more mesic habitats, such as those of coastal Volusia and Dade counties, also exhibit caulescence. These plants grow in what appears to be "mesic scrub," a scrub in the process of succession toward a mesic hammock (Kurz 1942). The short-emergent trunks of these individuals may be the result of mesic edaphic conditions. There also exist individuals of *S. palmetto* with only shortly emergent trunks to 1 m tall. Such individuals may be seen in dry coastal dunes such as those near Cedar Key (Levy Co.) or Merritt Island (Brevard Co.). There are also acaulescent to short-emergent plants on the Everglades pine keys of Dade County. These "stunted" plants also are likely the result of edaphic conditions. It appears that either excessively dry soil or a confined root system results in acaulescent or short-trunked *S. palmetto*. The morphological plasticity of these species has not been fully appreciated by many taxonomists.

The trunk of *Sabal etonia* is smooth, even on those plants with emergent trunks. The trunk of *S. palmetto* may be more or less smooth or clad with old leaf bases. The petioles, and consequently, the leaf bases are smaller in *S. etonia* as compared with those of *S. palmetto*.

As indicated above, the leaves of *Sabal etonia* are smaller on average than those of *S. palmetto*: the hastula and petiole are narrower and shorter, and there are fewer, shorter and narrower segments. The lamina of *S. etonia* and of *S. miamiensis* is characteristically yellow-green, but that of *S. palmetto* is slightly blue-green.

The inflorescence structure is variable and of taxonomic importance in the genus *Sabal*. Inflorescences of the group are axillary and enclosed by a series of open-ended tubular bracts which protect the primary axis of the inflorescence. The inflorescence of *S. etonia* is nearly erect, but as the fruits develop, it frequently becomes prostrate on the ground from its own weight. The branches of the inflorescence of *S. palmetto* are arrayed loosely along the main axis. There are three orders of branches (discounting main axis). In *S. etonia* the branches are crowded tightly on the main axis and are ascending, and there are only two orders of branches. Terminology used here, particularly that of axis enumeration, corresponds to Tomlinson & Zimmermann (1968).

Floral morphology varies very little among these species, and the taxonomic usefulness of floral features is not great. The petals of *Sabal*

etonia average 3.1 mm long, while those of *S. palmetto* average slightly shorter (i.e., 2.9 mm), and those of *S. miamiensis* slightly longer (i.e., 3.5 mm). However, fruit and seed size has proved to be of taxonomic value in the species complex. As indicated above, the fruits of *S. etonia* are intermediate between those of *S. palmetto* and *S. miamiensis*.

Sabal etonia is a member of the characteristic and highly endemic flora occurring on the white or yellow sands of the upland areas of the central "backbone" of the Florida peninsula. One of the most common plant communities in this region is the sand pine/xerophytic oak scrub (e.g., vegetation dominated by *Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg., *Quercus geminata* Small, *Q. myrtifolia* Willd., *Q. inopina* Ashe, and *Q. chapmanii* Sarg.). The species occurs in central Florida from Clay Co. south to Highlands Co. along the Trail Ridge, Mount Dora Ridge, and Lake Wales Ridge, and along the Atlantic Coastal Ridge from St. Lucie to Dade County (Figure 1). (See White 1970, for a summary of the geology of these ridges). In contrast, *S. palmetto* occurs from coastal North Carolina (Brunswick Co.) south through South Carolina and Georgia to northeastern Florida, throughout peninsular Florida, and in the Bahama Archipelago. This species shows a distinctive affinity for water. It is abundant in mesic to hydric hammocks, tidal flats, river banks, coastal strand and dunes, and pine flatwoods and savannas. The species is the canopy dominate in peninsular Florida's tidal flats just above the *Juncus roemerianus* Scheele zone. *Sabal miamiensis* is limited to the pinelands (i.e., *Pinus elliottii* Engelm. var. *densa* Little & Dorman) occurring on the oolitic limestone of the Miami region. Thus *S. etonia* is typically ecologically isolated from both *S. palmetto* and *S. miamiensis*.

The authors conclude that *Sabal etonia* is clearly distinct from both *S. palmetto* and *S. miamiensis* in both morphology and ecology. This study has demonstrated the unreliability of cauline characters in this complex. The morphology of adult leaves, particularly leaf number, lamina color, segment number, and hastula length, has proven taxonomically valuable. Inflorescence structure is also an important and useful character, as is fruit and seed size. No one morphological character is reliable enough to separate the three species due to the amount of overlap in the range of variation, however, *S. etonia* is clearly delimited from related taxa when a suite of characters is used. A summary of the nomenclatural synonymy along with a brief description and citation of representative specimens for *S. etonia* is given below.

SABAL ETONIA Swingle ex Nash, Bull. Torrey Bot. Club 23:99-100.

1896. TYPE: FLORIDA: vicinity of Eustis, 16-30 Jun 1894, Nash 999 (HOLOTYPE: NY!; ISOTYPES: BH!, GH!, MO!, US!).

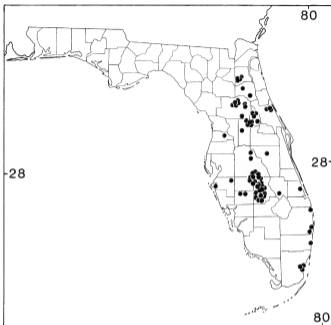


Figure 1. The distribution of *Sabal etonia*.

Sabal adansonii Guerns. var. *megacarpa* Chapm. Fl. South. U.S., 2nd ed. 651. 1883.

Sabal megacarpa (Chapm.) Small, Fl. SE. U.S. 223. 1903. TYPE: SOUTH FLORIDA: Garber s.n. (LECTOTYPE: MO!).

Plants usually acaulescent, rarely caulescent to 2 m, stems sigmoid, to 10–15 cm in diameter, or if upright, 15–20 cm in diameter. Leaves 3–5, usually yellow-green, costapalmate; petiole 23–55 cm long, 0.6–2(–2.1) cm wide; hastula triangular, 1–2.7 cm long, segments 20–46(–56), bifid, filiferous, 32–66(–69) cm long, 1.5–3 cm wide. Inflorescence paniculate, densely branched with two orders of branching (discounting main axis), upright at first then prostrate as fruits develop. Flowers subsessile, perfect, white, sweetly fragrant, protogynous; calyx three-lobed, 1–1.4 mm long, cup-shaped; petals three, 3–3.2 mm

long, ovate; stamens 6, the same length as the petals, connate slightly at the base and basally adnate to the petals; gynoecium composed of three fused carpels, 2.5–3.5 mm long; ovary superior, stigma papillose. Fruit a one-seeded berry developing from one carpel (rarely more than one carpel develops, the fruit is then a strongly lobed two- or three-seeded berry), globose, shiny black, (11-)12–15 mm in diameter with a fleshy pericarp; seed oblate, concave on the funicular end, brown, (6-)8–10(-11) mm in diameter, embryo sublateral, endosperm bony. (Figure 2, see also Bailey 1944, Small 1925).

Distribution and Ecology: Florida, from Clay Co. to Highlands Co. in the sand pine scrub of the Central Florida Ridge, also in the scrub on older coastal dunes of Volusia, St. Lucie, Palm Beach, Broward, and Dade counties, and in isolated patches of scrub in DeSoto, Hernando, Manatee, Okeechobee, and Seminole counties (Figure 1). Associated species are discussed by Harper (1914, 1915, 1927), Kurz (1942), and Mulvania (1931). Flowering occurs from late May through July.

Representative Specimens: UNITED STATES: FLORIDA. **Broward Co.:** Ft. Lauderdale, *Bailey 473* (BH). **Clay Co.:** Goldhead Branch State Park, *Shaw 850* (FLAS), *Ward 5490* (FLAS). **Dade Co.:** Miami, *Bailey 6472* (BH); North Miami, *Zona 68* (FLAS). **De Soto Co.:** west of Horse Creek, *Shaw 1853* (USF). **Highlands Co.:** Lake Placid, *Brass 33413* (USF); near Sebring, *Judd 2498* (FLAS); just west of Lake Jackson, *Judd 2846* (FLAS); without definite locality, *Small 11572* (NY); off U.S. Rt. 27, *Zona 10* (FLAS); south of Josephine Creek, *Zona 60* (FLAS). **Lake Co.:** near Eustis, *Nash 975* (US). *Savage 79* (BH). **Marion Co.:** near Salt Springs, *Judd 2774* (FLAS); Ocala National Forest, *Wunderlin, et al. 6549* (USF), *Zona 1* (FLAS). **Okeechobee Co.:** near Okeechobee City, *Bailey & Small 6211* (BH). **Osceola Co.:** east of Alligator Lake, *Shaw s.n.* 27 Oct 1974 (USF). **Palm Beach Co.:** Jupiter, *O'Neill s.n.* (FLAS, US); Boca Raton, *Zona 63* (FLAS); Boynton Beach, *Zona 104* (FLAS). **Polk Co.:** near Frostproof, *Judd 2840* (FLAS), *Zona 3* (FLAS). **Putnam Co.:** north of Florahome, *Wilson s.n.* 16 May 1959 (FLAS). **Volusia Co.:** near Ormond Beach, *Zona 31* (FLAS), *Zona 60* (FLAS).

Economic Uses: *Sabal etonia* is of potential ornamental use in areas where the edaphic conditions would permit its growth.

The sand pine/xerophytic oak scrub of the Central Florida Ridge supports many endemic species (Harper 1949, James 1961, Ward 1979). *Sabal etonia* is almost always found wherever there is scrub, and the taxonomy and distribution of this species may provide some insight into the probable origin of this and other scrub endemics. Noteworthy endemics of this region include: *Asclepias curtissii* A. Gray, *Bonamia grandiflora* (A. Gray) Heller, *Bumelia lacunum* Small, *Calamintha asbei* (Weatherby) Shinnery, *Carya floridana* Sarg., *Chapmannia floridana* Torr. & Gray, *Chionanthus pygmaeus* Small, *Clitoria fragrans* Small, *Conradina brevifolia* Shinnery, *Dicerandra frutescens* Shinnery, *Eriogonum floridanum* Small (*E.*

longifolium Nutt. var. *gnaphalifolium* Gandoger), *Eryngium cuneifolium* Small, *Garberia heterophylla* (Bart.) Merr. & Harper, *Hypericum cumulicola* (Small) P. Adams, *H. edisonianum* (Small) P. Adams & Robson, *Ilex opaca* Ait. var. *arenicola* (Ashe) Ashe, *Lechea cernua* Small, *Liatris oblongifera* (Blake) Robins., *Lupinus aridorum* McFarlin ex Beckner, *L. cumulicola* Small, *Nolina brittoniana* Nash, *Osmanthus megacarpus* (Small) Small ex Little, *Palafoxia feayi* Gray, *Paronychia chartacea* Fern., *Persea humilis* Nash, *Pityopsis graminifolia* (Michx.) Nutt. var. *aequilifolia* Bowen & Semple, *Polygala lewtonii* Small, *Polygonella basiramia* (Small) Nesom & Bates, *P. robusta* (Small) Nesom & Bates, *P. myriophylla* (Small) Horton, *Prunus geniculata* Harper, *Quercus inopina* Ashe, *Sabal etonia* Swingle ex Nash, *Sisyrinchium xerophyllum* Greene, *Stylisma abdita* Myint, *Warea amplexifolia* (Nutt.) Nutt., *W. carteri* Small, and *Ziziphus celtata* Judd & Hall.

An understanding of the origin of many of the scrub endemics is aided through a study of the distribution and morphological variation of the various endemics and their close relatives, an appreciation of past geological events in the area of endemism, and a knowledge of the region's edaphic and climatic conditions [see discussion of endemism in Stebbins (1942), Mason (1946), and Woodson (1947)].

The Central Highlands of the Florida peninsula, as they are called by Cooke (1945), are a series of disconnected ridges which may represent the remnants of a single ridge extending through Florida from Baker to Highlands County (White 1970). This geomorphological feature is now seen as a series of separate smaller ridges including the Trail Ridge to the north in Baker, Bradford, and Clay counties; the Mount Dora Ridge extending through eastern Marion, Lake, and Orange counties; and, by far the largest of the individual ridges, the Lake Wales Ridge of Lake, Orange, Osceola, Polk, and Highlands counties. McNeil (1949) showed that much of the land that is now the Trail Ridge and Lake Wales Ridge was exposed even during the Pleistocene interglacial periods when the sea level was considerably higher than its present level. In the Pliocene, portions of the Florida-Georgia border and probably portions of the ridges were above sea level (White 1970). Another ridge which is relevant to this discussion is the Atlantic Coastal Ridge which extends down the entire Atlantic coast but supports scrub only in its higher areas such as those found in Volusia, St. Lucie, Palm Beach, Broward, and Dade counties. In its southerly parts the Atlantic Coastal Ridge was formed from sand dune deposits overlaid on the Miami Ridge, a calcareous bar formed in Pamlico times (100,000 B.P.) and was submerged until very recently (White 1970). The areas of Florida that were exposed in the Pleistocene presumably were suitable for plant habitation. Watts (1969) noted that sclerophyllous oak pollen is well



Figure 2. Habite of *Sabal etonia*; photograph taken in Highlands Co., Fla.

represented in Pleistocene lake sediment in Marion County. Discontinuities in sedimentation suggest periods of time when the environment was drier than it is now. In addition, Watts (1975) reported that the fossil pollen record from a lake in Highlands County indicated a dominate scrub community in the Pleistocene.

The genus *Sabal* is well represented in fossil deposits in the southeastern United States (Daghlian 1978, Moore 1973, Read & Hickey 1974). Many of these deposits predate the formation of the land masses in Florida. The fossil record of *Sabal* suggests that it has long occurred in North America, and a refugium, similar to that suggested by Woodson (1947), may have been instrumental in the speciation of the genus in Florida. Moore and Uhl (1982) stated that dwarfism in palms is an evolutionarily advanced condition, so it is likely that *S. etonia* evolved from caulescent ancestors that colonized the ridges of Florida as they formed. *Sabal etonia* now inhabits some of the geologically oldest formations in Florida. However, the Atlantic Coastal Ridge is geologically recent and has been colonized successfully by *S. etonia*. Thus *S. etonia* is likely capable of invading new scrub habitats as they form.

Mason (1946) stated that the area occupied by any species is determined by environmental conditions and that, of the many factors contributing to the overall environment, only edaphic factors occur in sharply defined, often small areas. The soil of the central ridges of peninsular Florida is clearly extreme; Mulvania (1931) described the sand pine scrub inhabitants as "rooted in a bed of silica, to which the term soil is but remotely applicable." The soil underlying the scrub is a coarse white or yellow silica sand that extends to a depth of ca 3.5–4.5 m, and the scrub vegetation, including *Sabal etonia*, is found almost exclusively on these xeric sands. This specificity suggests that the distribution of *S. etonia* is the result of the limited occurrence of xeric white sands, and the species may have developed through selection in response to the extreme xeric environment of these sandy ridges.

Stebbins (1942) maintained that species with a great deal of genetic variability within populations are more likely to spread over large areas and many habitats than are species whose populations are genetically homogeneous. It is of interest that *Sabal etonia* is morphologically uniform, especially when compared with *S. palmetto*, a species found in many habitats throughout the southeastern United States and the Bahamas (Brown 1976, Zona 1983). Furthermore, Stebbins (1942) defined two different kinds of rare genetically homogeneous species: the "depleted species" and the "insular species." Depleted species are those which were once more common but their present rarity is due to depletion of the store of genetic variability. An insular species, which need not be found only on islands, is one which was never common but has diverged from a more widespread ancestor and has become established in a small insular or isolated area. Stebbins suggested that if the endemic is closely related to a widespread species, which occurs on an adjacent continental area, it is probably a strictly insular species, but if it is closely related to no other living species, or has its close relatives in a geographically distant region, it is more likely a depleted species. A second criterion given by Stebbins (1942) is that an insular species is typically morphologically and/or ecologically specialized in relation to its continental relatives. According to these guidelines *Sabal etonia* is clearly an insular endemic, and likely evolved from mesophytic, more widespread, *S. palmetto*-like ancestors. Many of the other characteristic scrub species also appear to be insular, e.g., *Asclepias curtissii* (related to *A. purpurascens*, Woodson 1954), *Chionanthus pygmaeus* Small (*C. virginicus* L., Hardin 1974), *Ilex opaca* var. *arenicola* (Ashe) Ashe (*I. opaca* var. *opaca*, Wunderlin 1982), *Osmantbus megacarpa* (*O. americana* (L.) Benth. & Hook. f. ex A. Gray, Hardin 1974), *Persea humilis* Nash (*P. borbonia* (L.) Spreng., Wofford 1973), *Polygonella basiramia* (*P. ciliata* Meisn., Nesom & Bates 1984), *P.*

robusta (*P. fimbriata* (Ell.) Horton, Nesom & Bates 1984), *Prunus geniculata* (*P. angustifolia* Marsh., Harper 1911), *Quercus inopina* (*Q. myrtifolia* Willd., Johnson & Abrahamson 1982). *Sabal etonia* is typical of these endemics. The ancestral species presumably inhabited the southeastern United States, and *S. etonia* shows the morphological specializations so typical of scrub endemics: dwarf stature, small leaves, large fruits, and large seeds (see Hardin 1974). These morphological features are likely adaptations to the xeric conditions of the sand pine scrub. Isolation, both in past refugia of emergent land masses and present-day "ecological islands," has preserved the genetically divergent biotypes of the scrub endemics. However, the floristic affinities of the scrub endemics are complex, and some [e.g., *Ziziphus celata* and *Nolina brittoniana* (Judd & Hall 1984), *Eriogonum longifolium* var. *gnaphalifolium* (Horton 1972), *Bonamia grandiflora* (Myint & Ward 1968), *Palafoxia feayi* (Turner & Morris 1976), and *Carya floridana* (Hardin & Stone 1984)], appear to have western affinities. Additional systematic studies of the endemic species of the Central Florida Ridge are urgently needed.

It is the unique combination of historical and edaphic features which makes the sand pine scrub habitat so rich in endemic species. The Florida peninsula, by virtue of its absence of glaciation, recent geological activity characterized by many fluctuations in its coastline, relative isolation from the remainder of the continent, proximity to the species-rich tropics, and unique climatic patterns, is an area which supports many endemics. Peninsular Florida is also being subjected to rapid urban and agricultural development, and the natural plant communities of the Central Florida Ridge are very rapidly being destroyed. At this time less than 3% of the total land area of the southern Lake Wales Ridge is currently protected from development (Peroni & Abrahamson 1985). For these reasons, action to preserve the distinctive flora of the Central Florida Ridge is essential.

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NOTES ABOUT PSORALEA SENSU AUCT.,
AMORPHA, BAPTISIA, SESBANIA
AND CHAMAECRISTA (LEGUMINOSAE) IN THE
SOUTHEASTERN UNITED STATES¹

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ABSTRACT

The classic *Psoralea* is presented as *Orbexilum*, *Pediomelum* and *Psoralidium*: *Pediomelum digitatum* (Nutt. ex T. & G.) comb. nov.; *Orbexilum pedunculatum* var. *eglandulosum* (Elliott) comb. nov.; *Orbexilum lupinellum* (Michx.) comb. nov. *Amorpha* essentially follows Wilbur's monograph: *Amorpha herbacea* Walter var. *crenulata* (Rydberg) comb. nov. *Baptisia lactua* (Raf.) Thieret (*B. leucantha* T. & G.) and *B. alba* (L.) Vent. of prior literature must change names; *Baptisia alba* var. *macrophylla* (Larisey) comb. nov. *Sesbania* concerns the delimitation of *Sesbania macrocarpa* and *S. emerus* (Aubl.) Urban, and the distribution of *S. virgata* (Cav.) Poit. in the United States. An author alteration for *Chamaecrista nictitans* var. *aspera* is noted.

This is one of several contributions in which rationale for floristic treatment of the Leguminosae for the Vascular Flora of the Southeastern United States (University of North Carolina) is presented.

GENERIC DELIMITATION IN THE PSORALEEAE:
ORBEXILUM, PEDIOMELUM AND PSORALIDIUM

Except for Rydberg (e.g. 1919–1920, and 1928) and the few other authors who followed him in floristic treatments (notably Small 1933), American authors have maintained a traditional, diverse *Psoralea* without generic segregation. Rydberg raised the traditional *Psoraleae* (spelled *Psoraleae* by authors prior to correction by Barneby 1977) from subtribal to tribal status and divided North American *Psoralea* into seven segregate genera. Isely (1962) accepted the first of Rydberg's premises, but not the second in that he maintained the U.S. species within the confines of a single genus. He felt that Rydberg's segregates represented, at least in part, natural groups but, because of the reticulate nature of variability, was unsuccessful in delimiting coherent sets on a multiple character basis.

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Since that time, the Psoraleae has been segregated into two tribes, the Amorpheae and Psoraleae (Barneby 1977, Stirton 1981). Stirton also divided the Old World representatives of the classic *Psoralea* into some five genera, *Psoralea* in this restricted sense being a small (ca 20 species) homogeneous group limited to South Africa. The circumscription of *Psoralea* is accepted (I do not pass judgment on the other Eurasian-African segregates), and therefore that name is not available for any American species. Were American "*Psoralea*" yet maintained as a single genus the available generic name would be *Orbexilum*.

Because of the evident diversity of the North American Psoraleae, and in connection with impending decisions for the SE Vascular Flora I have reexamined the problem with the hypothesis that fruit-calyx features (rather than foliage divergence for example) are the best markers for evolutionarily segregate groups and arrived at a classification that works at least for the region concerned. In stripped down key form, it is as follows.

1. Legume enclosed in the enlarging calyx except for the long, projecting beak; pericarp thin, commonly papery *Pediomelum*
1. Legume exerted above calyx remnants, shortly beaked; pericarp thick and coriaceous.
 2. Legume cross-rugose, eglandular *Orbexilum*
 2. Legume not cross-rugose, conspicuously glandular *Psoralidium*

This presentation is the same as Rydberg's except that his *Rhytidomene* is included in *Orbexilum* and (among southeast species) *Psoralidium digitatum* (that has enlarging calyx and long beak) is transferred to *Pediomelum*.

Because I have conducted no critical phylogenetic study of the American Psoraleae as a whole, this possibly should be regarded as a working arrangement for the immediate purpose of a coherent floristic interpretation. However, a study of New World Psoraleae, comparable to that of Stirton for Africa-Eurasia (*Cullen* to Australia), is presently underway by James Grimes of the University of Texas. The above generic segregation, within its limited context, seems approximately equivalent to his concepts.

Three new combinations resulting from these taxonomic decisions are listed under the subject genera.

PEDIOMELUM RYDBERG

PEDIOMELUM digitatum (Nutt. ex T. & G.) Isely, comb. nov. *Psoralea digitata* Nutt. ex T. & G., Fl. N. Amer. 1:300. 1838; *Psoralidium digitatum* (Nutt. ex T. & G.) Rydb., N. Amer. Fl. 24:16. 1919.

Although this species indeed superficially resembles some of *Psoralidium*, e.g., *P. tenuiflorum* (Pursh) Rydb., it has the fruit of *Pediomelum*.

ORBEXILUM RAFINESQUE

ORBEXILUM PEDUNCULATUM (Miller) Rydberg

Of the two varieties listed following, var. *pedunculatum*, the eastern Coastal Plain form, is usually glandular on all plant parts, conspicuously so on bracts, and the undersides of leaflets. Var. *eglandulosum*, lacking the glands or nearly so, is widely distributed from Texas and Oklahoma east into the Appalachians. Varietal segregation is not entirely "air-tight"; there is some intermediacy in the mountains and a few weakly glandular forms may be encountered farther west. But most material is clearly one or the other and it seems worthwhile to retain this now traditional varietal bifurcation despite, perhaps, its rather trivial nature.

ORBEXILUM PEDUNCULATUM (Miller) Rydb. var. PEDUNCULATUM, N.

Amer. Fl. 24:7. 1919. *Hedysarum pedunculatum* Miller, Gard. Dict. ed. 8. No. 17. 1768; non *Psoralea pedunculata* (Pursh) Poit. (1816) nec *P. pedunculata* Ker (1817).

Trifolium psoralioides Walt., Fl. Carl. 184. 1788; *Psoralea psoralioides* (Walt.) Cory, Rhodora 38:406. 1936.

As the above citations indicate, the familiar *Psoralea psoralioides* is lost on transfer to *Orbexilum* where the earlier epithet must be taken up. That the *Hedysarum pedunculatum* Miller is this species was verified for Freeman by C. A. Weatherby who, however, felt that it was a mixture of the two varieties (Freeman 1937).

Dr. C. E. Jarvis of the British Museum has kindly sent me a photocopy of the sheet of the Miller material that Weatherby examined. It includes the apices of two separate flowering stems that might or might not have come from the same plant. Both are easily, as Weatherby asserted, the now traditional *Psoralea psoralioides*. Dr. Jarvis kindly also examined the specimens and says "There are indeed numerous dark glands on the lower surfaces of the leaflets and bracts" thus contradicting Weatherby's assertion that the collection(s) includes a mixture of the two conventional varietal types.

While these specimens match the protologue, the secondary observations, i.e. "The seventeenth sort . . ." starts with the same subject but trails off into the statement that the flowers "are succeeded by jointed pods, straight on one side." In view of the fact that the specimen and diagnosis are confirmatory, it is reasonable to assume that Miller, perhaps writing his commentary at a later date, became confused about his subject, possibly then thinking of a *Desmodium*.

Dr. Jarvis has also noted that the specimen "bears on the verso the legend 'America septentrionalis' and was accordingly filed amongst the North American rather than amongst the cultivated material in our herbarium.

Miller clearly had material in cultivation, but I would not like to say whether this sheet was of cultivated or wild origin." Because of this ambiguity, I hesitate to designate the sheet as holotypic although I think it would be expedient to regard it in this light.

The British Museum also has a specimen in the Dale herbarium, presumably collected by Thomas Dale in South Carolina in 1730. It is almost an exact match for the Miller specimen.

ORBEXILUM PEDUNCULATUM var. **eglandulosum** (Elliott) Isely, comb.

nov. *Psoralea eglandulosa* Elliott, Skerch Bot. S. Carolina 2:198. 1822; *Psoralea psoralisoides* var. *eglandulosa* (Elliott) Freeman, Rhodora 39:426. 1937.

Freeman (1937) made no reference to Elliott's original material, and I have not had an opportunity to see it (if extant). Identification, however, seems evident from the protologue.

ORBEXILUM lupinellum (Michx.) Isely, comb. nov. *Psoralea lupinella* Michx.,

Fl. Boe. Amer. 2:58. 1803; *Rhytidonene lupinellus* (Michx.) Rydb., N. Amer. Fl. 24:12. 1919.

Orbexilum, though predominantly of species with pinnately trifoliolate leaves, as *O. pedunculatum* and *O. simplex* (Nutt. ex T. & G.) Rydb., includes *O. lupinellum* with linear-filiform, palmately foliolate leaves and *O. virgatum* (Nutt.) Rydb. with simple leaves. They all have the same fruit type. Michaux's protologue of *Psoralea lupinella* is explicit as to the identity of his material.

AMORPHA L.

I follow Wilbur's admirable revision (1964, 1975) of an amorphous genus except for reduction of a couple of taxa, noted following, in the dwarf *A. herbacea* complex. The major problems, however, are not with the so-called dwarf group. They are instead with the segregation of *A. fruticosa* and its immediate relatives. These include all of the remaining species save *A. schwerinii* Schneider, *A. paniculata* T. & G. and *A. californica* Nutt. Herein the omnipresent *A. fruticosa* not only overlaps with the others in its geographic range, but also in its plethora of variability (in pubescence, number of leaflets, the level and type of exertion of the leaflet midrib, calyx lobe length, level of glandular development on all plant parts). I follow Wilbur because I believe the species that he delineated from the overlying blanket of *A. fruticosa* represent real entities, although it is possible that some of the southwestern (e.g. Texas, Arkansas) segregates should be considered peripheral varieties. Also, among those I have recently studied, I find that I cannot always confidently distinguish some

specimens, e.g. of *A. glabra* Poir., *A. nitens* Boynton, and *A. onachitensis* Wilbur from *A. fruticosa*. I believe that the problem is not hybridization, rather that the evident exomorphic features are less than consistently diagnostic, and that perhaps we have yet to discern characters that clearly differentiate the taxa.

AMORPHA HERBACEA Walter and *A. CRENULATA* Rydb.

I confirm Wilbur's lucid (1964, 1975) characterization of geographic-morphological variation in this complex that includes the relatively wide-ranging and variable *Amorpha herbacea*, North Carolina to Lake Co., Florida and *A. crenulata*, a monotype in Dade Co., Florida.

Amorpha herbacea is normally conspicuously pubescent, but the typical form fades to thinly hairy in various parts of the range, and to glabrate in two disjunct areas in Florida, specifically Hillsborough and contiguous counties, and separately in Franklin and Wakulla counties in the Panhandle. The glabrate forms are the basis of var. *floridana* (Rydb.) Wilbur. Because pubescence is a quantitative feature that is regionally variable, I prefer to regard the glabrous forms as local extremes and withdraw var. *floridana* from nomenclatural listing. The name is, of course, available for those who wish to call attention to glabrate forms.

Amorpha crenulata, exclusively of Dade Co., Florida, differs, in Wilbur's analysis, from the glabrate forms of *A. herbacea* in that it is usually white-flowered and that the revolute margins of its leaflets are slightly crenulate. But I have seen white-flowered forms of *A. herbacea*, and the flowers of *A. crenulata* (as to herbarium labels) may range to pale lavender. Wilbur (1964) called *A. crenulata* a "weakly differentiated species," and I reduce it to a slightly isolated variant of *A. herbacea* as follows.

- Plants conspicuously pubescent to almost glabrous; leaflets usually 1.8-3 times as long as wide, entire or subcrenulate, petioluled 1-1.5 mm; flowers blue-purple (-white) var. *herbacea*
 Plants glabrous; leaflets mostly 2.8-3.5 times as long as wide, usually evidently crenulate along the incurved (revolute) margin, usually petioluled 1.5-2 mm; flowers white (-lavender) var. *crenulata*

AMORPHA HERBACEA Walter var. *crenulata* (Rydb.) Isely, comb. nov. *A. crenulata* Rydb., N. Amer. Fl. 24:30. 1919.

BAPTISIA VENTENAT

BAPTISIA LEUCANTHA - LACTEA - ALBA SEQUENCE.

The relatively common *Baptisia* with large, white flowers of the central states has traditionally been known as *B. leucantha* T. & G. The similar eastern plants were referred to the same species by Small (1933), but were

mostly relegated to *B. pendula* Larisey and *B. psammophila* Larisey in Larisey's (1940) monograph of the genus. Thieret (1969) identified Rafinesque's *Dolichos lacteus* with *B. leucantha* and took up *B. lactea* (Raf.) Thieret for the subject species. His determination was confirmed by Isely (1981) with reasonable assurance, and *B. leucantha*, therefore, was relegated to synonymy.

The name *Baptisia alba* (L.) Vent. has traditionally been applied to the eastern (primarily North Carolina to Georgia) white-flowered *Baptisia* that, though with entirely different fruits, considerably resembles *B. leucantha* (*lactea*) in flower except that the corolla is usually smaller. The identity of the Linnaean basionym (*Crotalaria alba*) has been assumed rather than definitively identified and Isely remarked (1981, p. 219) "*Crotalaria alba*... traces to 'Hort Cliff 499' and the associated specimen (BM). The specimen in LINN (microfiche!) marked by Linnacus as 'alba' lacks fruit and could be *Baptisia lactea*." But Isely had no opportunity to see the Hortus Cliffortianus material and indeed was happy to leave the reference of *B. alba* as it has been for over 150 years. That is no longer possible. For Turner (1982), in a critique of Isely's treatment, wrote that he had had opportunity with Stearn to examine the Hort. Cliff. specimen at the British Museum and that it was indeed the species that had been called *B. leucantha* and subsequently *B. lactea*. The consequences of the Turner-Stearn identification, sadly, result in a further scrambling of names for both of the white-flowered species. *B. leucantha*, recently to *B. lactea*, now becomes *B. alba* (L.) Vent. and the shift follows to the varietal names for the eastern and western components of that species because the Linnaean type (Habitat Carolina) is of the eastern rather than the western variety. And the prior *B. alba* of all U.S. treatments must become *B. albescens* Small. In the following listing only the names mentioned above and essential synonyms are cited; complete synonymy is given in Isely (1981).

BAPTISIA ALBESCENS Small, Fl. SE. U.S. 600, 1331. 1903.

B. albiflora Raf., New Fl. N. Amer. 2:47. 1837 sensu Merrill (1949).

B. alba sensu auct. pl.

Merrill (1949) identified the Rafinesque name with *Baptisia albescens* (as *B. alba*) but this determination is patently unwarranted because Rafinesque described the pods as obovate. *Baptisia albescens* has cylindrical pods while those of *B. alba* (= *B. leucantha*, *lactea*) are obovate. Furthermore the range given, "Carolina to Alabama and Louisiana," is impossible because *B. albescens* is exclusively an eastern species. Granting that Rafinesque might have had a mixture of the two, the reference to *B. albescens* is rejected.

BAPTISIA ALBA (L.) Vent., Dec. Gen. Nov. 9. 1808. *Crotalaria alba* L., Sp. Pl. 716. 1753.

Dolichos lacteus Raf., Fl. Lud. 102. 1817; *B. lactea* (Raf.) Thieret, Sida 3:496. 1969.
Baptisia leucantha T. & G., Fl. N. Amer. 1:385. 1840.

The identity of *Crotalaria alba* has been discussed in foregoing text. Eastern and western varieties of *B. alba* may be distinguished as follows:

Legume usually 1.5–2(-3) cm in diam., thin-walled and brittle (-thick-walled); eastern U.S.: North Carolina, south to northern Florida, west to Alabama var. *alba*
Legume usually 0.9–1.2(-1.5) cm in diam., rigidly coriaceous; central U.S.: Mississippi to eastern Texas, north to Minnesota, Wisconsin and Ohio var. *macrophylla*

BAPTISIA ALBA VBL ALBA

B. leucantha T. & G., Fl. N. Amer. 1:385. 1840 sensu authors in part.
B. pendula Larisey, Ann. Missouri Bot. Gard. 27:170. 1940.
B. psammophila Larisey, Ann. Missouri Bot. Gard. 27:180. 1940.
B. pendula Larisey var. *obovata* Larisey, Ann. Missouri Bot. Gard. 27:171. 1940; *B. lactea* Raf. var. *obovata* (Larisey) Isely, Brittonia 30:471. 1978.

BAPTISIA ALBA var. macrophylla (Larisey) Isely, comb. nov. *B. pendula* var. *macrophylla* Larisey, Ann. Missouri Bot. Gard. 27:172. 1940 as to type, nor Georgia citations.

B. leucantha T. & G., Fl. N. Amer. 1:385. 1840.
B. lactea (Raf.) Thieret, Sida 3:446. 1969 as to var. *lactea*.

SESBANIA SCOPOLI

This genus has been known under two similar names: *Sesban* Adanson, Fam. 2:327, 604. 1763 and *Sesbania* Scopoli, Introd. 308. 1777. The fact that they were once considered orthographic variants, but are now treated as different names, *Sesbania* being conserved over the earlier *Sesban*, has produced some interpretational problems in author citation of several species that are listed in both genera.

SESBANIA MACROCARPA Muhl., Cat. 65. 1813; also Muhl. ex Nutt. Gen. 2:112. 1818; also Muhl. ex Elliott, Sketch Bot. S. Carolina 2:221. 1822.

Darwinia exaltata Raf., Fl. Ludoviciana 106. 1817; *Sesban exaltatus* (Raf.) Rydb., N. Amer. Fl. 24:204. 1924; *Sesbania exaltata* (Raf.) Hill, Index Kewensis, Suppl. 7: 223, 1929 (of authors); *Sesbania exaltata* (Raf.) Cory, Rhodora 38:406. 1936.

Sesbania macrocarpa is an abundant weedy species that ranges in the southern United States from Florida to California. In vegetative condition and flower, *S. macrocarpa* resembles *Glottidium vesicarium* (Jacquin) Harper (this species is commonly treated as a *Sesbania*), which ordinarily has fewer

leaflets, considerably smaller flowers and a calyx that is but slightly toothed. It is easily known in fruit because, except for *S. emerus* (Aubl.) Urban and *S. sericea* (Willd.) Link of subtropical Florida, the linear pods are essentially unique among our herbaceous legumes. The *S. macrocarpa-emerus* problem will be discussed under the latter species following.

The flowers of *S. macrocarpa* are ordinarily yellow or mottled, but there is a race in western peninsular Florida (Bay and Santa Rosa counties) that has a conspicuously dark red standard.

Merrill and Hu (1949) regarded the Muhlenberg entry for *Sesbania macrocarpa* as a nom. nud. and attributed first validation of the name to Elliott in 1822. Consequently the synonym *S. exaltata* has been taken up by many recent authors.

Muhlenberg (loc. cit.) listed two species under *Sesbania* as follows:

- rubr. 1. *platycarpa* broad-podded
- lut. 2. *macrocarpa* long-podded

These statements, contrasting both flower color and pod conformation of the two kinds, meet the minimum, technical requirements of a diagnosis. *Sesbania macrocarpa* is retained.

The synonym *Sesbania exaltata* (Raf.) Hill enters the literature under the presumption that Hill (then editor of *Index Kewensis*) made an inadvertent combination. This is not the case, the listing is *Sesbania exaltatus* Rydberg. Hill only corrected Rydberg's spelling.

SESBANIA EMERUS (Aublet) Urban, Repert. Spec. Nov. Regni Veg. 16: 149. 1919. *Aechynomene emerus* Aublet, Hist. Pl. Guiane 775, table des noms p. 1, 1775; *Sesban emerus* (Aublet) Britt. & Wilson, Sci. Surv. Porto Rico 5:395. 1924 (of Rydberg, N. Amer. Fl. 24:204. 1924).

?*Emerus herbacea* Miller, Gard. Dict. ed. 8. *Emerus* no. 3. 1768.

The differences between the herbaceous to suffrutescent *Sesbania emerus* and the ubiquitous, probably derivative United States annual, *S. macrocarpa* are of uncertain dimensions. On the basis of Antilles and Central American specimens and descriptions (e.g. Standley and Steyermark 1946; White 1980), *S. emerus* is a branched, presumably perennial or potentially perennial herb or a shrub 1–2(-5) m tall with larger flowers (corolla ca 15–20 mm long) than those usually possessed by *S. macrocarpa*.

In the United States, interpretations of these species and their distribution have been various. Rydberg (1924) listed both *Sesban emerus* of Florida and *Sesban exaltatus* (= *Sesbania macrocarpa*) "Missouri to Louisiana and Texas." Small (1933) postulated a similar distribution but said of *Sesban emerus*, "one of our very vigorous annuals," surely primarily with reference to *Sesbania macrocarpa*.

Long and Lakela (1971; subtropical Florida) reported only *Sesbania macrocarpa* without inclusion of *Sesbania emerus* as a synonym; Ward (1972) listed both species for Florida; and Wunderlin (1982; central Florida) included only *Sesbania emerus* "Disturbed sites. Frequent; throughout." *Sesbania macrocarpa* (as *Sesbania exaltata* (Raf.) Cory) was relegated to synonymy.

Thus, United States authors have reduced *Sesbania macrocarpa* to *Sesbania emerus* or ignored the latter (Long and Lakela), or attempted differentiation. Distinction, where attempted, as indicated both by descriptions and annotation of specimens seems to be entirely on the basis of flower size. Most Florida material seen has been identified as *Sesbania macrocarpa* (or by its synonym, *Sesbania exaltata*) except that a few specimens from the southern half of the peninsula with flowers more than ca 15 mm long are identified as *Sesbania emerus*.

Those United States plants that I tentatively take to be *Sesbania emerus* are of my own collections (ISC) from Key West where the species is not uncommon in ruderal areas. These plants are suffrutescent or woody, to 3 m tall, much branched and spring-flowering, i.e., blooming in April and abundantly fruiting by June. At least some *Sesbania emerus* from the Antilles are also spring-flowering. The large-flowered (corolla 15–20 mm long) specimens from peninsular Florida otherwise, which botanists have identified as *Sesbania emerus*, I presently consider to be the annual, often wand-like and fall-flowering *Sesbania macrocarpa*. Similar plants are occasional elsewhere in the United States. It is true that duration cannot always be determined from the specimens but, so far as discernible, the plants are not branched as are those of Key West, and all are late summer- or fall-flowering, typical of *Sesbania macrocarpa* throughout its range.

KEY DIFFERENTIATION IN SUMMARY

- A scarcely branched, annual herb, flowering middle to late summer; flowers 11–15(-20) mm long; a widely distributed and abundant weed across the entire southern U.S. *Sesbania macrocarpa*
 A branched shrub, flowering in the spring; flowers 15–22 mm long; Fla, Key West, and possibly farther north. *Sesbania emerus*

The name *Aeschynomene emerus* of Aublet is derived from a Plumier plate that I have not seen. Since Urban, who made the combination in *Sesbania*, published an extensive commentary about the Plumier taxa (Rep. Spec. Nov. Beih. 5:1–196. 1920), the identity may be reasonably assumed.

Britton and Wilson credited the combination *Sesbania emerus* to Urban; i.e., they only corrected the spelling to that of the earlier orthographic variant and did not claim authorship. It was Rydberg (1924) who initially assigned the combination to them.

But the epithet "emerus" possibly should be superseded by the earlier *Emerus herbacea* cited in synonymy above. Miller said, of his *Emerus herbacea*, "It was found growing in plenty in La Vera Cruz, New Spain by the late Dr. Houston, who sent me the seeds—which succeeded in the Chelsea garden." and this is verified by the annotations on the type specimen (Photo of type: photographs of Miller collections BH!) that I have examined. The specimen, which consists of pods and a few leaves, is either *Sesbania emerus* or *Sesbania macrocarpa*, but it seems impossible to tell which, and the name is therefore rejected.

SESBANIA VIRGATA (Cav.) Poit., Lam. Encyl. 7:129. 1806. *Aeschynomene virgata* Cav., Icon. Pl. 3:47, pl. 293. 1797.

Sesbania marginata Benth., Mart., Fl. Bras. 15:43. 1859.

Sesbania virgata, introduced from South America, is similar to the well known *S. drummondii* and *S. punicea* but the flowers are smaller and the fruit, the indehiscent *Daubentonia* type, lacks wings. United States specimens seen range from coastal Florida panhandle to southern Mississippi. Most of them, collected by Demaree in the vicinity of Ocean Springs, Harrison Co., Mississippi match South American *S. virgata* except that the flowers may be either red or yellow, whereas those of *S. virgata* are said to be yellow only. There is evident introgression between *S. drummondii* and the red-flowered *S. punicea* about Ocean Springs, and it is possible that *S. virgata* is also genetically affected by the latter species.

The preponderance of U.S. collections were initially identified as *S. marginata* Benth., possibly because Pierce (1942) felt that the original Cavanilles material of *Aeschynomene virgata* was *Glottidium vesicarium*. The identity of the Cavanilles plant (completely unlike the *Glottidium*, both as to description and plate) has been verified by Burkhart (1967).

CHAMAECRISTA (L.) MOENCH

CHAMAECRISTA NICTITANS VAR. *ASPERA* (Muhl. ex Ell.) Irwin & Barneby, Mem. New York Bot. Gard. 35:838. 1982. *Cassia aspera* Muhl. ex Ell., Sketch Bot. S. Carolina 1:474. 1817; *Cassia nictitans* var. *aspera* (Muhl. ex Ell.) T. & G., Fl. N. Amer. 1:396. 1838.

Irwin & Barneby inadvertently attributed their combination to Torrey & Gray who published the equivalent trinomial in *Cassia*.

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AN UNDESCRIBED PANAMANIAN VACCINIUM: *VACCINIUM BOCATORENSIS* (ERICACEAE)

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Among the strikingly different species still being discovered along the relatively uncollected Caribbean slope of Panama is a vaccinioid unlike any previously described from Central America. In view of the recent attention played to this group of plants in Panama (Wilbur and Luteyn 1978, 1981), these continuing discoveries are surprising. They emphasize the need for critical collecting even in an area as intensively explored botanically as Panama, a country blessed with the most recent flora of any Central American nation as well as the most intensive collecting of any country in the area—a continuing program that reportedly has resulted in over 300,000 collections.

VACCINIUM bocatorensis Wilbur, sp. nov.

Frutex ut videtur epiphyticus, plus minusve scandens. Petioli 2–3 mm longi. Laminae foliorum coriaceae, integrae, ovatae vel ovato-ellipticae, 4–6.5 cm longae et 3.5–5 cm latae, apice rotundatae, basi rotundatae et cordatae, pinnatinerviae. Inflorescentia racemosa vel subcorymbosa; rhachis 2–5 cm longa, pilosula; bractae florales lanceolatae vel lanceo-ovatae, 3–6 mm longae; pedicelli puberulenti eglandulari, 10–15(20) mm longi. Calyx et hypanthium 7–10 mm longus et ca 6 mm diametro, cylindricus, pilosulus; lobi calycis 4–5 mm longi. Corolla carnea tuba cylindrica, glabra extra, tomentosa intra distalis; lobi corollae 2 mm longi et 2.5 mm lati. Stamina 5 mm longa; filamenta ca 2.5 mm longa, moderate vel dense sericea; antherae ca 3 mm longae, tubulis 2, 1–1.2 mm longis. Stylus ca 7 mm longus, glaber.

Reportedly an epiphytic, scandent treelet. Mature stems drying brownish, \pm terete; bark thin, longitudinally splitting. Leaves coriaceous, entire, ovate to ovate-elliptic, 4–6.5 cm long \times 3.5–5 cm wide, basally rounded and slightly cordate, apically \pm rounded, glabrous above and moderately but inconspicuously erect-pilosulose beneath with widely spaced, slender, hyaline trichomes 0.2–0.3 mm long, apparently eglandular; venation pinnate with 3 pair of lateral veins arising within 5–10 mm of the base, the midvein and secondary veins impressed above and elevated beneath but the tertiary venation not apparent; petiole 2–3 mm long, shortly puberulent adaxially, \pm glabrous abaxially. Inflorescence axillary but congregated distally and sometimes appearing

terminal, racemose to subcorymbose, 6–12-flowered, 3–7 cm long; rachis 2–5 cm long, \pm terete, moderately and inconspicuously pilosulose; floral bracts lanceolate to lance-ovate, acute to acuminate, sparingly puberulent to pilosulose externally, 3–6 mm long; bracteoles borne on the proximal third of the pedicel, lanceolate to lance-oblong, 4–6 mm long and 0.6–1.5(1.8) mm wide, adaxially glabrous and abaxially sparingly puberulent to pilosulose and marginally ciliate; pedicels terete, densely but inconspicuously puberulent with erect hyaline trichomes, striate, eglandular, 10–15(20) mm long and about 1 mm in diameter, articulate with the flower. Calyx (and hypanthium) 7–10 mm long and about 6 mm in diameter, inconspicuously and moderately pilosulose with spreading erect trichomes, "purplish red," the hypanthium broadly cylindrical, pilosulose and glandular-pustulate throughout, the calyx lobes narrowly triangular to lanceolate, spreading recurved or reflexed, 4–5 mm long and about 2–3 mm wide at base; corolla thick and fleshy, 7–9 mm long and 6–7 mm in diameter, externally glabrous, internally glabrous or very nearly so for the basal half and increasingly tangled pilose distally and the broadly deltoid lobes exceedingly densely matted tomentose and about 2 mm long and 2.5 mm wide at base, "livid red" externally; stamens about 5 mm long, the filaments very weakly connate basally, very much flattened and rather broad, about 2.5 mm long and medially about 0.5 mm wide, marginally and on both surfaces moderately to densely sericeous especially on the connective abaxially, the anthers golden, finely or moderately granular, about 3 mm long, strongly incurved basally, the tubules 2/anther and each 1–1.2 mm long, about as wide as the thecae, glabrous, dehiscent by obliquely introrse pores; style included, glabrous, about 7 mm long.

TYPE: PANAMA. Bocas del Toro: headwaters of Rio Colubre, 2400–2550 m (Colubre Camp), 3 Mar 1984, L. D. Gomez, I. Chacon, G. Davids & G. Herrera 22368 (HOLOTYPE: DUKE; ISOTYPE: MO).

Generic limits within the vaccinioid ericads are not as precise as might be implied or expected and the placement of this species is not above question. It is here placed in the genus *Vaccinium* because of certain resemblances in shape and pubescence of the corolla and of the androecium to such species as *Vaccinium poasanum* Donn. Sm., *V. floccosum* (L.O. Wms.) Wilbur & Luteyn and even *V. jefensis* Luteyn & Wilbur. At first glance it might equally be placed in the neotropical genus *Macleania* but its relatively short corolla and very short antherial tubules and finely granular thecae suggest a closer relationship with the very diverse genus *Vaccinium*. A broadly based reappraisal of generic limits within the vaccinioid ericads seems very much overdue, and until completed, generic placement will in

large part be rather speculative. In reference to this it should be noted that this species belongs in the same complex of species that has engendered a continuing debate as to the validity of the segregate genus *Symphysia* (Vander Kloet 1985).

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SCAEVOLA (GOODENIACEAE) IN SOUTHEASTERN UNITED STATES

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ABSTRACT

Two species of *Scaevola* (Goodeniaceae) occur in southeastern United States: *S. plumieri* (L.) Vahl, a native strand plant, and *S. sericea* Vahl, a shrub used as an ornamental and sparingly escaped and naturalized. Notes on biology, and keys to and descriptions of taxa, including two varieties of *S. sericea*, are given.

Two species of *Scaevola* (Goodeniaceae)—a genus of about 80 species—are littoral plants widely distributed in warm regions. The Indo-Atlantic *S. plumieri* (L.) Vahl (Fig. 1) occurs from Ceylon and India west through the Mascarenes (Guillaumet 1976) and eastern, southern, and western Africa (Somalia to Cape Province to São Tomé) (Davies 1978) to Florida, Louisiana, Texas, the West Indies, the Galápagos, and continental tropical America. The Indo-Pacific *S. sericea* Vahl (Fig. 2) is native from eastern Africa (Kenya, Tanzania, and Natal) (Davies 1978), Madagascar, the Mascarenes, and the Seychelles east through India, southeastern Asia, Malaysia, and tropical Australia to Melanesia, Micronesia, and Hawaii; it is naturalized elsewhere, e.g., in Florida and in the Bahamas (Correll and Correll 1982). Thus, as Guppy (1917) pointed out, the two taxa divide between them the tropical shores of the world.

Scaevola plumieri and *S. sericea* owe their wide distribution primarily to the ocean-current-dispersed stones of their fruits. The stones of *S. sericea* are buoyant because of a corky outer layer; in contrast, those of *S. plumieri* lack such a layer but usually have one empty, watertight locule (Brizicky 1966; Guppy 1906, 1917). Stones of the former species can float in sea water for at least a year (Guppy 1890, 1906, 1917); those of the latter, for only 4 or 5 months (Guppy 1917).

Fruits of *S. sericea* float with or without their fleshy outer layer; this portion, if not worn off by beach sand before the fruits reach the water, is



Figure 1. *Sarcola plumieri*: flowering-fruiting branch, $\times 1$; upper left, flower, adaxial view, $\times 2$.



Figure 2. *Scaevola sericea*: flowering-fruiting branch, $\times 1$; upper left, flower, adaxial view, $\times 2$.

said to disintegrate "during the early days of . . . immersion" (Guppy 1890). Fresh drupes of *S. plumieri*, upon getting into the sea, will, according to Guppy (1917), "sink in two days, the buoyant stone, on being freed from the decaying fruit, soon floating to the top," an observation somewhat at variance with ours. Drupes we placed in sea water on 23 July 1985 never did sink but remain, 15 months later, as buoyant as ever. The fleshy portion is still intact (but barely so), doubtless because the fruits have been in still water in a beaker rather than in the moving, often turbulent sea.

Lesko and Walker (1969) found that stones of *S. sericea* showed no "significant loss" in viability after 50 days of floating in sea water. Indeed, such fruits germinated 1–2 weeks sooner than dry ones when placed in non-saline environments.

Dispersal of the two taxa may also be accomplished by frugivorous birds. Indeed, the fruits seem as well suited for ornithochory as for hydrochory; Guppy (1917) and Schimper (1891) suggested the agency of birds for local dispersal, that of ocean currents for long distances. A note on a specimen of *S. plumieri* from Barbuda (*J. S. Beard* 367, GH) reads: "fruit said to be eaten by gulls" (Altschul 1973). Julia E. Morton (pers. comm.) was told in 1982 by D. S. Correll that, on Pine Key in the Caicos Islands, he watched seagulls devouring all the fruits on *S. plumieri*, coming in great flocks to feast on them. Millspaugh (1907), in his paper on the Florida Keys, stated that "the black, pulpy fruits of [*S. plumieri*] form a very attractive food for land birds; it thus becomes scattered far throughout the Antillean region." Louda and Zedler (1985) wrote that, among the four Pacific atoll species whose fruit and seed predation they studied, *S. sericea* (as *S. taccada*) had the highest rate of fruit disappearance, due to hermit crabs and, possibly, birds.

Scaevola sericea is apparently a recent introduction to the naturalized flora of Florida. It is mentioned as a plant "confined to the Eastern Hemisphere," but not as one cultivated or spontaneous in the southeast, by Brizicky (1966) and is absent from Long and Lakela (1971). It is not included in Shelter and Skog (1978) or in the "United States and Canada" section of *National List of Scientific Plant Names* (Soil Conservation Service, U.S.D.A. 1982) (it is listed, of course, in the "Hawaii" section). Kartesz and Kartesz (1980) listed the species—in four varieties—but there is no way to tell from their listing which, if any, of the varieties was known to them from conterminous United States as opposed to Hawaii, where all four varieties occur (Hawaiian plants are accounted for in the Kartesz and Kartesz work). Finally, the presence of the species—but only the sericeous variety—in Florida is acknowledged in Wunderlin's (1982) central Florida manual.

Scaevola sericea is cultivated as an ornamental in southern Florida, where its use is increasing. We have seen it as a hedge plant on Sanibel Island and on Key Biscayne. With its glossy, bright green leaves, its white to lavender flowers, and its white fruits, it is indeed attractive. The appearance of the fruits is recalled in one common name we heard for the plant, "hailstones" (see also Neal 1965).

In Florida, *S. sericea* spreads from cultivation—presumably by seeds—to nearby thickets, woodland borders, canal banks, and waste places, as on Sanibel Island. Its stones are obviously dispersed by ocean currents, too. For example, on the foredune near Marathon High School, Key Vaca, Monroe County, both varieties of *S. sericea* grow with *S. plumieri*—all certainly spontaneous—just 2 or 3 meters from waters of the Straits of Florida. We noted, on Key Biscayne, an individual of *S. sericea* var. *sericea* about 40 cm tall rooted in sand between beached sailboats on the upper strand; we suspect that it could have originated from a washed-up stone or from a fruit produced on a hedge of *S. sericea* about 100 m away. It certainly was *not* deliberately planted where it was growing.

The pollen-presentation mechanism of Goodeniaceae is an outstanding feature of the flowers (Brizicky 1966; Carolin 1960; Krause 1912; Kugler 1973). The style bears at its apex a pollen-collecting cup (or "cupular indusium") within which is the stigma. The anthers, more or less coherent, release their pollen introrsely while the flower is still in bud; the pollen collects in the cup as the style elongates. At anthesis, the enlarging stigma pushes at least some of the pollen out of the cup onto the trichomes of the cup's apex and exterior. Pollen from the cup and the trichomes is then dusted onto visiting insects (bees, wasps, beetles, and butterflies; perhaps only the first two mentioned are effective pollinators). The stigma finally becomes receptive after the pollen is all or mostly gone from the cup. Hairs of the cup then brush pollen off visitors, bringing it to the stigma.

The nomenclature of *S. plumieri* and *S. sericea* has been reviewed by Jeffrey (1980). It is hoped that his conclusion that *S. sericea* is indeed the correct name of this species will lay to rest the long-standing controversy and confusion over the matter.

Jeppesen (1981) wrote that *S. plumieri* and *S. sericea* (as *S. taccada*) are "very similar and . . . may prove to be one polymorphous pantropical species," a suggestion that seems to us untenable. The taxa are, at least in Florida, certainly easily separable. Guppy (1917) noted: "The two plants, as was evident to me when I first met *Sc. plumieri* in the West Indies, are quite distinct, and could not be mistaken by any one with both before him." To the other features that characterize the two should be added the

fact that *S. sericea* is frequently grown as an ornamental and *S. plumeri* is not—at least we have not seen it so, although the species is offered by at least one southern Florida nursery specializing in native plants. *Scaevola sericea* is propagated with ease by cuttings; *S. plumeri*, only with difficulty by this means (A. Sprunt, Jr., pers. comm.).

TAXONOMIC ACCOUNT

The account below follows, in general, the format established for *Vascular Flora of the Southeastern United States*.

SCAEVOLA L.

Evergreen, monoclinous shrubs. Leaves simple, alternate, often crowded at branch tips, blade tapering to a sessile or subpetioled base. Inflorescence cymose, axillary, bracteate. Flowers perfect, zygomorphic, epigynous; calyx of 5 sepals; corolla of 5 united petals, split to base adaxially, tube woolly inside, limb 1-lipped, spreading, resembling an outstretched hand, lobes more or less equal, narrowly ovate, apex acute, margins with thin, induplicate wings; stamens 5, free, the pollen subprolate to prolate, 3-colporate (Dunbar 1975; Moreira and Belem 1978); carpels 4 but appearing as 2 (Carolin 1959, 1966); stigma within a ciliate, pollen-collecting cup; style elongate; ovary inferior, 2-loculed, ovule 1 per locule. Fruit a fleshy drupe, 1–2 seeded.

Cyme with central flowers sessile, laterals pedicelled; calyx more or less obsolete to clearly 5-lobed, the lobes broadly ovate to broadly triangular, 0.2–1 mm long; drupe black

..... 1. *S. plumeri*
 Cyme with all flowers pedicelled; calyx 5-lobed, the lobes linear to narrowly obovate or narrowly elliptic, 3.5–5 mm long; drupe white to yellowish-white 2. *S. sericea*

1. *S. PLUMERI* (L.) Vahl. Beachberry, inkberry. Shrub 15–150 cm tall, often colonial; stems glabrous or essentially so, often glandular, the leaf axils white-pilose with hairs 0.5–2 mm long. Blades narrowly to broadly elliptic or obovate, 2.5–10 cm long, 0.5–5 cm wide, glabrous or nearly so, sometimes minutely glandular, apex rounded to obtuse, sometimes apiculate, margin entire. Cymes simple to 1-compound, or 1-flowered by reduction; central flowers sessile, laterals pedicelled. Calyx more or less obsolete to clearly 5-lobed, the lobes broadly ovate to broadly triangular, 0.2–1 mm long, glabrous, rounded to obtuse; corolla white to pinkish-white adaxially, pale greenish to pale yellowish abaxially, 1.8–2.4 cm long. Drupe subglobose to ellipsoid, 1–1.8 cm long, 1–1.6 cm wide, black. ($n=8$; Kausik 1939). Spring-fall. Coastal dunes and beaches; cp.

Fla (all coastal counties north to and including Hillsborough and Pinellas on the west coast and Brevard on the east); La (Jefferson Parish [Timbalier Island], where collected in 1937: *E. B. West 123*, LSU; Brown 1945); and Tex (Kleberg County, where collected in 1954: *F. B. Jones 1082*, SMU). The Louisiana and Texas (?) populations may be "one-time" introductions and possibly not persistent.

2. *S. SERICEA* Vahl. Beach naupaka, hailstones. Shrub 0.5–2 m tall (7 m maximum recorded in *Flora Malesiana*; Leenhouts 1957); stems glabrous or essentially so or lightly to heavily sericeous or glandular-sericeous, the leaf axils conspicuously white-pilose with hairs 1.5–7 mm long. Blades elliptic to spatulate or obovate, 4–21 cm long, 1.8–9 cm wide, often minutely glandular, apex truncate or slightly emarginate to obtuse, sometimes apiculate, margin entire to shallowly crenate. Cymes usually 2–4 compound; all flowers pedicelled. Calyx 5-lobed, the lobes linear to narrowly obovate or narrowly elliptic, 3.5–5 mm long, acute to obtuse; corolla white to pale lavender adaxially, pale greenish-yellow abaxially, 1.8–2 cm long. Drupe subglobose to ellipsoid, 1–1.7 cm long, 1–1.5 cm wide, white to yellowish-white. ($n=8$; Carr 1978; Skottsberg 1953). Spring-summer. Coastal dunes, beaches, woodland borders, thickets, canal banks, and waste places; cp. Fla [*S. frutescens* Krause; *S. koenigii* Vahl] The two taxa below are cultivated in Fla; both are sparingly escaped and extending their ranges as naturalized plants.

Leaves lightly to heavily sericeous (Fig. 3a) 2a. var. *sericea*
 Leaves glabrous or essentially so (Fig. 3b) 2b. var. *taccada*

2a. var. *SERICEA*. Stem lightly to heavily sericeous; inflorescence sericeous. Fla: Dade, Lee, and Monroe counties.

2b. var. *TACCADA* (Gaertn.) Thieret & Lipscomb. Stem glabrous or essentially so; inflorescence glabrous to sericeous. [*S. taccada* (Gaertn.) Roxb.] Fla: Monroe County.

The status of the infraspecific taxa of *S. sericea*, a most variable species, is subject to verification following study of the plant throughout its natural range.

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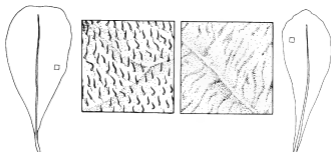


Figure 3. *Scariosa sericea*, leaves, showing vestiture: left, var. *sericea*, leaf, $\times 1/2$, inset, $\times 20$; right, var. *tucuala*, leaf, $\times 1/2$, inset, $\times 20$.

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The publication of *A Flora of New Mexico* (Martin and Hutchins 1980, 1981; for brevity cited as M&H from hereon) was a long awaited and welcome event. To have access to geographic ranges and nomenclature updated over the 65 years since the publication of the *Flora of New Mexico* (Wootton & Standley 1915) has been a stimulus to floristic research in the state and has allowed the easy determination of plant species here-to-fore unknown in New Mexico or in portions of the state. Also, since 1975 increased knowledge of the flora of New Mexico has resulted from vegetation studies concerned with the distribution of endangered or threatened plant species, from environmental impact studies, or both. In addition to the 79 records that we present here, at least another 138 are now scattered in the literature and are compiled in the Appendix to aid individuals who wish to identify plants from New Mexico or are interested in floristics of the Southwest. The taxa presented here add 8 genera, 43 species, and 9 subspecific taxa to the NM flora. Those given in the appendix bring the total taxa reported here and not recorded as present in NM by M&H to one family, 25 genera, 144 species, and 28 subspecies or varieties.

The following records are arranged in alphabetic order by family and genus. Those that represent taxa not recorded for the state in M&H are marked by an asterisk before the name of the taxon in this list or in the appendix; most of these are first records as indicated by specimen citations. Others are significant range extensions within the state. Abbreviations for

collectors are: F = Fletcher, K = Knight, S = Spellenberg, W = Worthington. Deposition and date of the first known collection is indicated; later collections by F, K, S, or W can be found at ALBU, NMC, UTEP, or UNM.

ARISTOLOCHIACEAE

ARISTOLOCHIA *WRIGHTII Seem. Luna Co.: S 1/2 Florida Mts, 9 Apr 1978, W 2581, 5316, 7046 (COLO, UTEP); *McIntosh*, s.n. (NMC). A species of w TX and n Mex.

ASTERACEAE

*ANTHROPEAS LANOSUM (Gray) Rydb. (*Eriophyllum lanosum* Gray). Hidalgo Co.: Peloncillo Mts, Granite Gap, 9 Apr 1982, S 6455 (NMC, NY, UNM, ASU); near Steins, W 10221, 11721.5, near Lordsburg in Pyramid Mts, W 9919. Common spring annual formerly known from se AZ to nw Mex and s CA, in our region most frequent after moist winters.

ASTER LAEVIS L. var. *GUADALUPENSIS A. Jones. Eddy Co.: Guadalupe Mts in riparian of Big, Black, and Gunsight canyons, 15 Sep 1982, K 2370, 2374 (UNM). Variety previously known only from nw TX.

MACHAERANTHERA *RIPARIUS (Kunth) A. G. Jones. Known from several collections in Hidalgo Co., NM (NMC, UNM). Jones (1983) follows other authors such as Kearney and Peebles (1960) (who use the name *Aster riparius* Kunth) and has considered this and *A. sonorae* Gray as conspecific. None of these names appear in M&H, but *A. blepharophyllum* does, which is interpreted as a rare form of *M. riparia* by Almut Jones (pers. comm. to S., 26 Feb 1986).

CHRYSOTHAMNUS PARRYI (Gray) Greene subsp. *PARRYI. Rio Arriba Co.: Toltec Mesa 8 km airline ne of Lagunitas, 13 Oct 1984, F 7912 (ALBU, UNM). This subspecies was previously known to range from WY to NV, UT, CO.

CIRSIUM *SCOPULORUM (Greene) Cockll. Taos Co.: Sangre de Cristo Mts, above E. Fork Santa Barbara Cr., 6 Aug 1985, F 8414 (ALBU, NMC). Extension from the alpine of s CO.

CONYZA *RAMOSISSIMA Cronq. Doña Ana Co.: Las Cruces, 4 Oct 1985, *McIntosh* 1824 (NMC). Common weed in e US; established in Las Cruces in lawn and cracks of sidewalk.

ERIGERON *BIGELOVII Gray. Hidalgo Co.: Sierra Rica, 13 May 1980, S & Ward 5524 (NMC, NY). Otero Co.: Sacramento Mts., *Soreng* 2808 (NMC). M&H map as potential for se NM; previous United States records apparently from TX near El Paso. Nesom (pers. comm.) says species is frequent in CHIH.

ERIGERON *SCOPULINUS Nesom & Roth. **Sierra Co.:** Black Range, ca 3 km W of James Brothers Cabin, T11S, R10W, S28, 24 May 1981, *Todien 810524-01* (NMC). **Catron Co.:** Mogollon Mts, *K 1759*. **Socorro Co.:** San Mateo Mts, *K & F 1781*, etc.). Previously known only from se AZ.

ERIGERON *URSINUS D.C. Eaton. **Rio Arriba—Mora cos line:** Sangre de Cristo Mts, vicinity Santa Barbara Peak, 6 Aug 1985, *F 8384* (ALBU, NMC). Extension from the alpine of S CO; only ca 6 plants observed.

***FILAGO CALIFORNICA** Nutt. **Hidalgo Co.:** U.S. Hwy. 80, Peloncillo Mts, 20 Apr 1973, *S 3039* (NMC, NY); Pyramid Mts, *W 9908*. **Grant Co.:** Little Hatchet Mts, *W 8195B*. **Luna Co.:** Tres Hermanas Mts, *W 10371*. Spring annual formerly known from se AZ to s CA and nw Mex. The species may occur in collections under the names *Stylocline micropoides* Gray or *Evax multicaulis* DC., both reported for the region, all three of similar appearance, and for the casual collector, at least, difficult to distinguish.

HYMENOPAPPUS FILIFOLIUS Hook. var. ***PAUCIFLORUS** (I. M. Johnston) B. L. Turner. **San Juan Co.:** ca 10 km ssw of Waterflow in sand, 31 May 1985, *S 8199* (NMC, TEX). Confirms presence for NM; said by M&H to be expected in nw corner.

MALACOTHRIX *SONORAE Davis & Raven. **Grant Co.:** Little Hatchet Mts, 24 Apr 1982, *W 8157* (UTEP). **Luna Co.:** Tres Hermanas Mts, *W 9545*. **Catron Co.:** ca 9 km se of Glenwood, Sheridan Gulch Trail, *Soreng & Ward 2130b* (NMC). Known previously from s AZ and n SON.

***PRENANTHELLA EXIGUA** (Gray) Rydb. **Hidalgo Co.:** Pyramid Mts, 7 Apr 1984, *W 11739* (UTEP). Mostly a species from the Sonoran Desert, but type collection is from near El Paso, TX. Postulated distribution by M&H for se NM counties unlikely.

PRIONOPSIS CILIATA Nutt. **San Juan Co.:** 21 km w of Farmington, US Hwy 550, 16 Sep 1984, *S 7875* (NMC, NY). **Doña Ana Co.:** Las Cruces (*S* in 1985, visual w/o specimen). **Eddy Co.:** Carlsbad, *S 8259*. A plains species recorded by M&H from Otero Co.

SENECIO *CANUS Hook. **Harding Co.:** 26 km ne of Roy, 2 Jul 1981, *S et al. 6053; S 7203* (NMC, KSC), a record ca 150 km se of nearest known populations. Diminutive, monocephalic form on caliche, with *Parthenium alpinum*. Other collections from n CO and central UT resemble this phase but none are as dwarfed (specimens examined at BYU, CSU, ID, UNM, UT, UTC, WS).

SENECIO *DIMORPHOPHYLLUS Greene var. **DIMORPHOPHYLLUS**. **Taos Co.:** Wheeler Peak Cirque, 5 Aug 1980, *F 4690* (ALBU, UNM). Previously known from high mts of CO and WY.

SENECIO *SOLDANELLA Gray. **Taos Co.:** Red Dome e of Wheeler Peak,

5 Aug 1980, *F* 4659 (ALBU). Previously known from high mts of CO.

**SILYBUM MARIANUM* (L.) Gaertn. Doña Ana Co.: NM Hwy 404 11 km e of Interstate 25, roadside, 8 May 1985, *S* 8155 (NMC, UTEP). A widespread weed introduced here in straw used to stabilize roadside. Confirms presence for New Mexico; said to be expected in northern tier of counties by M&H.

THELESPERMA SIMPLICIFOLIUM Gray. San Miguel Co.: Rowe Mesa s of Pecos, 22 Aug 1985, *F* 8443 (ALBU). A N range extension of ca 200 km from Chaves Co.

BORAGINACEAE

CRYPTANTHA **BARBIGERA* (Gray) Greene. Luna Co.: Florida Mts, 4 Apr 1980, *W* 5709 (UTEP). Common to the w, reported as far e as w TX (Correll & Johnston 1970), and said to be expected in s NM by M&H. Numerous collections by *W* (UTEP, etc.) from Doña Ana, Grant, Hidalgo, Luna cos. confirm its presence.

PECTOCARYA **HETEROCARPA* (I. M. Johnst.) I. M. Johnst. Luna Co.: Victorio Mts, 23 Apr 1983, *W* 9995 (NMC, UCR, UNM, UTEP). Indicated by M&H to be expected in three sw counties of NM; easternmost record in w TX (Correll & Johnston 1970). Recent records of this, *P. platycarpa* (Munz & I.M. Johnst.) Munz & I.M. Johnst., and *P. recurvata* I. M. Johnston well e of previously known ranges may be due to spread of bristly fruits by livestock. However, a number of spring annuals, common to the w, have been found in this region during the past two decades. Increased botanical activity may be one explanation, their comparatively introduction from the w another, and their spread from small sites of suitable microhabitat after degradation of arid grassland and increase of desert scrub (Van Devender 1980, York & Dick-Peddie 1969) yet a third. The region was inadequately botanized earlier to give strong support to any one explanation.

BRASSICACEAE

CHORISPORA TENELLA (Pall.) DC. Doña Ana Co.: Las Cruces, 4 Apr 1981, *Leyendecker s.n.* (ASU, NMC, NMCR, NY, TEX, UNM). Reported by Marley & Wagner (1981) and mapped by M&H 300 km to n; also in w TX near NM border (Lipscomb 1984). Apparently rapidly spreading and to be expected throughout NM.

DIPLTAXIS **TENUIFOLIA* (L.) DC. Otero Co.: US Hwy 82, 8 km e of US Hwy 70, 15 Aug 1972, *Jackson* 295 (NMC). Collections by *W* and students (UTEP) from the same general vicinity, and sightings of the

species in Doña Ana Co. and in El Paso, TX, indicate this Old World weed to be well established and spreading.

LEPIDIUM *CAMPESTRE (L.) R. Br. **Sierra Co.:** n end of Black Range e of Beaverhead, 2 Jun 1982, *F & K 6124* (ALBU, UNM). Confirms presence for NM; said by M&H to be expected in n.

LEPIDIUM *LATIFOLIUM L. **Doña Ana Co.:** near TX border, 8 Jun 1976, *Alpers 19* (NMC, GH). **Guadalupe Co.:** 5 km n of Pastura, *S et al.* 5984. European weed now widespread in N. Amer., said M&H to be expected in central NM.

LEPIDIUM *RAMOSISSIMUM A. Nels. **Santa Fe Co.:** nw portion of co. in Guaje Canyon, 1 Jun 1984, *S 7766* (NMC). Confirms presence for NM; said to be expected by M&H.

STREPTANTHUS *SPARSIFLORUS Rollins. **Eddy Co.:** Guadalupe Mts, Black River Canyon, 17 May 1979, *F 3827* (UNM); others in general vicinity *F 3807*, *K 1966*. An endemic of the Guadalupe Mts, previously known only in TX.

THYSANOCARPUS AMPLECTENS Greene. M&H write that this occurs in sw NM, but map it "to be expected." Rollins (pers. comm. to W) says that the type locality is in that portion of the state, and that the name is a synonym of *Thysanocarpus curvipes* Hook. var. *elegans* (E & M.) Robins. Records at NMC, UNM, and UTEP, and probably elsewhere, indicate it to be fairly common there.

CAMPANULACEAE

TRIODANIS *BIFLORA (Ruiz & Pavon) Greene. **Grant Co.:** 11 km nnw of Buckhorn, base of Mogollon Mts, 22 May 1983, *Soreng & Ward 2143a* (NMC). A species of the s U.S. from CA to VA, s to MEX and S.A. Inter-mixed with *T. perfoliata* (L.) Nieuwl. at this site.

CARYOPHYLLACEAE

CERASTIUM *AXILLARE Correll. **Otero Co.:** ca 3 km nw of Orogrande at s end of Jarillo Mts, 12 Apr 1985, *McIntosh 1665* (NMC). Previously known from w TX and n CHIH.

STELLARIA *WEBERI Boiv. **Taos Co.:** Latir Peaks, 1 Aug 1979, *F 4028* (ALBU, UNM). S extension of taxon from CO. Considered a dwarf alpine form of *S. umbellata* Turcz. (Weber 1976), the latter known from several localities in NM.

CHENOPODIACEAE

ATRIPLEX *PLEIANTHA W. A. Weber. **San Juan Co.:** Navajo Mine, Fruitland, 5 June 1979, *Pace et al.* 2388 (RM); collected in same area with-

out knowledge of previous record in 1983, 1984, *S* 7087, 7091, 7795. Sporadic on Fruitland Clay knolls; common at 7091 in 1983, where co-occurring with two other state records, *Phacelia demissa*, *Mentzelia thompsoni* (Soreng 1984a), but absent at this site in the drier spring of 1984. Previously known only from one site in extreme sw CO (Ecology Consultants 1978), but now also known in se UT.

CUCURBITACEAE

CITRULLUS VULGARIS Schrad. var. **CITROIDES* Bailey. **Eddy Co.:** ca 42 km airline ese of Carlsbad on large, active dunes at Los Medanos, 21 Jul 1978, *K* 394 (UNM); *K* 786 (UNM). About 30–40 plants were found over an area of ca 20 km near an abandoned dwelling. Collections from two consecutive years indicates that population is at least weakly persistent.

IBERVILLEA **TRIPARTITA* (Naud.) Greene. **Eddy Co.:** ca 45 km airline ese of Carlsbad in Los Medanos dunes, 29 Apr 1983, *K* 2467 (UNM). A species common in the Trans-Pecos region of TX.

CYPERACEAE

CAREX PITYOPHILA Mackenz. **Cibola Co.:** ca 40 km ssw of Grants at s end of Grants Malpais, 19 May 1979, *S* & *Repass* 5131 (NMC, NY); Zuni Mts, *F* 6210 (ALBU). M&H map this for Rio Arriba Co., ca 100 km to ne. Hermann (1970) indicates this species to be rare and local in s CO and n NM.

EUPHORBIACEAE

EUPHORBIA **ERIANTHA* Benth. **Eddy Co.:** Guadalupe Mts, Big Canyon, infrequent in riparian, 16 Sep 1982, *K* 2400 (UNM). A weedy species common in much of s U.S.

EUPHORBIA *GEYERI* Engelm. var. **WHEELERIANA* Warnock & M. C. Johnston. **Doña Ana Co.:** near boundary monument 4 on Mexican border, 25 Jul 1984, *McIntosh* 1588 (NMC). Formerly known only from dunes of extreme w TX, where it is said to be rare and local (Correll & Johnston 1970). It has also been found very near the NM border at Anthony, TX (UCR, UTEP).

FABACEAE

ACACIA ANGSTISSIMA (P. Miller) Kuntze var. **SUFFRUTESCENS* (Rose) Isely. **Hidalgo Co.:** Peloncillo Mts, Guadalupe Pass, T34S, R21W, s edge S16, 15 Aug 1979, *S* & *Repass* 5301 (NMC). Isely (1973) shows this variety to be widespread in s AZ. Variety *texensis* (T. & G.) Isely is common in sw NM.

ACACIA *MILLEFOLIA S. Wats. **Hidalgo Co.:** very near MEX and AZ borders in Guadalupe Canyon and tributaries, 17 Aug 1979, *S & Repass 5371* (NMC, NY). Isely (1973) indicates this species to occur in extreme se AZ, virtually on the NM border. Observed several times within 1 km of AZ border by S.

ASTRAGALUS *DESPERATUS Jones var. **DESPERATUS.** **San Juan Co.:** near AZ border, 3.5 km airline s of Hwy 504 near Beclabito, 27 Apr 1983, *K 2446* (UNM); 14 km airline n of "The Thumb," *K 2448*. Members of the section *Desperati* are common in se UT and ne AZ, but uncommon in NM.

ASTRAGALUS FEENSIS M. E. Jones. **Hidalgo Co.:** low pass s of Pyramid Mts e of Animas, 1 Jun 1985, *Barneby 17985* (NMC). A 370 km range extension to sw for a species previously known only as an endemic of central NM.

ASTRAGALUS FUCATUS Barneby. **Socorro Co.:** 22 km n of Magdalena, 8 May 1977, *S 4653* (NMC). A single plant in heavily grazed grassland, sandy soil, ca 200 km to se of localities in San Juan Co. in M&H and Barneby (1964).

DALEA PURPUREA VENT. var. **PURPUREA** (= *Petalostemum purpureum* [Vent.] Rydb). **Grant Co.:** 3.2 km s of Silver City on Hwy 90, 26 Apr 1983, *W 10777* (NMC, UTEP). A plains species mapped as far sw in NM as the central counties by M&H; this a range extension of 250 km to the sw, where probably introduced.

LATHYRUS *LATIFOLIUS L. **Otero Co.:** Cloudcroft, 19 Oct 1969, *Smart 84* (UTEP); Haynes Canyon, *Gonzalez 44*. **Lincoln Co.:** 3 km nw Ruidoso, *Berry 19*. **Sierra Co.:** Kingston, *W 13302*. This is a common escape from cultivation and is used in roadside stabilization in many parts of the w U.S.

PROSOPIS GLANDULOSA Torr. var. **GLANDULOSA.** **Doña Ana Co.:** 5 km e of Akela on I-10, 16 Apr 1984, *S & Leiva 7797* (NMC). Along freeway right-of-way where it receives somewhat more water than the sympatric var. *torreyana* (L. Benson) M. C. Johnston. M&H map the variety as far w as Lincoln and Eddy cos. in NM, and Johnston (1962) does not indicate it to occur in NM at all. It is a common ornamental in Las Cruces, a possible source of seed for plants along the highway.

***SCHRANKIA UNCINATA** Willd. **Hidalgo Co.:** along I-10 at Lordsburg, 5 Apr 1983, *W 10688* (UTEP); Peloncillo Mts, Granite Gap, *W 10703*. **Grant Co.:** 3.2 km s Silver City, *W 10779*. Known from much of central U.S., probably introduced in sw NM through hay to control roadside erosion.

VICIA *VILLOSA Roth. **Doña Ana Co.:** College Farm (in Mesilla Park), both 16 Apr 1895, *Sweet s.n.* and *Peacock s.n.* (NMC). M&H indicate in a footnote that species "probably occurs near cultivated areas" in the state.

Apparently has not been seen in NM since these two simultaneous early records, probably collected by students of Wootton.

HALORAGACEAE

MYRIOPHYLLUM **PINNATUM* (Walt.) B.S.P. **Harding Co.:** 1 km ne Abbott Lake, 1 Jul 1981, *F & S* 5339 (UNM). A species widespread to the east.

LAMIACEAE

CALAMINTHA* *ARKANSANA* (Nutt.) Shinners. **Otero Co.: Sacramento Mrs, T15S, R13E, S22, 1 Aug 1971, *Todten s.n.* (NMC); e of Cloudcroft, T15S, R13E, S33, 7 Oct 1978, *F s.n.* (ALBU). Nearest known localities are apparently in central TX.

HEDEOMA **DENTATUM* Torr. **Hidalgo Co.:** Peloncillo Mts, Skeleton Canyon, 6 Sep 1981, *S* 6287-B (NMC, NY); 15 air km ssw of Animas, *W* 13395. Irving (1980) shows this species to approach NM only a few km to the w in se AZ.

MONARDA *CITRIODORA* Cerv. var. *CITRIODORA*. **Hidalgo Co.:** Peloncillo Mts, Granite Gap, Hwy 180, 6 Jun 1983, *W* 10705 (NMC, UTEP). A species of s-c U.S. reaching se NM (Scora 1967), possibly introduced in sw NM through hay used in control of roadside erosion.

LILIACEAE

ALLIUM **ACUMINATUM* Hook. **San Juan Co.:** above e side of Navajo Lake adjacent to sandstone rimrock, T30N, R8W, S25, 2 May 1984, *K* 3031 (UNM). **Hidalgo Co.:** 10 km ne of Virden, *S* 8408. A species widespread to the n and w.

ALLIUM *GOODINGII* M. Ownbey. **Lincoln Co.:** Sierra Blanca, 7 Jul 1977, *K* 148 (UNM) with subsequent independent collections by each of us since then. Known for a number of years in c AZ, and for about a decade in w-c NM. Extension ca 240 km se of closest populations, where it is sporadic in moist areas in spruce/fir forest on ne slope of the mountain. This population has passed as *A. brevistylum* Wats. in M&H.

ASPHODELUS* *FISTULOSUS* L. **Luna Co.: 34 km w of Deming on I-10, 19 Apr 1981, *S* 5975 (NMC, NY, TEX); *W* 10783, 11848. A Mediterranean plant common as a weed along roadsides in nc Mex. Also introduced in s CA (Munz 1968).

LINACEAE

LINUM *LEWISII* Pursh. This perennial is widespread in the west. In the sw corner of NM there are annual plants with styles about 3 mm long or

less, shorter than or equal to the anthers. These plants do not have the erose or ciliate inner sepals characteristic of *L. angustifolium* Huds. or *L. usitatis-simum* L. They will "key" to *L. pratense* (Nort.) Small in Correll & Johnston (1970) and in M&H, and match the description of this species rather well. *Linum pratense* is recorded in M&H only from extreme e-c NM. Observations in Hidalgo Co., near Cloverdale, by Spellenberg indicate that populations are entirely annual and short-styled. To the north, near Virden, perennials and plants blooming their first year grow together; less than 10% are short-styled. These populations of short-styled annuals may be arid grassland ecotypes derived from adjacent perennial *L. lewisii*, and probably do not represent *L. pratense* of the Great Plains. Records are: *Hershey 141, S 3070, Hess & Sticky 3446*, NMC, all from Hidalgo Co., and *Metcalfe 1580*, NMC from Sierra Co. The phase also barely enters AZ in se Cochise Co. w of Guadalupe Cyn. (*F 3187*, ALBU).

MALVACEAE

ABUTILON *SONORAE Gray. Hidalgo Co.: Peloncillo Mts, Skeleton Cyn., 6 Sep 1981, *S 6294* (NMC). Luna Co.: s end Florida Mts., *McKintosh s.n.* (NMC). Formerly known from w TX, n MEX, se AZ.

***ALTHAEA ROSEA** (L.) Cav. Doña Ana Co.: Las Cruces, Del Rio Drainage Canal, 20 Sep 1984, *Green s.n.* (NMC). Lincoln Co.: Ruidoso, *Berry s.n.* (UTEP). Sparingly established at both sites; young plants apparent.

NYCTAGINACEAE

BOERHAVIA SPICATA Choisy. Many of the collections of spicate *Boerhavia* from sandy areas in NM will key to *B. spicata* in Kearney & Peebles (1960) or in Standley (1918). These are comparatively robust plants with densely-flowered racemes, ovate floral bracts that are as long as or longer than the ovary at anthesis, and that have stems that are viscid-pubescent below the inflorescence. They will key to *B. torreyana* (Wats.) Standl. in M&H, a common form with narrower, shorter bracts, and usually with less densely pubescent stems. The extremes of this form are on the rockier sites. If the two forms are kept as separate species, then *B. spicata* occurs in NM; if not, then all forms are included in *B. spicata*, the older name, a taxonomy followed by C. E. Reed in Correll & Johnston (1970).

ONAGRACEAE

CALYLOPHUS *BERLANDIERI Spach. subsp. PINIFOLIUS (Engelm. ex Gray) Towner. Socorro Co.: 13 km s of San Antonio along I-25, 24 May 1983, *S 7017* (NMC, MO). San Juan Co.: Little Water, road shoulder, *S*

8492. About 160 km to w of known range of species in NM (subsp. *berlandieri*) and a state record for the subspecies, a native of central Oklahoma and Texas (Towner 1977). It may have been introduced in hay spread on road banks and shoulders. Species not in M&H.

CALYLOPHUS SERRULATUS (Nutt.) Raven. **Hidalgo Co.:** Peloncillo Mts, Granite Gap, Hwy 80, 5 Apr 1983, W 10708 (NMC, UTEP). Mapped mostly e of mountains in NM by M&H, and shown to "skip" to e AZ in Towner (1977). Possibly introduced in hay to control roadside erosion.

OROBANCHACEAE

OROBANCHE LUDOVICIANA Nutt. var. **ARENOSA* (Suksd.) Cronq. **San Juan Co.:** ca 6 km n of La Plata, 11 Aug 1981, S 6119 (NMC). Confirms presence for state; said to be expected by M&H (as *O. multiflora*).

OXALIDACEAE

*OXALIS *PILOSA* Nutt. **Hidalgo Co.:** Peloncillo Mts, Guadalupe Cyn, T34S, R21W, S6, 7 Apr 1979, S 5072. Infrequent; a species of AZ, CA, and SON.

POLEMONIACEAE

IPOMOPSIS CONGESTA (Hook.) V. Grant. **Sandoval Co.:** 35 km nw of San Ysidro, 4 Apr 1984, S 7789 (NMC, ID, NY, CSU, ASU, UNM). Dominant on clay road bank, about a 100 km se range extension from San Juan Co.

*PHLOX *VARIABILIS* Brand. **Taos Co.:** Little Costilla Peak, 29 Jul 1982, F 6396 (ALBU, NMC). Previously known from the high mts of CO and UT.

POLYGONACEAE

*ERIOGONUM *FLEXUM* M. E. Jones. **San Juan Co.:** 10.5 km s of Waterflow, Navajo Mine, 5 Jun 1985, S 8222 (NMC, NY, RSA, UNM). Rare on steep, n-facing clay slope. Reveal and Ertter (1976) map this species (in *Stenogonum*) very near to the border of NM in sw CO.

OXYRIA DIGYNA (L.) Hill. **Otero Co.:** Sierra Blanca, cliff face at 3350 m elev, 16 Aug 1980, W 6355 (COLO, UTEP). M&H indicate this occurs in NM only in high mountains of northern counties; this a range extension of ca 400 km to south.

RANUNCULACEAE

*DELPHINIUM *AJACIS* L. **Eddy Co.:** ca 30 km e of Carlsbad, roadside

below Maroon Cliffs, 14 May 1979, *K* 878 (UNM). A garden escape, native of Europe, found occasionally in several states in U.S.

RANUNCULUS **ABORTIVUS* L. var. *ABORTIVUS*. Taos Co.: Rio Santa Barbara 5 km airline se of Peñasco, 4 Jul 1982, *F* 6252 (ALBU, UNM). A transcontinental species.

ROSACEAE

POTENTILLA CONCIANNA Rich. in Frankl. var. **RUBRIPES* (Rydb.) C. L. Hitchc. Taos Co.: Latir Peaks, 1 Aug 1979, *F* 4062 (ALBU, UNM). An alpine variety widely distributed in w N. Amer.

RUBUS **PROCERUS* P. J. Muell. Sierra Co.: Kingston, along N. Percha Creek, 23 Aug 1980, *W* 6392 (UTEP). Catron Co.: Glenwood, weed along road and in creek, *S* 7742. Doña Ana Co.: Organ Mts, Haynor Resort (*S* visual, w/o record). A blackberry adventive in AZ (Kearney and Peebles 1960) and a well established and unwelcome weed in the Pacific States.

SCROPHULARIACEAE

CORDYLANTHUS **LAXIFLORUS* Gray. Grant Co.: 5 km n of Redrock, single plant in heavily grazed area, 7 Sept 1985, *S* 8286 (NMC, NY, UC). Species previously known only from AZ.

LINARIA VULGARIS Mill. Lincoln Co.: s of Nogal along Hwy 37, 25 Aug 1984, *Soreng* 2601 (NMC). An aggressive Eurasian weed 200 km s of the two NM counties where mapped by M&H. Found throughout much of the U.S.; to be expected in much of NM.

PENSTEMON BRIDGESII Gray. San Juan Co.: 6.4 km n of La Plata, 11 Aug 1981, *S* 6126 (NMC, NY). Kearney and Peebles (1960) indicate this species to occur from sw CO across much of n AZ. It was known from NM only from one old record in extreme w Catron Co. nearly 300 km to the south.

SOLANACEAE

SOLANUM AMERICANUM Mill. Hidalgo Co.: Peloncillo Mts, Guadalupe Cyn, 14 Aug 1979, *S & Repass* 5276 (NMC, NY). Doña Ana Co.: Organ Mts, *W* 6594. These records extend the known range ca 300 km to s from central NM and central Arizona.

SOLANUM **CAROLINENSE* L. Mora Co.: 29 km w of Roy, 3 July 1981, *Ward et al.* 81-269 (NMC, NY). M&H indicate the species is to be expected in the extreme se counties.

TYPHACEAE

TYPHA **DOMINGENSIS* Pers. San Juan Co.: Navajo Coal Mine, ca 5 km

s of Fruitland, 8 Sep 1983, *S & Ward 7585* (NMC), where it grew with *T. latifolia* L. Correll & Correll (1972) indicate the species to occur across the U.S., but M&H do not include the name.

ULMACEAE

CELTIS **OCCIDENTALIS* L. **Harding Co.:** along the Canadian River 11 km airline w of Mills, 3 Jul 1981, *F & K 5353* (UNM). A western extension from TX & OK, possibly escaped from cultivation.

VIOLACEAE

VIOLA **VIARUM* Pollard. **Eddy Co.:** 46–59 km sw of Whites City in Guadalupe Mts, shaded, moist crevices of limestone in Big, Black, and Gunsight canyons, 27 Mar 1982, *K 1822, 1823* (UNM). A w range extension of ca 800 km from OK. The plants from this region have been previously misidentified as *V. missouriensis*; R. Barneby kindly identified Knight's material. The Guadalupe Mts presently harbor several relict species of the southeastern hardwood forest, and this violet may have been part of a more inclusive flora of such affinity. Plants are consistently different from those of more eastern populations, and study may show them to be taxonomically distinct.

APPENDIX

Additional records and literature citation for distribution records of plant taxa reported for New Mexico. This list serves to up-date Martin & Hutchins (1980, 1981) but does not repeat range extensions or new species mapped in Fletcher, et al., 1984. For taxa new to the state or otherwise not included in Martin & Hutchins (1980, 1981) an asterisk appears next to the name of the taxon added to the flora.

ACANTHACEAE: *Carlsonrightia* **texana*; **Justicia wrightii*; **Tetramerium nevadense*;—Daniel 1984. **APIACEAE:** *Lomatium* **nevadense* var. *parisii*—Mathias & Constance 1945; *Perideridia* **parisii* subsp. *parisii*—Chuang & Constance 1969; *Pteryxia* **bendersonii*—Mathias & Constance 1945. **APOCYNACEAE:** *Ansonia* **fugatei*—McLaughlin 1985. **ASCLEPIADACEAE:** **Cynanchium arizonicum*—Todsén 1984. **ASTERACEAE:** *Chaetopappa* **elegans*—Soreng & Spellenberg 1984; **C. berbeyi*—Shinners 1946; *Chrysothamnus nauseosus* subsp. **arenarius*, *C. n.* subsp. **nitidus*—Anderson 1978; *C. n.* ssp. **texasensis*—Anderson 1980; *Erigeron compactus* var. **consimilis*—Marley & Wagner 1981; *E. excimius*—Nesom 1978; *E. rybius*—Nesom 1982; *Evax* **prolifera*—Spellenberg 1984; *Helianthus* **paradoxus*—Seiler, et al. 1981; *Lygodesmia* **arizonica*—Tomb 1980; *Parthenium* **alpinum* var. *alpinum*—Spellenberg 1984; *Perityle* **lemonii* (Gray) MacBride—Todsén 1973; *P. stansophylla* var. **homiflora*—Todsén 1983; *Tetradymia* **spissa*—Marley & Wagner 1981. **BORAGINACEAE:** *Cryptantha* **bakeri*; *C. gracilis*; *C. recurvata*; *C. setosissima*—Sivinski in press. **BRASSICACEAE:** **Alyssum minus* var. *microanthum*—Hartman et al. 1980; **Diploxixis muralis*—Marley & Wagner 1981; *Lepidium oblongum*—Wagner 1983; *Malosmia* **africana*—Marley & Wagner 1981; *Thelypodopsis* **parpasii*—Ward & Spellenberg 1981. **BROMELIACEAE:** *Tillandsia*

- recurvata*—Wagner 1979. CACTACEAE: *Echinocereus emucanthus* var. **emucanthus*. *Opuntia *ficus-indica*—Benson 1982. CAMPANULACEAE: **Nemacladus glandulosiferus* var. *orientalis*—Ward & Spellenberg 1981. CAPPARACEAE: *Psolanisia *janatii*—Willson et al. 1979. CARYOPHYLLACEAE: *Arenaria *stricta* subsp. *texana*—Wagner 1983; *Stellaria *nitens*—Soreng & Spellenberg 1981. CHENOPODIACEAE: **Grayia brandegei*—Levin 1985. *Suaeda suffrutescens* var. **detonsa*—Hopkins & Blackwell 1977. COMMELINACEAE: *Tradescantia *wrightii*—Spellenberg 1979. CONVULVULACEAE: *Ipomoea *egregia*—Soreng & Spellenberg 1981. CROSSOSOMATAACEAE: **Apacheria chircabuenis*—Knight et al. 1984; *Glossopetalon *plantiterum*—Brooks 1984. CUPRESSACEAE: *Juniperus *erythrocarpa*—Adams & Zaccari 1979. CYPERACEAE: *Cyperus *ovularis* var. *cylindricus*—Kessler 1984. EUPHORBIACEAE: *Phyllanthus *abnormis* var. *abnormis*—Urbatsch et al. 1975. FABACEAE: *Astragalus cobrensis* var. **maguirei*—Isely 1984; *A. *monumentalis*—Marley & Wagner 1981; *A. punicus* cf. var. **punicus*; *A. *sericeolens*—Spellenberg 1984; *Dalca *cylindricus*—Barneby 1977; **Teprosia tenella*—Todsén 1984. HYDROPHYLLACEAE: *Nama bipidum* var. *mentzelii*, *N. *retrosum*, *N. *stevensii*—Bacon 1984; *Phacelia *bakeri*—Arwood 1975; *P. *dewissa*—Soreng 1984a; *P. integrifolia* var. **texana*—Arwood 1975; *P. *splendens*—Knight 1984. LAMIACEAE: *Hedeoma *reverbonii* var. *serpyllifolium*; *H. *todsenii*—Irving 1980; *Monarda punctata* var. **occidentalis* (replacing var. *lasiodonta*, mis-mapped for NM in M&H)—Scoa 1967; *Salvia *microphylla* var. *wilzizenii*—Marley & Wagner 1981; *S. *summa*—Worthington 1982. LOASACEAE: *Mentzelia *thompsonii*—Soreng 1984a. LYTHRACEAE: **Nesaea longiper*—Graham 1977. MALPIGHIACEAE: *Aspicarpa *hirtella*—Todsén 1982. MALVACEAE: *Sphaeralcea *polychroma*—La Duke 1985. MARTYNIACEAE: *Proboscidea *subulosa* Bretting 1982. OPHIOGLOSSACEAE: *Botrychium *matricariifolium*—Spellenberg 1978. POACEAE: *Agrostis *variabilis*; *Alopecurus *pratensis*; *Apera *interrupta*; *Aristida *brevensis*; *Bohrischloa *bladhii*, *B. *zchaenium* var. *songarica*; **Brachiaria ciliatissima*, *B. *texana*; *Bromus *disandrus*, *B. *mollis*; *Cbloris *submutica*; *Dichanthelium *linearifolium*; *Echinochloa *crus-gannis*, *E. muricata* var. **microstachys*, *E. m.* var. **muricata*; *Elymus *sanderi*; *Elytrigia *pontica*; *Eragrostis *lutescens*, *E. *palmeri*, *E. *superba*; *Eremopyrum *triticum*; *Festuca *arundinacea*, *F. ovina* var. **rylbergii*; *Hilaria *rigida*; *Leymus *ambiguus*, *L. *solinus*; *Muhlenbergia *villota*; *Panicum *antidoteale*, *P. *coloratum*, *P. *hillmanii*, *P. *stramineum*; *Paspalum *setaceum* var. *setaceum*; *Pennisetum *ciliare*; *Poa *arabifera*, *P. *bulbosa*, *P. fendleriana* var. **albicans*, *P. *trivialis*; **Pithecolobium juncea*; **Rhynchosyrum repens*; *Sclerobloa dura*; *Setaria *leucopila*, *S. *ramiseta*; *Sporobolus *heterolepis*; **Urochloa panicoides*—Allred et al. 1986. POLEMONIACEAE: *Ipomopsis longiflora* subsp. **australis*—Fletcher & Wagner 1984; *I. *pinnata*—Soreng 1984b. POLYGALACEAE: *Polygala rindicola* var. **mesalerorum*—Wendt & Todsén 1982. POLYGONACEAE: *Eriogonum *aliquantum*—Reveal 1976; *E. *atorabens* var. *atorabens*—Soreng 1984a; *E. *gordonii*—Reveal 1976; *E. *bookeri*—Soreng 1984a; *E. *microthecum*, *E. *palmerianum*—Reveal 1976; *E. *cabrellaw*—Soreng 1984a; *E. *schackleyi*; *E. *umbellatum*—Reveal 1976. POLYPODIACEAE: *Cheilanthes *springii*—Wagner 1979. RANUNCULACEAE: *Ranunculus *testiculatus*—Marley & Wagner 1981. ROSACEAE: *Cercocarpus *intricatus*—Marley & Wagner 1981. RUBIACEAE: *Galium *emeryense* subsp. *emeryense*—Wagner 1983. SAXIFRAGACEAE: *Hesperia *glowerulata*—Todsén 1982. SCROPHULARIACEAE: **Mearnsia vandellioides*—Todsén 1984. *Penstemon *ramosus*—Crosswhite 1966. SOLANACEAE: *Chamaecrista *pallida* Avenet 1973. VERBENACEAE: *Glandularia bipinnatifida* var. **brevispicata*, *G. *chircabuenis*—Umber 1979. VIOLACEAE: *Viola *pratensis*—Russell 1965.

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TAXONOMIC AND NOMENCLATURAL NOTES ON *HOUSTONIA NIGRICANS* (RUBIACEAE)¹

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ABSTRACT

Herbarium and field studies on Florida and Texas representatives of *Houstonia nigricans* sens. lat. resulted in the recognition of three varieties in Florida: var. *nigricans*, var. *floridana*, and var. *pulvinata*. Taxonomic and nomenclatural confusion surrounding the name *H. filifolia* and its parent combinations are discussed, and these names and the Texas taxa *H. salina* and *H. tenuis* are relegated to synonymy under var. *nigricans*. A key to Florida varieties and a nomenclatural summary are provided.

INTRODUCTION

Houstonia nigricans (Lamarck) Fernald is a perennial, tap-rooted, polymorphic species occurring from southern Michigan to southern Florida and the Bahamas, west to eastern Colorado and Arizona, and south through northern Mexico. Over this wide range it grows in a great variety of habitats, including prairies and plains in the central United States, shale outcrops in southern Ohio, cedar glades in Tennessee, and sandy sea coasts in Florida. These notes deal with varieties and so-called species from Florida and Texas related to *H. nigricans* and conclude that var. *nigricans*, var. *floridana*, and var. *pulvinata* should be recognized in Florida. *Houstonia filifolia* and its parent combinations are relegated to synonymy under var. *nigricans*, as are also *H. salina* and *H. tenuis*.

Terrell (1975) discussed generic delimitations and pointed out the distinctness of the type species of *Hedyotis*, *Houstonia*, and *Oldenlandia* and their heterogeneity if all included under *Hedyotis*. Furthermore, recent research (Terrell et al. 1986) shows that *Houstonia* itself in North America includes several distinct groups of species based on seed and pollen morphology and chromosome number. The present paper deals with *Houstonia*, which is restricted to North America, while *Hedyotis* has an Asian type and is centered in Asia.

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MATERIALS AND METHODS

Herbarium and field studies were carried out on *Houstonia nigricans* sens. lat. using standard taxonomic methods and emphasizing morphological, chromosomal, ecological, and geographical data. Taxa described from Florida and Texas were the main objects of study. Specimens examined to compile the data appearing in the tables were lent from herbaria at FSU and US. Other specimens came from the herbaria cited in the nomenclatural summary. Additional Florida collections were recorded during visits to FLAS and USE. Field observations and collections in Florida were accomplished in 1965 and 1980. Samples of the handwriting of A. W. Chapman were accessed at NA.

RESULTS AND DISCUSSION

HOUSTONIA FLORIDANA

In 1918 Standley described *H. floridana* from the vicinity of Miami, Florida (see nomenclatural summary below). The protologue and type specimens clearly apply to a group of populations that differ from typical *H. nigricans* primarily in having globose or subglobose instead of turbinate or oblong capsules. These populations are restricted almost entirely to oolitic limestone outcrops and soil over limestone in open places and rocky pinelands in Dade County from the Miami area south to Everglades National Park, in Monroe County on Big Pine Key and Key West in Florida (Fig. 1), and in the Bahama Islands (Abaco and Grand Bahama Islands). The name here adopted for these populations is var. *floridana*. In contrast, *Houstonia nigricans* var. *nigricans* occurs in Florida in coastal sands along the Gulf coast from Collier County north to Pinellas and Levy counties, in these and other habitats in several northwest counties, and in Palm Beach and Osceola counties (Fig. 1). Variety *nigricans* and var. *floridana* are allopatric.

Comparison of the more important morphological characters in ten samples of var. *floridana* and seven of var. *nigricans* from the southern one-half of Florida shows some overlap except in the capsule character (Table 1). Capsules in var. *floridana* are always globose or subglobose (superficially suggesting a relationship to the *H. purpurea* group), whereas var. *nigricans* has turbinate or oblong capsules. Variety *floridana* always has filiform leaves, but var. *nigricans* leaves vary from filiform to somewhat wider. There appear to be clines in var. *nigricans*: plants from northern Florida tend to have wider leaves, taller stems, and longer capsules; thus, southern Florida populations of var. *nigricans* are more like var. *floridana* than are northern Florida populations.

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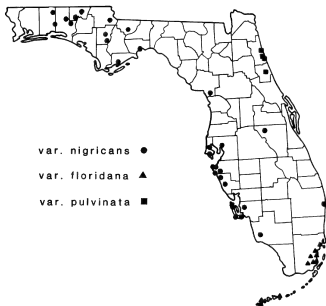


Figure 1. Distribution in Florida of three varieties of *Houstonia nigricans*; Bahama occurrences of var. *floridana* not shown.

Subglobose capsules and other parts of plants of var. *floridana* from the Bahamas were illustrated by Correll and Correll (1982) under the name *Hedyotis nigricans* var. *filifolia*.

Seed characters are very important to differentiate among species in *Houstonia*. Seeds of the two varieties of *H. nigricans* differ only in size. Seeds of three collections of var. *floridana* were 0.45–0.75 mm long and 0.3–0.45 mm wide compared to 0.45–1.15 mm long and 0.3–0.6 mm wide for var. *nigricans* for collections from Mexico and United States.

Chromosome counts for var. *nigricans* are $n=9$ and 10 (Lewis 1959, 1962). The chromosome number for var. *floridana* is $n=9$ for two Dade County collections (Lewis 1962, reported as *Hedyotis nigricans* var. *filifolia*). To these may be added another recently published count of $n=9$ (Terrell et al. 1986).

HOUSTONIA FILIFOLIA

The epithet, *filifolia*, has been used in both varietal and specific combinations to refer to south Florida specimens of *H. nigricans* with filiform leaves (see synonymy for var. *nigricans*). The epithet began with Chapman (1860) who described *Oldenlandia angustifolia* var. *filifolia*. The protologue includes the phrase, "Flowers and capsules very small." This could refer to var. *floridana* which tends to have small flowers and capsules, but so also do some plants of var. *nigricans* from south Florida. Chapman's protologue also mentions obcordate capsules rather longer than the calyx teeth. This and other phrases do not differentiate var. *filifolia* from var. *nigricans*, especially as Chapman did not mention the hallmark character of the Dade County-Monroe County populations (var. *floridana*)—the globose or subglobose capsules. The second and third editions of Chapman's flora repeat the protologue of the first (1860) edition. In the third edition, however, Chapman (1897) changed the name to *Houstonia angustifolia* var. *filifolia*, following Gray (1884).

Chapman did not designate a type specimen. To determine whether there are any extant collections by Chapman which might typify var. *filifolia*, I contacted or visited a number of herbaria, including most of those mentioned by Stafleu and Cowan (1976) as having Chapman collections: AUA, BM, E, GH, K, MO, NA, NY, OXF, PH, US. Results were negative from all but two of these herbaria. The GH has one collection which is discussed below. The US has three collections bearing Chapman's handwriting (verified by comparison with specimens of Chapman's handwriting on file at the National Arboretum) and variously labelled *Oldenlandia angustifolia*, *Oldenlandia angustifolia* var. *filifolia*, and *Houstonia angustifolia* var. *filifolia*. These three specimens are included in Table 1 for the purposes of comparison with other collections of both varieties. All three of the collections fit var. *nigricans* rather than var. *floridana*, as they have longer, more turbinate capsules with length-width ratios of 1.3 to 1.9. One of the three collections, US 83375, labelled as *Oldenlandia angustifolia* var. *filifolia* from "S. Florida," is here chosen as the lectotype of var. *filifolia* (see synonymy below).

Consideration of Chapman's (1860) protologue and his available collections suggests, therefore, that var. *filifolia* applies to filiform-leaved southern Florida populations of var. *nigricans* and perhaps also to var. *floridana*, indiscriminately; i.e., Chapman did not distinguish the Dade Co.-Monroe Co. populations (var. *floridana*) as being distinct from other southern Florida populations.

Subsequently, two other authors made new combinations using the epi-

TABLE 1. Comparison of some Florida collections of var. *nigricans*, var. *floridana*, and Chapman collections (var. *nigricans*).

	VAR. NIGRICANS	VAR. FLORIDANA	CHAPMAN COLLECTIONS: VAR. NIGRICANS		
	n = 7	n = 10	US 83375	US 1390549	US 956984
Height (cm)	17-53	12-35	30	--	15-35
Leaf width (mm)	0.5-2(-5)	0.5-1.2	0.5-1.2	0.5-1	0.4-1.3
Corolla length (mm)	3-7	3-5	4-8	4.8(one)	4-7
vestiture	pubescent to densely hirsutulous	glabrate to densely pubescent	densely pubescent	densely pubescent	densely pubescent
Anther length (mm)	1.0-1.5	0.8-1.2	--	--	0.9-1.2
Capsule length (mm)	1.7-3.2	1.2-2.5	2.0-2.8	2.1-3.2	1.9-3.0
width (mm)	1.3-2.0	1.2-2.2	1.2-1.8	1.3-2.2	1.0-1.7
L/W	1.2-2.2	1-1.3	1.3-1.75	1.3-1.7	1.5-1.9
shape	turbinate or oblong	subglobose or globose	turbinate	turbinate	turbinate

thet *filifolia*. Gray (1884) in his Synoptic Flora of North America cited Chapman's name and transferred it as *Houstonia angustifolia* var. *filifolia*. His description does not mention the subglobose capsules of var. *floridana*, thus could refer to either var. *floridana* or var. *nigricans*, although he mentions "Rocky pine barrens near the coast, Florida," suggesting the habitat of var. *floridana*. The GH has on file a designated "type specimen" which matches var. *floridana*. The collection is labelled as *Houstonia angustifolia* var. *filifolia* and "Syn. Fl. N. Amer.," "Blodgett," and "Key West." None of the labelling is in Chapman's handwriting. Key West probably supported var. *floridana* at one time, although I have not seen any other collections from there. "Blodgett" must refer to John Loomis Blodgett (1809–1853), born in Massachusetts. He went to Key West in 1838 and while there sent specimens to Torrey and Nuttall. This particular specimen may indicate Gray's idea of var. *filifolia*, but has no connection with Chapman nor any validity as a type specimen of Chapman's name.

Later, Small (1903) raised var. *filifolia* to the rank of species, but incorrectly cited Gray instead of Chapman. Small's description fits var. *floridana* by recognizing the subglobose or globose capsules. The combinations by Gray and Small are discussed above to present a complete record of the nomenclature, but do not alter the facts that the var. *filifolia* originated with Chapman (1860) and the application of the name depends on Chapman's protologue and type. Furthermore, adherence to the present nomenclature code does not allow the citation of "Chapman ex Gray," as Chapman provided a full description.

Standley (1918) in describing *H. floridana* dealt with the vars. *filifolia* of Chapman and Gray by relegating them to synonymy under *Houstonia angustifolia* (it was not until 1940 that Fernald showed that the name *H. nigricans* must supplant *H. angustifolia*). Standley listed Small's name, *H. filifolia*, as a synonym of *H. floridana* as to the description only. Thus, Standley reached essentially the same conclusions expressed here.

HOUSTONIA PULVINATA

Small (1899) described *Houstonia pulvinata* from St. Augustine, Florida, based on collections by Mary C. Reynolds and A. P. Garber (see nomenclatural summary). He believed that the short leaves, congested cymes, smaller corollas, and shorter, more obovoid capsules of *H. pulvinata* were "sufficient to warrant its treatment as a species." Fosberg (1954), however, merely listed *H. pulvinata* as a variety of *Hedyotis nigricans*.

In addition to the type specimens six collections of *Houstonia pulvinata*

have been examined from several herbaria (cited below). *Houstonia pulvinata* is now known only from St. Johns and Flagler counties in northeast Florida along the Atlantic coast (Fig. 1). The usual habitats are beaches, in sand, and more recent collections prior to 1984 mention sea shells and coquina rock. Because of the rapid expansion of building along the ocean front, there is some question whether *H. pulvinata* should be considered threatened or endangered; however, at present there are not definitive data concerning its abundance.

A 1984 collection of *H. pulvinata* by K. J. Wurdack has provided the first chromosome count and new information on its habitat. The locality for the collection was in southernmost St. Johns County in a vacant lot between two houses in a developing beach front community, where plants grew in sand among a dense mass of coquina shells about 100 feet from the ocean. Wurdack searched unsuccessfully for *H. pulvinata* at the Bunnell locality (cited below) in Flagler County, but he did not search for it elsewhere in St. Johns County. Without a complete survey it is uncertain whether *H. pulvinata* always occurs with coquina shells, thus the role of a possibly physiologically stressful habitat is not known.

To judge *H. pulvinata* more objectively, ten geographically scattered Florida collections (from herbarium FSU) of *H. nigricans* were compared with the isotype, lectoparatype, and the four recent cited collections of *H. pulvinata*. The results (Table 2) show that *H. pulvinata* differs mainly in having a consistently subprostrate habit (described as cushion-like masses), shortened internodes and pedicels, and congested inflorescences. Other differences, including corolla size and capsule shape and size, overlap greatly with var. *nigricans*.

Walter H. Lewis obtained a chromosome count of $n = 10$ for var. *pulvinata* from buds collected as part of Wurdack 106 (Terrell et al. 1986). Generally, *H. nigricans* var. *nigricans* is known (Lewis 1959, 1962) on the basis of several counts to have both $n = 9$ and 10; however, the $n = 10$ counts came from plants in Brewster Co., Texas, and Nuevo Leon, Mexico. The $n = 9$ plants came from New Mexico, Texas, and Mexico. In addition, *H. nigricans* var. *floridana* has $n = 9$. There are no counts of *H. nigricans* var. *nigricans* from Florida plants; consequently we do not know whether there are $n = 10$ plants elsewhere in Florida.

Considering the polymorphic nature of *H. nigricans* sens. lat., it seems best to recognize *H. pulvinata* on the varietal level. Its morphological differences are consistent but mainly in vegetative characters. It is allopatric (Fig. 1). The importance of the $n = 10$ chromosome number cannot be evaluated without chromosomal data on *H. nigricans* var. *nigricans* in Florida.

TABLE 2. Comparison of 10 Florida collections of var. *nigricans* and 6 of var. *pulvinata* (see text).

	VAR. NIGRICANS	VAR. PULVINATA
Height or dia. (cm)	18-54	8-26
Habit	erect or decumbent	cushion-like masses
Internode length (mm)	6-46	2-20
Leaf length (mm)	5-32	5-15
width (mm)	0.3-2.4	0.4-2.1
Inflor. congested	somewhat to very	very
Pedicel length (mm)	0-3	0-1.5
Corolla length (mm)	4-7.5	3.5-6.5
color	purplish or pinkish to white	pink to white
Capsule length (mm)	2.0-3.0	2.0-3.0
width (mm)	1.3-2.2	1.5-2.2
L/W ratio	1.25-1.9	1.1-1.6
shape	oblong to turbinate, sometimes broadly ellipsoid	oblong to turbinate or obovoid

HOUSTONIA SALINA and H. TENUIS

Houstonia salina A. A. Heller appears to be possibly an ecological equivalent of var. *pulvinata*, as it occurs on beaches along the Gulf coast of Texas. The type collection has linear-oblong leaves and somewhat congested internodes, but otherwise falls within the limits of var. *nigricans*. There are a number of other collections from the Gulf coast of Texas including at least one from or near the type locality. Some of these collections are smaller and more congested, but others are very similar to var. *nigricans* from Texas and elsewhere. Generally, *H. salina* is variable and does not seem sufficiently distinct from var. *nigricans* to warrant recognition. There is a chromosome count of $n=9$ reported for *Hedyotis nigricans* f. *salina* (Lewis, 1962). Later, Lewis (1970) merely listed *Houstonia salina* as a synonym of *Hedyotis nigricans*.

Houstonia tenuis Small was described from east central Texas. The leaves are more filiform than most Texas populations of *H. nigricans*. Although *H. tenuis* somewhat resembles *H. nigricans* var. *floridana*, the capsules in the protologue and type specimen are distinctly longer than wide, which places it in var. *nigricans*. Standley (1918) listed *H. tenuis*, *H. pulvinata*, and *H. salina* all as synonyms of *H. angustifolia* (*H. nigricans*).

A key to the three varieties and a nomenclatural summary of var. *nigricans* are provided below. Following these is an appendix of specimens examined for Tables 1 and 2.

ABBREVIATED KEY TO FLORIDA VARIETIES OF *H. NIGRICANS*

- A. Stem internodes short, 2–20 mm long; (inflorescence congested; plants in mats) var. *pulvinata*
- AA. Stem internodes usually 6–46 mm long (or sometimes longer); inflorescence open or at least not congested; plants not matted.
- B. Mature capsules subglobose, 1.0–1.3 times longer than wide var. *floridana*
- BB. Mature capsules turbinate, oblong, or broadly ellipsoid, 1.5–2.2 times longer than wide (Florida plants only) var. *nigricans*

NOMENCLATORIAL SUMMARY

1. *HOUSTONIA NIGRICANS* (Lamarck) Fernald var. *NIGRICANS*, Rhodora 42:299, 1940. *Gentiana nigricans* Lamarck, Encycl. 2:645, 1788. TYPE: Herb. Jussieu (HOLOTYPE: P; PHOTO: FERNALD 1940). *Hedyotis nigricans* (Lamarck) Fosberg, Lloydia 4:287, 1941.

Partial synonymy follows:

Haustonia angustifolia Michaux, Fl. Bor. Amer. 1:85, 1803. TYPE: "submaritimis Floridae" (HOLOTYPE: P?). *Oldenlandia angustifolia* (Michaux) A. Gray, Pl. Wright. 2:68, 1853. *Chamisso angustifolia* (Michaux) Nicuwl., Amer. Midl. Naturalist 4:92, 1915.

Oldenlandia angustifolia var. *filifolia* Chapman, Fl. S. U.S. 181, 1860. TYPE: "S. Florida," Chapman *s.n.* (LECTOTYPE: US-83375). Lectotype here designated. *Haustonia angustifolia* var. *filifolia* (Chapman) A. Gray, Syn. Fl. N. Am. 1(2):27, 1884. *Haustonia filifolia* (Chapman) Small, Fl. S.E. U.S. 1109, 1338, 1903, as "(A. Gray) Small." *Hedyotis nigricans* var. *filifolia* (Chapman) Shinnery, Field and Lab. 17:168, 1949.

Houstonia salina A. A. Heller, Contr. Herb. Franklin and Marshall Coll. 1:96, pl. 9, 1895. TYPE: TEXAS. Corpus Christi, shell deposit along beach, 31 May 1894, A. A. Heller 1812 (LECTOTYPE: GH!; ISOTYPES: BM!, ILL!, K!, MO!, NY!, PH!, US-3!). Lectotype here designated. *Hedyotis salina* (A. A. Heller) Shinnery, Field and Lab 17:169, 1949. *Hedyotis nigricans* f. *salina* (A. A. Heller) W.H. Lewis, Rhodora 63:222, 1961.

Haustonia tenuis Small, Fl. S.E. U.S. 1109, 1338, 1903. TYPE: TEXAS. San Saba Co.: San Saba, October 1850(?), Thurber 67 (HOLOTYPE: NY!).

2. *HOUSTONIA NIGRICANS* var. *FLORIDANA* (Standley) Terrell, Phytologia 59:79, 1985. *Houstonia floridana* Standley, N. Amer. Fl. 32(1):36, 1918. TYPE: FLORIDA. Dade Co.: Coconut Grove, Biscayne Bay, Jul 1895, A. H. Curtis 5484 (HOLOTYPE: US!; ISOTYPES: FLAS!, NY!). *Hedyotis purpurea* var. *floridana* (Standley) Fosberg, Castanea 19:36, 1954.
3. *HOUSTONIA NIGRICANS* var. *PULVINATA* (Small) Terrell, Phytologia 59:79, 1985. *Houstonia pulvinata* Small, Bull. New York Bot. Gard. 1:289–290, 1899. TYPE: FLORIDA. Se. Johns Co.: Se. Augustine, sandy soil, Jul 1876, Mary C. Reynolds *s.n.* (LECTOTYPE: NY!; ISOTYPE: NA!). Lectoparatypes, same locality and date, A. P. Garber *s.n.* (NY!, US-2!). Lectotype here designated. *Hedyotis nigricans* var. *pulvinata* (Small) Fosberg, Castanea 19:37, 1954.

ACKNOWLEDGMENTS

I wish to thank Kenneth J. Wurdack for his collection and cytological material of var. *pulvinata*. Type and other collections were lent or seen during visits, thanks to the curators of BM, FLAS, FSU, GH, ILL, K, MO, NA, NY, PH, US, and USE D. H. Nicolson helpfully contributed advice on nomenclature, but is not responsible for any errors. Appreciation is also expressed for help from E. G. Meyer, Julia Morton, J. L. Reveal, and R. P. Wunderlin.

APPENDIX

Specimens included in Table 1 (all in herbarium US):

Variety *NIGRICANS*: FLORIDA. Lee Co.: Sanibel Island, Tracy 7493; Lower Captiva Island, *Brambach* 8769. Manatee Co.: Longboat Key, *Wilbur and Webster* 2518. Pinellas Co.: St. Petersburg, *Buckwith* 80; Clearwater Beach, *Beckwith* 803. Sarasota Co.: Keys, Sarasota, Jun 1876, *Garber s.n.* County unknown: Tampa Bay, *Rugel* 323.

Variety *FLORIDANA*: FLORIDA. Dade Co.: Miami, Tracy 9247; Miami, *Pollard and Collins* 222; south of Miami, *Fosberg* 56758; Homestead, *Killip* 44238; 6 mi east of Royal Palm Park, *O'Neill* 7584; Sykes Hammock, *Small et al.* 6755; between Everglades and Biscayne Bay, *Cartis* 1137 (type). Monroe Co.: Big Pine Key, *Killip* 31434, 43372; *Killip and Swallen* 40443.

Specimens included in Table 2 (all FSU):

Variety *NIGRICANS*: FLORIDA. Collier Co.: NW of Naples, *Long et al.* 28121. Franklin Co.: Camp Weed, *Godfrey* 58816; Alligator Point, *Godfrey* 79017. Holmes Co.: 3.7 mi west of Ponce de Leon, *McDaniel* 4845. Jackson Co.: 6 mi south of Sneads, *Godfrey* 75206. Okaloosa Co.: west of Laurel Hill, *Godfrey* 61275. Pinellas Co.: town of St. Petersburg Beach, *D. B. and S. S. Ward* 2345. Sarasota Co.: Longboat Key, *Godfrey* 65247. Wakulla Co.: Shell Point, *Godfrey* 58899; Live Oak Point, *Ward* 2751.

Variety *PULVINATA*: all collections seen are listed as follows, but the Williamson and Crawford collections were not included in data in Table 2.

FLORIDA. St. Johns Co.: dry sand, Anastasia Island, Aug 1894, *C. S. Williamson s.n.* (PH); Anastasia Island, 26 Jul 1923, *J. Crawford s.n.* (PH); Marineland, 2 Jul 1959, *W. A. Merrill* 741 (GA, US); abundant on sand-shell flats behind the foredunes along the coast between Matanzas and Marineland, 5 Aug 1971, *R. K. Godfrey* 70664 (FSU); caespitose mats, fls. pink to white, tap root angling toward the ocean, inner dunes of coquina sands, west side of old Fla. A1A, 0.8 mi north of Flagler Co. line, S39, T9S, R31E, 10 Aug 1984, *K. J. Wurdack* 106 (NY, US). Flagler Co.: near coquina rock quarry just east of Bunnell, flowers pink, 23 May 1979, *J. Papowe et al.* 1783 (NCU).

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DOCUMENTED PLANT CHROMOSOME NUMBERS 1986:1. MISCELLANEOUS COUNTS IN *ASTER* (COMPOSITAE)

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Semple et al. (1983) stated the need for chromosome counts of asters and other genera for the purpose of determining cytogeographic patterns. These patterns in turn could be used to determine the limits of distribution of infraspecific variants; in reconstructing biogeographic histories of species; in testing hypotheses on the evolution of infraspecific polyploidy; and in biosystematic studies (Strother 1972, Semple et al. 1983). With this purpose in mind, this paper reports chromosome number determinations to supplement the available counts in the genus *Aster*.

MATERIALS AND METHODS

Chromosome counts were made from freshly prepared material following the procedures of Chmielewski and Semple (1983). Root-tips were taken from transplanted rootstocks of plants collected in the wild or from seedlings grown in the greenhouse. Mitotic metaphase cells were examined to determine the chromosome number of each individual. Voucher specimens were deposited in the Herbarium of the Department of Biology, University of Waterloo (WAT). In citation, *Chmielewski* is abbreviated to *C.*

RESULTS

ASTER (*VIRGULUS*) × *AMETHYSTINUS* Nutt. $2n = 10$. CANADA. ONTARIO. **Brant Co.**: Tuscarora Township, 2.3 km SW of Sixty-nine Corners, *C. 1768*. **Perth Co.**: Ellice Township, Ellice Con. 4-5, 2.5 km W of Perth 12, *C. 1864*. **Peterborough Co.**: Asphodel Township, W of Asphodel Line 6 and Hwy 7, *C. 2174*.

ASTER BOREALIS (T. & G.) Prov. $2n = 16$. CANADA. SASKATCHEWAN. 14.5 km SW of Armit, W of North Armit River, *Hooper & Baker 84091315, 84091316*.

_____. $2n = 32$. CANADA. ONTARIO. **Bruce Co.**: St. Edmunds Township, Hwy 6, S of entrance to Cyprus Lake Provincial Park, *C. & Ringuis 2040*. **Oxford Co.**: East Oxford Township, intersection of Hwy 2

and Hwy 53, SE of Eastwood, *C. 1600*. **Wellington Co.:** Puslinch Township, Puslinch 7, 5 km N of Gore Rd. *C. 1355*. **SASKATCHEWAN.** Nitenai River, 7 km W of Hwy 163 and Hwy 9, *Hooper & Baker 84090806*.

ASTER CILIOLATUS Lindl. $2n = 48$. **CANADA.** **SASKATCHEWAN.** 8 km N of Usherville, coulee W of Hwy 9, *Hooper & Baker 84090703*.

ASTER LANCEOLATUS Willd. $2n = 32$. **CANADA.** **ONTARIO.** Wentworth Reg. Mun.: West Flamborough Township, Con. 6, 1.3 km W of Hamilton-Wentworth 4, *C. 1360*.

—————. $2n = 48$. **CANADA.** **ONTARIO.** **Brant Co.:** Onondaga Township, Creek Rd., 2.1 km E of McBay Rd, *C. 1323*. **Essex Co.:** Sandwich West Township, Windsor Salt Factory, *C. 1515*. **Halton Co.:** Burlington City Limits; North Service Rd., S of Aldershot, *C. & C. 1541*. **Kent Co.:** Walpole Island, SE of town of Walpole Island, *C. 1526*. **Nipissing District:** Hwy 11, 1.4 km N of Strathcona Township line, S of Temagami. *C. & C. 1306*. **Nipissing District:** Gladman Township, Hwy 11, Marten River, *C. & C. 1310*. **Parry Sound District:** South Himsforth Township, Hwy 11, Trout Creek rest area, *C. & C. 1315*. **Timiskaming District,** Dymond Township, New Liskeard, intersection of Hwy 11 and 11B, *C. & C. 1281*. **Timiskaming District:** Casey Township, 3.4 km S of Belle Vallee, *C. & C. 1291*. **Timiskaming District:** Chamberlain Township, Hwy 11, picnic area S of intersection with Hwy 112, *C. & C. 1302*. **Timiskaming District:** Hwy 11, 5.9 km S of Latchford, *C. & C. 1304*. **Waterloo Reg. Mun.:** Wellesley Township, *C. 1337*. **Wellington Co.:** Guelph Township, Wellington 72, 0.5 km SE of Speedvale Rd. *C. 1350*. **QUEBEC.** Hwy 101, 9.6 km N of Ville Marie, Ile de College, *C. & C. 1285*. 0.5 km W of Hwy 101, at turnoff to Ile de College Rd., N of Ville Marie, *C. & C. 1289*. **SASKATCHEWAN.** 8 km SE of Somme, *Hooper & Baker 84090304*. Pepaw Lake, *Hooper & Baker 84090306*. McBride Lake, McBride Lake Rd. 1, *Hooper & Baker 84090307*. 3 km E and 3 km N of Somme, *Hooper 84091301*. Bertwell, 15 km NE Reserve, Etommami River, *Hooper & Baker 84091302*. 20 km S of Hudson Bay, intersection of Hwy 9 and Pepaw River, *Hooper & Baker 84091310*. 40 km N of Arran, Mink Creek and Woody Lake Rd, *Hooper 84091505*. 15 km NE of Weekes, S shore of Neely Lake, *Hooper 84091601*.

ASTER aff. LONGIFOLIUS Lam. $2n = 64$. **CANADA.** **ONTARIO.** **Oxford Co.:** East Zorra Township, NE of Cassel, *C. 1607*.

ASTER NEMORALIS Ait. $2n = 18$. **CANADA.** **ONTARIO.** **Nipissing District:** E of Huntsville, *C. & C. 1579, 1580*.

ASTER PILOSUS Willd. $2n = 32$. **CANADA.** **ONTARIO.** **Gray Co.:** Bentinck Township, 11 km E of Elmwood, *C. 2269*.

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NOTES

PANAX QUINQUEFOLIUS L. (ARALIACEAE) REDISCOVERED IN LOUISIANA—The American species *Panax quinquefolius* L. commonly known as ginseng and other Asiatic members of the genus have long been esteemed for their medicinal properties (Dixon 1976). *Panax quinquefolius* is fairly widespread in rich cool woods of the eastern United States. According to Fernald (1950) the species ranges from Quebec to Manitoba south to Florida and Oklahoma. Previously, ginseng was documented for Louisiana by a single specimen collected by C.A. Brown in 1938. The locality data on the specimen label is rather vague: "West Feliciana Parish in the vicinity of Plettenberg" [Brown 7293 (LSU)]. The species was recently found in the same general area. Twelve plants growing in two clumps of two and ten plants each were located on rich soil of a west-facing slope in West Feliciana Parish; aerial parts of the plant were collected to document its occurrence [private property along local road ca 5.0 mi NW of the jct. of LA 968 and LA 66; R4W, T1S, sect 47, 17 Jul 1986, Urbatsch, Meier, Cox, Lievens, and Harris 4106 (LSU)]. The ginseng plants were growing under *Arundinaria gigantea* (Walt.) Chapm.; *Schisandra coccinea* Michx. was observed nearby. Canopy trees included *Liriodendron tulipifera* L., *Carya glabra* (Mill.) Sweet, and *Fagus grandifolia* Ehrh. The ginseng plants were about 15 to 20 cm tall and a few had red fruit on them while others had immature or underdeveloped green fruit. By a later visit to the site the plants (5 Sep 1986) had lost their fruit and their riddled leaves were senescent as evidenced by their yellow to brown color.—Lowell E. Urbatsch, Department of Botany and Albert Meier, School of Forestry, Wildlife, and Fisheries, Louisiana State University, Baton Rouge, LA 70803, U.S.A.

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MUHLENBERGIA FRONDOSA (POACEAE) NEW TO LOUISIANA—According to Chase (1951) and Gould (1975) the range of *Muhlenbergia frondosa* (Poir.) Fernald extends from New Brunswick and Maine to North Dakota, and south to Georgia and Texas. A distribution map published by Pohl (1969) shows this species to be absent from all southern states including South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana and Arkansas and it is not reported from Louisiana

by Allen (1980). In Texas, the grass is known only from specimens taken in Dallas and Grayson counties (Correll and Johnston 1970, Gould 1975). On May 16, 1986, we collected several specimens, *McKenzie 284*, LSU, (duplicates sent to FLAS, LAF, TAES, US) of this species growing in shady woods in moist sandy-loam along the Mississippi River ca 0.1 mile south of the School of Veterinary Medicine on the LSU campus in Baton Rouge, East Baton Rouge Parish. Two small populations, each containing approximately 30 plants were located ca 300 meters apart. The grass was growing on a slightly elevated natural levee between the river and a constructed levee in association with *Arthraxon hispidus* (Thunb.) Makino, *Digitaria ciliaris* (Retz.) Koel., *Leersia lenticularis* Michx., *Leptochloa attenuata* (Nutt.) Steud., *Panicum capillare* L., *P. dichotomiflorum* Michx., *Paspalum fluitans* (Ell.) Kunth, *Brunnichia ovata* (Walt.) Shinnery, *Polygonum* spp., *Alternanthera philoxeroides* (Mart.) Griseb., *Celtis laevigata* Willd., *Acer negundo* L., *Forestiera acuminata* (Michx.) Poiret, *Physalis angulata* L., *Phyla lanceolata* (Michx.) Greene, *Teucrium canadense* L., *Cephalanthus occidentalis* L., *Artemisia annua* L., *Bidens cernua* L., *B. frondosa* L., *Eclipta alba* (L.) Hassk., *Eupatorium coelestinum* L., *E. serotinum* Michx., *Pluchea campborata* (L.) DC., and *Xanthium strumarium* L. The dominant overstory plants were of *Populus deltoides* Marsh. and *Salix nigra* Marsh. The discovery site is irregularly flooded during periods of high water and silt is deposited between the river and the constructed levee. Because this species is common in some north central states bordering the Mississippi River (Pohl 1969), it may have been introduced to Louisiana by floodwaters carrying seeds or rhizomes. Although areas north and south of the discovery sites were searched for additional specimens, no other populations were located. These collections constitute the first record for Louisiana and extend the range of this species ca 600 km.—*Paul M. McKenzie, Louisiana Cooperative Fish and Wildlife Research Unit, and Lovell E. Urbatsch, Department of Botany, Louisiana State University, Baton Rouge, LA 70803, U.S.A.*

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THASPIUM TRIFOLIATUM (APIACEAE) AND *RANUNCULUS MARGINATUS* (RANUNCULACEAE) NEW TO TEXAS—A collection of *Thaspium trifoliatum* (L.) Gray var. *flavum* Blake (13 Apr 1985, *McFarlane 30* [SBSC, SMU, TEX]) from the Damuth Nature Sanctuary near Cleveland, Liberty County is the first reported for Texas. *Thaspium trifoliatum* ranges throughout the eastern United States southwest to Louisiana, Arkansas and Oklahoma. Variety *flavum* is yellow-flowered and more common westward whereas variety *trifoliatum* is purple-flowered but more common eastward. (Cooperrider 1985, Gleason & Cronquist 1963, Smith 1978).

Ranunculus marginatus d'Urv. was taken 28 April 1984 from a weedy area in the Armand Bayou Nature Center near Clear Lake City in Harris County (*Brown 7249* [PAC, SBSC, SMU]). Because of the somewhat similar achene faces these plants keyed to *R. muricatus* L. (Correll & Johnston 1979), but they differ from *R. muricatus* in their longer peduncles, more pubescent habit, and shorter achene beaks (Keener 1976). *Ranunculus marginatus* is native to the Mediterranean region and Shinners (1962) reported it (as *R. trachycarpus* Fisch. & Meyer) new to North America from Avoyelles Parish, Louisiana. I wish to thank Carl S. Keener (PAC) for providing the identification of my collection.—Larry E. Brown, Spring Branch Science Center and Houston Community College, 726 Horncastle Street, Channelview, TX 77530, U.S.A.

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SCUTELLARIA MINOR (LAMIACEAE) NEW TO NORTH AMERICA—*Scutellaria minor* Hudson, a small skullcap with three leaf shapes and a pinkish corolla with purple spots, (fig. 1) was taken in April 1984 from a roadside ditch along East Knox Street near the junction of Loop 494 & North Park Drive near Kingwood, Montgomery Co., Texas (Ward 1378; SMU). In July 1985 a larger population was found, again in a roadside ditch, along highway U.S. 59, 0.5 miles north of junction with highway 1314 near the village of Porter, Montgomery Co. (Ward 1406; SBSC). These two collections are presumably the first in North America for this small mint which is native in Europe from the Azore and British Isles to East Germany and northern Italy (Clapham et al. 1962, Tutin et al. 1972).

The authors wish to thank Elizabeth Messenger for the illustration and Raymond McBen of the Houston Community College for some technical assistance.—Larry E. Brown, Spring Branch Science Center, 8856 Westview Drive, Houston, TX 77055, U.S.A., and John R. Ward 16010 Buccaneer St., Houston, TX 77062, U.S.A.

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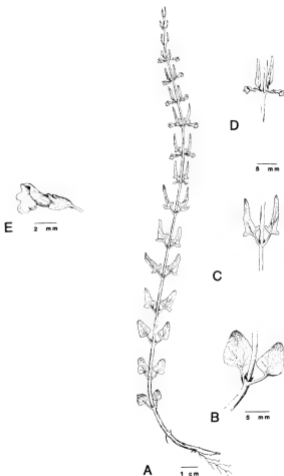


Figure 1. *Scutellaria missouriensis*: A. habit; B. ovate lower leaves; C. hastate middle leaves; D. linear upper leaves; E. flower (all from Ward 1378).

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