









# MADROÑO

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Volume 24 of *Madroño* is dedicated to Dr. Elizabeth McClintock in recognition of her long service as Curator of Botany at the California Academy of Sciences, San Francisco, her extensive knowledge of ornamental and economically useful plants which she willingly shared with others, and her knowledge of the California flora and her efforts towards its conservation.

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TAXONOMY OF THE GENUS CYMOPHORA  
(ASTERACEAE: HELIANTHEAE)

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Anderson and Beaman (1968) gave an excellent account of the monotypic genus *Cymophora* of southern Mexico. They compared it with *Tridax* and *Eleutheranthera*, noting that the single species, *Cymophora pringlei*, was sufficiently close to *Tridax accedens* to be included in *Tridax*. They accordingly made the transfer, assigning a new specific epithet, *T. oligantha*, the name *T. pringlei* having been previously applied.

Turner, Powell, and Watson (1973) questioned the immersion of *Cymophora* into *Tridax*, noting its seemingly closer relationship to *Sabazia* and *Galinsoga*. Anderson and Beaman's argument for a position in *Tridax* rested largely on its strong similarity to *T. accedens* and their belief that the latter was part of a reduction series out of *T. dubia*, a true *Tridax*, leading to *T. oligantha*.

As indicated by our discussion under *Cymophora accedens*, below, we do not now accept the position of either *C. pringlei* or *Tridax accedens* in *Tridax*. These taxa are very closely related, but presumably are more distantly related to *Tridax* proper than they are to other members of Galinsoginae.

We also describe here a third species of the genus, *Cymophora hintonii* (Fig. 1). Since Anderson and Beaman (1968) have made thorough comparative studies of both *C. pringlei* and *C. accedens*, we do no more than provide a somewhat amended generic description of *Cymophora*, along with a key and appropriate comments upon the several species recognized.

CYMOPHORA B. L. Robins., Proc. Amer. Acad. Arts 43:39. 1907.

Plants erect or suberect annuals, 12–65 cm high; stems pilose and glandular. Leaves opposite, blades sparsely pubescent, 2.0–6.5 cm long, 1–5 cm wide, progressively smaller upwards, broadly lanceolate, ovate, to subdeltoïd (flabellate), margins subentire, subrepand, serrulate, or distinctly serrate; petioles 0.1–4.0 cm long. Capitulescence paniculate or cymose; heads narrowly campanulate to subcylindrical; peduncles with copious glandular trichomes usually mixed with straight trichomes; receptacle convex to conical, naked, pilose, or chaffy, 0.5–2.0 mm wide; phyllaries in 1–3 series, pilose and glandular or glabrous, concave, oblong, obovate, or linear, greenish, or membranous, often purplish above.

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Ray florets absent, or disk-like, 4–5 in number, much like inner disk florets except that 3 outer lobes may be longer than inner 2, corollas white, achenes with or without a pappus, or with reduced pappus, rather densely pubescent; inner disk florets 4–40, corollas white, 2.8–3.5 mm long, tube 0.5–1.0 mm long, throat tubular or funnellform, 1.0–1.8 mm long, lobes nearly equal, 0.5–1.5 mm long; style branches subulate, 0.8–1.2 mm long; achenes black, narrowly obconical or obpyramidal, 1.2–2.3 mm long, 4–5 angled and sulcate, short pilose mostly in sulci or on basal half; pappus absent, or of 8–20 scales, the scales lanceolate, fimbriate-plumose, and 1–2 mm long, or oblong, fimbriate at the apexes only, and 0.8 mm long; anthers 1.5–2.0 mm long, often purplish, appendages triangular, bases sagittate. Base chromosome number,  $x = 8$ .  
Type species: *C. pringlei* B. L. Robins.

#### Key to Species of *Cymophora*

1. Leaves markedly flabellate, the blade 4–5 cm wide; florets 8–10  
     . . . . . 2. *C. hintonii*
1. Leaves ovate, the blades 1.0–3.5 cm wide; florets 10/40.
  2. Achenes without pappus, or seemingly so; plants of Guerrero .  
     . . . . . 1. *C. pringlei*
  2. Achenes, at least those of the disk, with well-developed pappus;  
     plants of Michoacan and northwestward . . . 3. *C. accedens*

1. CYMOPHORA PRINGLEI B. L. Robinson. Proc. Amer. Acad. Arts 43:39. 1907.—*Tridax oligantha* Anderson & Beaman, Rhodora 70:241–246. 1968.—TYPE: Mexico, Iguala Canyon, 2500 ft, 22 Sep 1905, C. G. Pringle 10068 (Holotype: GH; isotypes: LL (2), MICH, MSC, UC, US).

Anderson and Beaman gave a detailed description of this taxon and we see no reason to enlarge upon this except to note that the character that they use as a “ready means” for distinguishing between *C. pringlei* and *C. accedens* (florets 10 in the former; 30–40 in the latter) has been somewhat vitiated, for recent collections of the latter from Colima (*McVaugh 18075*, LL; *Feddema 2730*, TEX) have somewhat smaller heads and fewer florets (14–30) than previously reported. A more detailed account of the relationship of *C. pringlei* to *C. accedens* is given under the latter taxon.

2. *Cymophora hintonii* B. L. Turner & A. M. Powell, sp. nov. Fig. 1. TYPE: Mexico, Michoacan, Dist. Coalcomán, Huizontla, alt. 460 m, 17 Nov 1938, G. B. Hinton 12590 (Holotype: TEX; Isotypes: MICH, UC).—Additional collection examined: Jalisco, 17 mi by road SW of Autlán, 28 Oct 1970, *Webster & Breckon 16051* (MICH). Plantae 28 cm altae. Laminae foliorum 5–6 cm longae 3.5–5.0 cm latae subdeltoideae basi cuneatae margine serratae; petioli 2–4 cm longi; capitulescentia paniculata; capitula subcylindrica; involucrem 2–3 seri-



FIG. 1. Habit of *Cymophora hintonii* (Hinton 12590; holotype).

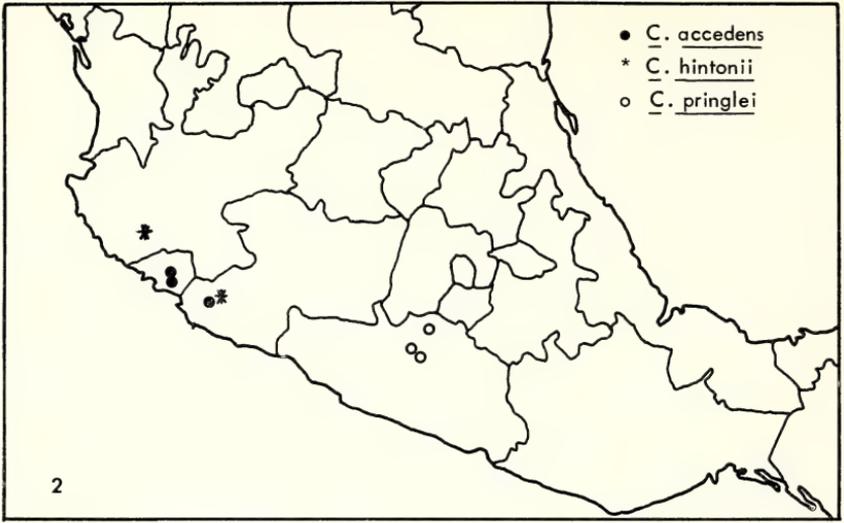


FIG. 2. Collection sites of *Cymophora* species.

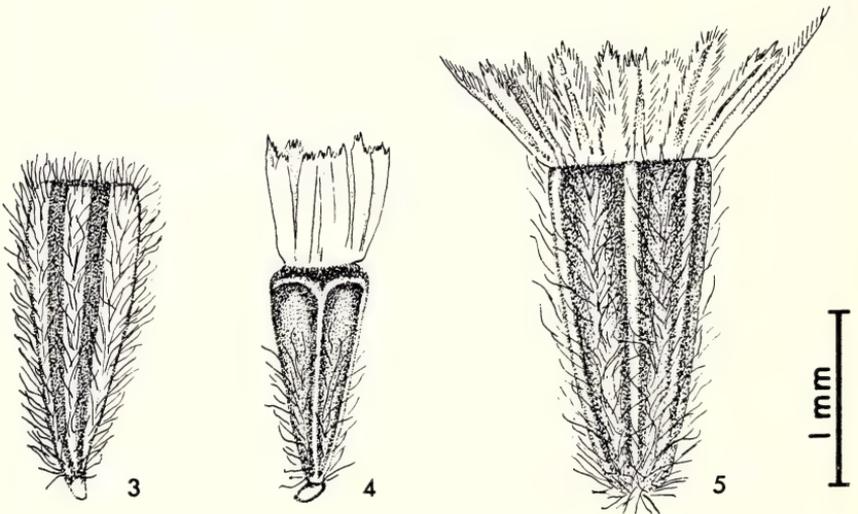


FIG. 3-5. Achenes of *Cymophora* species. 3. *C. pringlei* (Pringle 10068; isotype). 4. *C. hintonii* (Hinton 12590; holotype). 5. *C. accedens* (Hinton 12884; isotype).

atum; flores disci externi 4 epapposi interni 4–5 corollis 2.8–3.0 cm longis styli subulati; achaenia anguste obpyramidalia 1.2–1.5 mm longa 4–5 angulata; pappi squamae 8 oblongae (raro nullae).

Plants ca. 28 cm high; leaf blades 5–6 cm long, 3.5–5.0 cm wide, subdeltoid and basally cuneate (flabellate), margins serrate; petioles 2–4 cm long; capitulescence paniculate; heads subcylindrical; receptacle convex, naked, ca. 0.5 mm wide; phyllaries in 2–3 series, 2–3 mm long, glabrous, sublinear, rather membranous; ray florets (or outer disk florets) 4, corolla with 3 outer lobes longer than inner 2, achenes short-pilose, epappose; inner disk florets 4–5, corollas 2.8–3.0 mm long, tube 0.8–1.0 mm long, throat 1.0–1.2 mm long, subfunneliform, lobes 5, ca. 1.0 mm long, nearly equal; style branches subulate, ca. 1.0 mm long; achenes narrowly obpyramidal, 1.2–1.5 mm long, 4–5-ridged and sulcate, short pilose with hairs mostly in sulci and on basal half; pappus (when present) of ca. 8 oblong scales, ca. 0.8 mm long, rather closely enclosing the corolla tube, obtuse and fimbriate apically; anthers ca. 1.5 mm long; chromosome number, unknown.

3. *Cymophora accedens* (Blake) B. L. Turner & A. M. Powell, comb. nov.—*Tridax accedens* Blake, J. Wash. Acad. Sci. 33:270. 1943. See detailed description, Powell, 1965, p. 95.—Additional specimens examined: Mexico, Colima, 11 mi SW of Colima on Manzanillo rd, 500 m, 21 Sep 1958, R. McVaugh 18075 (TEX); ca. 20 km SW of Colima on the rd to Tecoman, 500 m, 25 Nov 1963, C. Feddema 2730 (TEX); Michoacan, Dist. Coalcoman, Ixtala, 22 Sep 1938, G. B. Hinton 12226 (LL, UC).

Powell (1965) recognized this taxon as belonging to *Tridax*, relating this to *T. dubia* Rose, much as proposed by Blake. However, at the time of his treatment Powell was unaware of the existence of *Cymophora pringlei* and would have surely perceived its closer relationship to the latter taxon were it known to him. Anderson and Beaman (1968) correctly noted this relationship, but instead of disengaging *Tridax accedens* from its seemingly comfortable position and placing this in *Cymophora*, they preferred to transfer the monotypic *Cymophora* to the larger genus. This seemed reasonable enough except that none of these workers was aware at that time of the chromosome number of *Cymophora pringlei* ( $2n = 16$ ; Turner et al., 1973), which is on a base of  $x = 4$  or 8, much as its presumably more closely related genera *Galinsoga* and *Sabazia* (including *Tricarpha* Longpre; Urbatsch and Turner, 1975). *Tridax* (including *T. dubia*, the taxon upon which both Powell and Anderson and Beaman hinge the relationship of *T. accedens*) is dibasic with  $x = 9$  and 10 (Powell, 1965), and we believe *Cymophora* (including *C. accedens*) is thus not correctly placed in *Tridax*. While the chromosome number is not known for *C. accedens*, considering its very similar habital and floral features in common with *C. pringlei* (Anderson and Beaman, 1968), we have little doubt that it too will be a base of  $x = 8$ .

Finally, it should be noted that with the description of the quite distinct *Cymophora hintonii* (above) the genus now has three well-marked species (Fig. 3-5), and presumably additional taxa will be uncovered as this poorly known region of Mexico in which they occur becomes better known.

#### ACKNOWLEDGMENTS

Professor M. C. Johnston provided the Latin description and Dr. Judith Canne made several helpful emendations to the original draft; for these contributions we are grateful.

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### A COMPARISON OF *EPILOBIUM MINUTUM* AND *E. FOLIOSUM* (ONAGRACEAE)

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All but six of the approximately 200 species comprised in the genus *Epilobium* have a gametic chromosome number of  $n = 18$ , with some polyploidy in sect. *Chamaenerion* Tausch. Among the unusual species, *E. minutum* Lindl. ex Lehm. (Fig. 1A) has  $n = 13$  (Kurabayashi et al., 1962; Taylor and Mulligan, 1968), and what has generally been regarded as a trivial form or variety of it, *E. foliosum* (T. & G.) Suksd. (Fig. 1B), has  $n = 16$ . These two closely related species together compose one of the sections of the genus, sect. *Crossostigma* (Spach) Raven (Raven, 1976). The purpose of this paper is to present the cytological and morphological evidence that distinguishes them and to outline their respective distributions in western North America. They were treated in a preliminary fashion, on the basis of information we provided, by Munz (1965, p. 208-9).

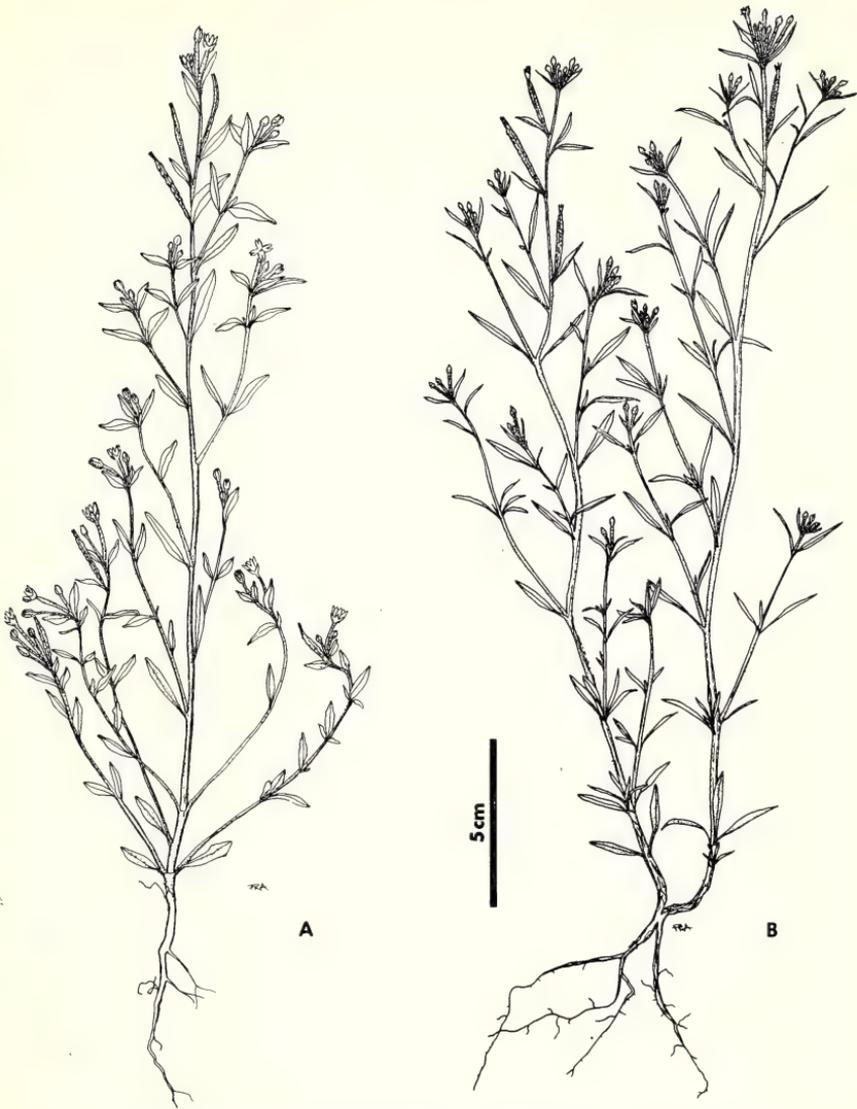


FIG. 1. The 2 species of *Epilobium* sect. *Crossostigma*. A, *E. minutum*. B, *E. foliosum*.

Both *Epilobium minutum* and *E. foliosum* are annuals, a habit they share with only one other species in the genus, *E. paniculatum* Nutt. ex T. & G. Unlike most of the other members of the genus, these three species are found in xeric habitats. We do not believe that there is a direct relationship between the spring-blooming sect. *Crossostigma*, considered here, and the summer-blooming *Epilobium paniculatum*. Consequently, we hypothesized that the annual habit has been derived independently in each line (Raven, 1976).

It is difficult to suggest a hypothesis for the derivation of the unique chromosome numbers of *Epilobium minutum* ( $n = 13$ ) and *E. foliosum* ( $n = 16$ ). In view of the absence of intermediate chromosome numbers, however, we believe that they are most likely derived independently from presumably extinct diploid ancestors with  $n = 8, 7$ , and  $6$  (Stebbins, 1971, p. 193).

Both *Epilobium minutum* and *E. foliosum* are highly autogamous, with *E. foliosum* often actually cleistogamous; as a result of this, many highly inbred morphologically distinguishable lines are apparent in both species. Several morphological characters, however, consistently distinguish the two species. The flowers of *E. minutum* are larger than those of *E. foliosum* (the petals up to 5 mm long), and the buds are broadly ovoid, often nodding, and borne in relatively uncrowded inflorescences. The narrowly elliptic cauline leaves are subacute at the apex and flat or nearly so. *Epilobium foliosum*, on the other hand, has erect, narrowly ovoid buds in a crowded inflorescence. The flowers are often cleistogamous and the petals rarely exceed 2 mm in length. The narrowly elliptic leaves are acuminate and often folded along the midrib. Axillary fascicles of leaves are more common than in *E. minutum*.

Additional differences between these two species include seed size and seed coat architecture. The seeds of *E. foliosum* are smaller, 0.64–0.85 mm long, and very slightly papillose when viewed with a dissecting microscope ( $\times 20$ ). When viewed with the scanning electron microscope, the seed coat is seen to be composed of a series of smooth raised areas, one over each cell lumen, with these raised areas separated by a reticulate network of minutely papillose side walls (Fig. 2, D–F). The larger seeds of *E. minutum*, 0.86–1.20 mm long, are smooth when viewed with a dissecting microscope and generally minutely papillose with a depressed area over each cell lumen when viewed with the scanning electron microscope (Fig. 2, A–C). Both of these seed coat types apparently are confined to sect. *Crossostigma* and unique to the respective species.

The distributions of these two species are similar (Fig. 3). Not only do they overlap geographically, but they are also often found growing sympatrically; a number of collections we examined included both species. *Epilobium minutum* is the more common northward, whereas *E. foliosum* is more frequent in the south. The prevalent autogamy of both species, coupled with their small, tufted seeds, makes them excellent colonizers, and they are often found in disturbed areas such as roadcuts and recently burned areas.

*Epilobium foliosum* has been found in California as far south as Los Angeles Co., and has been collected at least twice in Arizona (Gila Co., Peebles & Smith 13273, ARIZ, CAS, POM, US; Pinal Co., Nelson 1905, ARIZ, GH, NY, UC, US). Its northward distribution follows the coastal foothills from Ventura Co., California, through Oregon and Washington

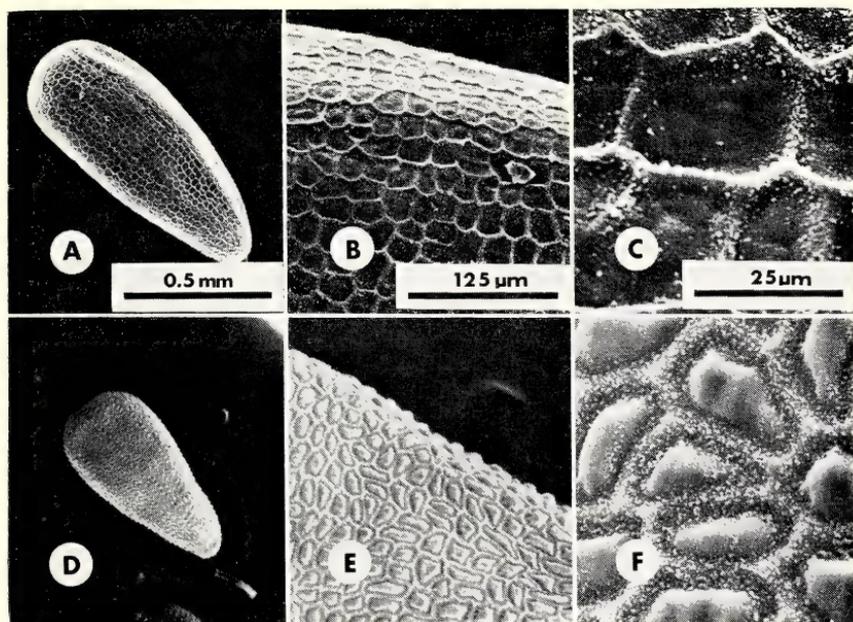


FIG. 2. Scanning electron micrographs of seeds. A-C, *Epilobium minutum*; D-F, *E. foliosum*.

into British Columbia, with northeastern limits in Idaho and northern limits on Vancouver Island, British Columbia (*Taylor 46108*, UC). The species is also scattered in the foothills of the Sierra Nevada of California, where it has been collected as far south as Tulare Co.

*Epilobium minutum* is less frequent in southern California, but ranges through the coastal foothills from Santa Barbara Co., California, to British Columbia. It is scattered in the Sierra foothills from Mariposa Co., California, northward and, like *E. foliosum*, is relatively poorly represented in this part of its range. The northern distribution of this species is more extensive than that of *E. foliosum*, and it reaches Stuiie (40 mi E of Bella Coola), British Columbia ( $52^{\circ}$  N, *McCabe 1546*, UC), and the Queen Charlotte Islands at nearly  $54^{\circ}$  N (*Calder and Taylor, 1968*, p. 438). The northeastern limits of *E. minutum* are in Montana (*Flathead Co., Holzinger & Blake 33*, US; *Missoula Co., Hitchcock 1662*, POM).

A collection from Guadalupe Island, Baja California (*Palmer 4217*, in 1875, K, MO, NY, UC) is difficult to assign to either species on the basis of the available material. No plants of either species have been collected on Guadalupe Island subsequently, and perhaps the plant is extinct there. For the present, we place this collection in *E. foliosum*, mainly on the basis of flower size. Additional material, if it were to become available, might cause us to alter this determination.

*EPILOBIUM MINUTUM* Lindl. ex Lehm., in Hook., Fl. Bor.-Am. 1:207. 1833.—*Crossostigma lindleyi* Spach, Nouv. Ann. Mus. Paris 4:404. 1835; based on *Epilobium minutum* Lindl. ex Lehm.—*Epilobium lindleyi* (Spach) Rydb., Fl. Rocky Mts. 586. 1917.—*Epilobium adscendens* Suksd., Deutsch. Bot. Monats. 18:87. 1900; illeg. subs. for *E. minutum* Lindl. ex Hook.—LECTOTYPE: Washington, Skamania Co., abundant on a mountain near Stevenson, 3–5 Sep 1825, David Douglas (Holotype: K, isotype: NY; selected by Munz, N. Amer. Fl. II. 5:208. 1965).

*Epilobium minutum* var. *canescens* Suksd., Deutsch. Bot. Monats. 18:87. 1900. TYPE: Washington, Klickitat Co., Falcon Valley, 27 June 1892, N. Suksdorf (WS).

Annual, simple or diffusely branched, (3–)5–25(40) cm tall, suberect; leaves mostly alternate, narrowly elliptic, entire or remotely and obscurely denticulate, 1–2(–2.5) cm long, the lowest ones opposite, lanceolate or oblanceolate; buds broadly ovoid, not crowded, often nodding individually; petals (1.5–)2–4(–5) mm long; stigma 4-lobed or entire; seeds obovoid, smooth, 0.86–1.20 mm long, the coma easily deciduous; gametic chromosome number,  $n = 13$ .

Chromosome count vouchers, all  $n = 13$ : U.S. CALIFORNIA. Butte Co.: Magalia, seeds from *Howell 37457*, CAS, grown at Stanford Univ., *Raven 19088* (MO). Del Norte Co.: Patrick Ck., *Raven 18380* (MO); 7.6 mi NE of Crescent City along Hwy. 199, seeds from *Breedlove 3087* (MO), grown at Stanford Univ., *Raven 19761* (MO). Lake Co.: 0.2 mi E of Lakeport on road to Hopland, *Raven 18236* (MO); 5.9 mi E of Houghs Springs, *Raven 18402* (MO). San Benito Co.: 5.4 mi from Hernandez on road to New Idria, *Raven 10585* (MO). San Mateo Co.: Jasper Ridge, Stanford Univ., *Raven 18258* (MO). Santa Barbara Co.: road from Davey Brown Public Camp to Sargent Cypress Forest, seeds from *Hardham 3381* (CAS), *Raven 18774* (MO). Santa Clara Co.: near Red Mt., on J17, *Seavey 1090* (MO). Sonoma Co.: intersection of Joy and Bittner Roads, SW of Occidental, *Seavey 1092* (MO). Stanislaus Co.: Arroyo del Puerto, 6 mi E of Junction in San Antonio Valley, *Raven 18229* (MO). Trinity Co.: 6.3 mi S of Trinity Center on road to Miner-ville, *Raven & Snow 13571* (RSA; Kurabayashi et al., 1962). OREGON. Douglas Co.: bluffs of the Umpqua, opposite Roseburg, *Raven 18383* (MO). WASHINGTON. Kittitas Co.: DeRoux Forest Camp, upper N Fork of Teanaway R., seeds from Kruckeberg, *Raven 18990* (MO); Denny Moore Forest upper Cle Elum R., seeds from Kruckeberg, *Raven 18991* (MO).

CANADA. BRITISH COLUMBIA: Queen Charlotte Islands (Taylor and Mulligan, 1968, p. 92; three localities). South Pender I., near Victoria, seeds from *Calder 29886* (DAO, MO). Lillouet Dist., above Piebiter Ck., Bralorne, seeds from *Kruckeberg 5733* (WTU), *Raven 19090* (MO); N end of Butte L., Vancouver Is., seeds from *Calder 30566* (DAO).

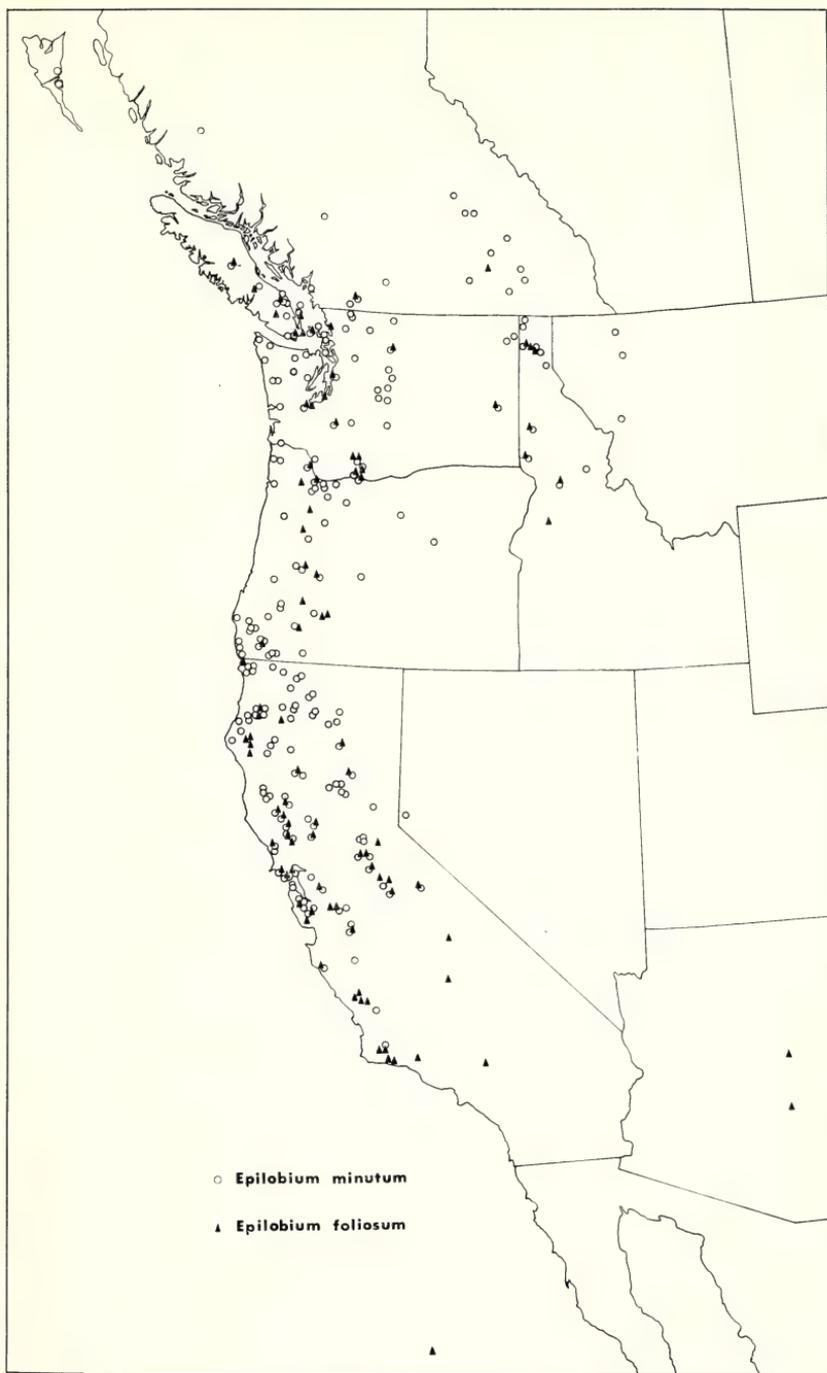


FIG. 3. Ranges of *Epilobium minutum* and *E. foliosum*.

- EPILOBIUM FOLIOSUM (T. & G.) Suksd., Deutsch. Bot. Monats. 18:87. 1900.—*Epilobium minutum* var. *foliosum* T. & G., Fl. N. Am. 1:490. 1840. TYPE: Dry rocks, Oregon and the Rocky Mountains of California, 1834–5, *Thomas Nuttall* (Holotype: NY; isotopes: BM, K).  
*Epilobium minutum* var. *biolettii* Greene, Pittonia 2:296. 1892. TYPE: California, Marin Co., Sequoia Canyon above Mill Valley, Mt. Tamalpais, May 1892, *Bioletti* (Holotype: UC).  
*Epilobium foliosum* var. *glabrum* (T. & G.) Suksd., Deutsch. Bot. Monats. 18:87. 1900. TYPE: Washington, Klickitat Co., moist, stony places, rare, on western plains, 17 May 1892, *N. Suksdorf 2108* (Holotype: WS; isotypes: NY, UC, US).

Like *E. minutum*, but leaves more pointed, very narrowly elliptic, the lowest ones narrowly lanceolate, often folded along midrib; axillary fascicles more frequent; flowers smaller, often cleistogamous, pointed in bud, usually crowded, erect; petals 1–2(–2.5) mm long; seeds slightly papillose, 0.64–0.85 mm long. Gametic chromosome number,  $n = 16$ .

Chromosome count vouchers, all  $n = 16$ . U.S. CALIFORNIA. Fresno Co.: Simpson Meadow, Middle Fork Kings R. (seeds from *Howell 33792*, CAS), *Raven 19083* (MO). Mariposa Co.: 3.7 mi NW of Coulterville, along Hwy. 49, *Raven 18348* (MO). Monterey Co.: Twin Valley, El Piojo (seeds from *Hardham 5650*, RSA), *Raven 17528* (MO). Tuolumne Co.: ridge above Twain Harte (seeds from *Lewis & Snow 1243*, LA), *Raven 16025* (MO). Ventura Co.: Rose L. (seeds from *Hardham 6126*, RSA), *Raven 17741* (MO). IDAHO. Valley Co.: E side of Big Payette L., *Raven 18518* (MO). OREGON. Douglas Co.: 20 mi E of Roseburg (seeds from *Gratkowski*, OSC), *Raven 19089* (MO).

#### ACKNOWLEDGMENTS

This study has been supported by a series of grants from the U.S. National Science Foundation to P. H. R., and a California State College Bakersfield Foundation grant to S. S. We are grateful to the curators of herbaria who made material of these species available to us: ARIZ, CAS, DS, GH, ID, JEPS, K, LA, MO, NY, ORE, OSC, POM, RSA, UC, US, WS, WTU.

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A NEW SPECIES OF FLAVERIA (COMPOSITAE:  
FLAVERIINAE) FROM GRAND CANYON, ARIZONA<sup>1</sup>

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Recent collections from remote areas of the Grand Canyon National Park, Coconino and Mohave Counties, Arizona, include a hitherto undescribed endemic species of *Flaveria* Juss. *Flaveria* is a widespread genus of mostly American distribution. Our new species, *Flaveria mcdougallii*, is the second member of the genus known from Arizona and extends the range of the genus into the Mohave Desert region.

We are naming the new species in honor of Dr. Walter B. McDougall, Curator of Botany at the Museum of Northern Arizona since 1955 and a long-time student of the flora of the National Parks System and northern Arizona. His many contributions are summarized by Hamann (1974).

***Flaveria mcdougallii*** Theroux, Pinkava & Keil, sp. nov. (Fig. 1) Suffrutex robustus usque ad 1 m diametro, basi crassa rhizomata lignea 1–3 cm diametro, caulibus numerosis erectis vel ascendentibus, usque ad 1 m altis, glabris, fragilibus, in dimidio superiore herbaceis virentibus, porcis decurrentibus leviter angulosis, in dimidio inferiore aetate lignescens et tephro-brunnescentibus. Folia opposita, carnosa, basi connata, linearia vel anguste lineari-lanceolata saepe falcata, 5–14 cm longa, 2–8 mm lata, apice acuta, basi cuneata, margine integra, 1–5-nervata, glabra. Capitula discoidea, sessilia vel brevipedunculata (1–2 mm), in fasciculis oligocephalis in cymis corymbiformibus 4–5 cm diametro aggregatis; ramuli capitulae a bracteolis subtenti; bracteolae infimae foliaceae, supernae reductae et squamiformes, 1–2 mm longae. Involucrum turbinatum; phyllaria 3–6, oblongo-lanceolata, 2.0–3.5 mm longa, 0.6–0.8 mm lata, dorsaliter 3–5 nervata, apicibus acutis erectis vel vix patentibus, basibus truncatis, in marginibus et adaxiale prope apicem trichomatibus multicellularibus 0.02–0.04 mm longis puberulenta vel glabrescentia. Flosculi ligulati nulli. Flosculi tubuliflori 3–6; corollae flavae, 3.5–4.0 mm longae, glabrae, tubis 1–2 mm longis, faucibus 1.0–1.5 mm longis, lobis 1 mm longis ad maturitatem reflexis; antherae exsertae thecis 1.0–1.5 mm longis, basaliter rotundatae vel truncatae, appendicibus terminalibus oblongis, 0.3 mm longis et 0.1 mm latis, subacutis; pollenis granum circa 23  $\mu$ m diametro; styli basaliter bulboso-incrassati, glabri, altitudine fere antheras aequantes, ramulis exilibus recurvatis apice peni-

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cillatis, extus papillosis. Achenia 1.5–2.5 mm longa, brunnescentia vel nigrescentia, cylindrica, circa 0.4 mm diametro, 10-costata, trichomatibus duplicibus 0.05–0.08 mm longis puberulenta vel glabra, carpodio eburneo obliquo 0.1 mm longo et 0.3 mm lata; pappus coroniformis, squamellis fimbriatis 0.2–0.4 mm longis, plus minusve connatis. Chromosome numerus:  $2n = 18_{II}$ .

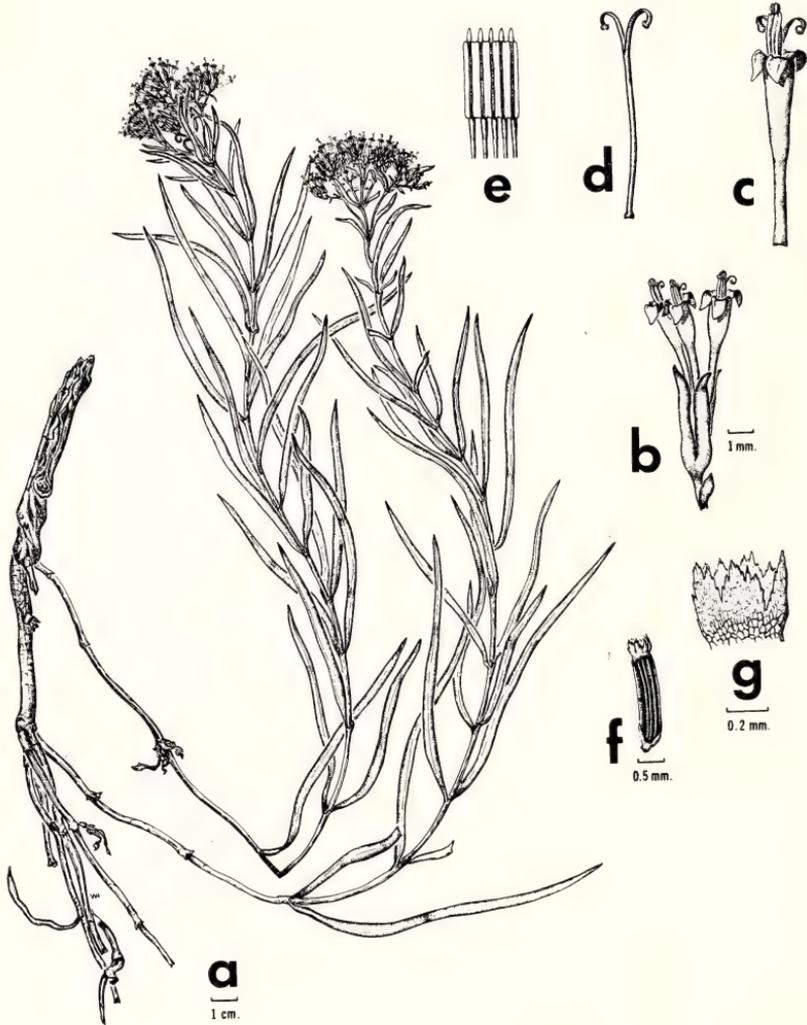


FIG. 1. *Flaveria mcdougallii*. a, Habit; b, Head; c, Corolla; d, Style; e, Stamens; f, Achene; g, Pappus. c, d, e, f, same scale.

TYPE: United States, Arizona, Mohave Co., Grand Canyon National Park, Cove Canyon (174.2 mi below Lee's Ferry), 27 Jan 1976, *M. E. Theroux 1675* (Holotype: US; isotypes: ARIZ, ASC, ASU, DES, GCNP, GH, MNA, NY, RSA, SRSC, TEX, UC).

PARATYPES: United States, Arizona, Coconino Co., Grand Canyon National Park, Matkatamiba Canyon (148.8 mi below Lee's Ferry), 1 Oct 1975, *M. E. Theroux 1519* (MNA); Mohave Co., Grand Canyon National Park, Cove Canyon, 5 Oct 1975, *M. E. Theroux 1567* (MNA).

The type locality of *Flaveria mcdougallii* is a permanent saline spring situated near the mouth of a remote tributary canyon in the Grand Canyon. The spring, located at ca. 550 m on an ESE-facing slope, is fed by seepage from the Muav Limestone at its contact with the underlying Bright Angel Shale. Direct sunlight reaches the site for a period of only a few hours per day because of shading by surrounding canyon walls. The soil where *F. mcdougallii* grows is a saturated, highly organic varying mixture of sand and silt bound together by roots and rhizomes of two grass species, *Muhlenbergia asperifolia* (Nees & My.) Parodi and *Sporobolus airoides* (Torr.) Torr. The A-horizon averages about 30 cm deep and overlies an unstable, shifting aggregation of coarse shale talus. *Flaveria mcdougallii* grows in soils ranging from a loose mud to consolidated travertine oxides. The other site where *F. mcdougallii* has been collected is very similar to the type locality.

Both collection localities for *F. mcdougallii* are situated in the narrow strip of Mohave Desert vegetation that parallels the Colorado River through the western two-thirds of the Grand Canyon. The most common woody species represented in the area are *Acacia greggii* A. Gray, *Lycium pallidum* Miers, and *Zizyphus obtusifolia* (T. & G.) A. Gray. The new species is the dominant shrub at the springy sites. In addition to the grasses and shrubs mentioned above, associated species include *Brickellia longifolia* S. Wats. and *Mentzelia pumila* (Nutt.) T. & G. in wet soil and *Adiantum capillus-veneris* L., *Mimulus cardinalis* Dougl., and *Petrophytum caespitosum* (Nutt.) Rydb. on seepage rock-faces.

Reproduction in the known populations of *Flaveria mcdougallii* is apparently predominately vegetative. Woody horizontal rhizomes 4–5 cm below the soil surface connect adjacent clumps. Seed set is low with many ovaries shrunken and apparently abortive. According to Dr. A. M. Powell (pers. comm.) perennial *Flaveria* taxa are self-sterile. The low seed set of *F. mcdougallii* may indicate a low incidence of cross-pollination. Our success in germinating a few achenes on moistened filter paper indicates that at least some of the seeds that do form are viable.

*Flaveria* is morphologically similar in many respects to both *Sartwellia* A. Gray and *Haploësthes* A. Gray (Turner, 1971, 1975). All three genera are characterized by opposite, often fleshy, basally connate leaves; yellow-flowered, cymosely-clustered heads with distinct, uniseriate or biseriate involucre bracts; penicillate-tipped, recurved style branches;

TABLE 1. COMPARISON OF CHARACTERISTICS OF MEMBERS OF THE FLAVERINAE

Character	<i>Flaveria</i>	<i>Flaveria mcdougallii</i>	<i>Sartwellia</i>	<i>Haploësthes</i>
Leaf shape	Linear, linear-lanceolate, or ovate	Linear or linear-lanceolate	Linear	Linear or linear-lanceolate
Phyllary shape	Narrowly oblong to lanceolate	Oblong-lanceolate	Ovate	Ovate
Number of ray florets	0-1	0	2-5	5 or 8
Number of disc florets	1-15	3-6	10-40	20-100
Pappus type	No pappus or separate scales (in one species)	Crown of united scales	Alternating bristles and scales or crown of united scales (in one species)	Many bristles
Corolla pubescence	Multicellular trichomes (or glabrous in some plants from coastal region)	Glabrous	Glabrous	Glabrous
Achene pubescence	Glabrous	Glabrous or double-hairs	Double-hairs	Double-hairs
Photosynthetic pathways	C <sub>3</sub> and C <sub>4</sub> (Smith and Turner, 1975)	C <sub>3</sub> ( <sup>13</sup> C‰ = -30.0)	C <sub>3</sub> (one species reported by Smith and Turner, 1975)	.....
Distribution	Widespread (but not Mohave Desert)	Mohave Desert Region	Chihuahuan Desert Region	Chihuahuan Desert Region
Habitat	Various moist substrates including gypsum	Saline springs	Dry gypseous soils	Dry gypseous soils

and brown to black, cylindrical, 8–10-ribbed achenes. All apparently have the same chromosome base number,  $x = 18$  (Turner, 1975). Recent authors (Turner and Johnston, 1961; Turner, 1971, 1975; Powell, pers. comm.) have maintained the three as separate genera. The principal morphological differences among the three genera are number of flowers per head, pappus structure, and pubescence of florets (Table 1).

The features of *Flaveria mcdougallii* are to some extent intermediate between those of *Flaveria* and *Sartwellia* as traditionally delimited (Table 1). *Flaveria mcdougallii* has slightly broadened leaves and eradiate, few-flowered heads with narrow phyllaries, characteristics that it shares with other *Flaveria* taxa. It also has a coroniform pappus and glabrous corollas, features that have until now been characteristic of *Sartwellia*. Some plants from one population of *F. mcdougallii* have glabrous achenes whereas other members of the same population and representatives of the other population have achenes puberulent with double-hairs (Zwillingshaare). According to Powell (pers. comm.), the double-hairs are characteristic of *Sartwellia* and until now have not been known in *Flaveria*.

If morphology alone were the deciding factor, the continued acceptance of *Flaveria* and *Sartwellia*, and possibly even *Haploësthes* as distinct genera might be questioned. Fortunately, systematists have at their disposal a battery of experimental techniques for gathering information about relationships. Powell (pers. comm.) is currently carrying on an experimental investigation of taxa in the Flaveriinae that hopefully will clarify the biological relationships among the genera. We have made material of *F. mcdougallii* available to Dr. Powell for his study.

#### ACKNOWLEDGMENTS

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## NORTHERN COASTAL SCRUB ON POINT REYES PENINSULA, CALIFORNIA

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According to Munz (1959) and Ornduff (1974), northern coastal scrub extends in a narrow coastal strip from southern Oregon to Point Sur, Monterey County. The vegetation type has recently been reviewed by Heady et al. (1977), who showed it to be a discontinuous community within a grassland matrix, dominated either by *Baccharis pilularis* var. *consanguinea* or *Lupinus arboreus*. Few quantitative studies for the type exist. The grassland-scrub mosaic is complex, and Howell (1970) pointed out that the scrub "... is perhaps the least definite in its boundaries ... " of any Marin County community.

Our objective was to document quantitatively the composition and structure of northern coastal scrub for an area representative of its range. Point Reyes Peninsula was selected as the study site because of its proximity to Davis, its topographic and soil diversity, its protected (National Park) status, and its relatively well-known land-use history. Within the Peninsula, major sample areas were on the slopes of Mt. Vision and near Laguna Ranch (Fig. 1). The elevation of Mt. Vision sites made the vegetation typical of scrub to the north, in the center of its distributional range. Additional, minor sample areas were near Tomales Point and in Tomales State Park.

### DESCRIPTION OF THE AREA

The climate of Pt. Reyes Peninsula is Mediterranean, modified by a maritime influence. It is characterized by cool, foggy but otherwise dry summers and cool, wet winters.

Temperature and rainfall data were obtained from unpublished National Park Service records from the Bear Valley Weather Station (24 m elevation) for 1964-75. Due to topography, annual rainfall varies markedly within short distances, but only sporadic climatic records exist for the Mt. Vision area (395 m), and this prohibits comparison between our high and low elevation sample sites. Mean annual precipitation at Bear Valley was 1,052 mm over the 11-yr. period, with the greatest amount occurring October through April. The driest months are July-September and total rainfall then averages 7 mm. According to Howell (1970), the average annual temperature is 11.4°C. The range of average temperature from warmest to coldest months is less than 2°C, although the extremes have ranged from 38.9°C (September, 1971) to -9.4°C (December, 1972) at Bear Valley. Sub-freezing temperatures occur any-time from October to May but are infrequent and seldom include hard frosts. Prevailing winds are WNW.

Pt. Reyes is gently rolling to hilly; elevation ranges from sea level to 435 m on Mt. Wittenburg. Inverness Ridge, averaging 300 m, runs parallel to Tomales Bay from Tomales Point south to the Park boundary and beyond. Ocean-facing cliffs, about 20–50 m high, are common along most of Drakes Bay and the Pacific Ocean coast.

The vegetation was mapped by Donald Lauer in 1973 (Point Reyes National Seashore, 1973), and his map shows a mosaic of coastal prairie, northern coastal scrub, closed-cone pine forest, mixed evergreen forest, and localized patches of dune scrub close to shore.

Point Reyes Peninsula is joined to the mainland along the San Andreas Fault. According to Howell (1970) and Feray et al. (1968), the peninsula is composed of three major geologic formations. The NE quarter and the tip of the point is Montara granitic formation of Mesozoic origin. The SE half of the peninsula is Monterey shale formation of Miocene origin. Some stabilized sand dune deposits overlay the Monterey shale in the central coastal portion.

The U.S. Soil Survey is in the process of mapping soil types of Point Reyes Peninsula. Through personal communication with Gordon Shipman of the Marin County Soil Survey staff, we were able to define the general soil types of the primary study locations. The soil of Mt. Vision sites is a clay loam, over a clay hardpan, about 50–100 cm deep, over quartz diorite parent material. It is similar to the Auberry series as defined by the National Cooperative Soil Survey (NCSS). Soil at the Laguna Ranch sites is a shaley clay loam, over shaley clay, about 50–100 cm deep, over shale parent material. It is similar to the NCSS Santa Lucia series in color, and in shallowness it is much like the NCSS Lopez series. The soil at Tomales State Park is a coarse sandy loam up to 1.5 m deep. It has developed on a stabilized sand dune deposit and is similar to the NCSS Sheridan series. We have no data for soil beneath the Tomales Point site.

#### SELECTION OF SAMPLE SITES AND SAMPLING METHOD

Sampling areas were chosen because they represent, with one exception, undisturbed, extensive, distinct examples of northern coastal scrub. The exception was a site on Tomales Point in an area actively grazed by cattle. The areas provided a variety of slope, aspect, soil type, and elevation which seemed to include the full range of habitat occupied by the vegetation type.

The method of sampling was by line transect. A total of 20 transects was established at 15 different sites (Fig. 1). Transects were 20 m long, but sometimes they were subdivided into two smaller units and placed apart from each other, depending on homogeneity of the site. Preliminary observations indicated that a length of 15 m included most variability and gave a representative sample. Within a given site, transects were subjectively located after reconnaissance. Plant cover of each species

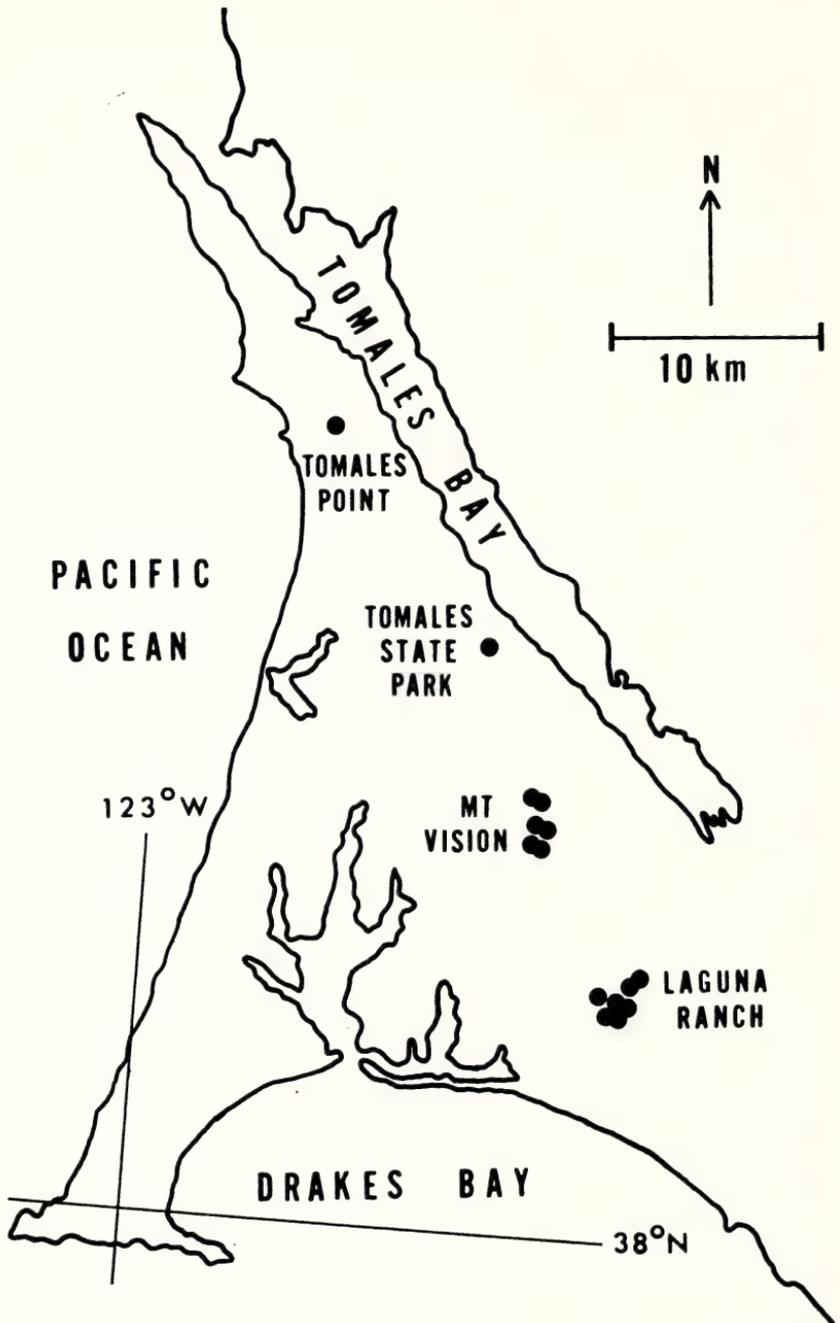


FIG. 1. Point Reyes Peninsula and location of northern coastal scrub sampling sites (dots).

TABLE 1. ABSOLUTE COVER (%) OF ALL SPECIES ENCOUNTERED ON 15 NORTHERN COASTAL SCRUB SITES ON POINT REYES PENINSULA. t &lt; 0.1% cover.

Taxa	Average	"N-facing"	"S-facing"
<i>Anaphalis margaritacea</i>	0.3	0.5	....
<i>Artemisia californica</i>	2.7	....	6.0
<i>Baccharis pilularis</i> var. <i>consanguinea</i>	31.2	25.7	38.0
<i>Corylus cornuta</i>	3.1	5.5	....
<i>Elymus condensatus</i>	2.0	3.5	0.1
<i>Erechtites prenanthoides</i>	0.3	0.3	0.2
<i>Fragaria californica</i>	0.4	0.6	0.3
<i>Galium nuttallii</i>	0.5	0.2	0.8
<i>Gaultheria shallon</i>	3.9	7.0	....
<i>Heracleum lanatum</i>	1.6	1.6	1.6
<i>Holodiscus discolor</i>	0.1	0.2	....
<i>Lupinus arboreus</i>	t	0.1	....
<i>Mimulus aurantiacus</i>	7.0	1.0	14.5
<i>Picris echioides</i>	t	0.1	....
<i>Polystichum munitum</i>	28.6	44.5	8.4
<i>Pteridium aquilinum</i>	6.4	3.5	10.0
<i>Rhamnus californica</i>	20.1	4.3	40.0
<i>Rhus diversiloba</i>	2.2	0.2	4.6
<i>Rubus ursinus</i> and/or <i>R. vitifolius</i>	5.8	3.6	8.7
<i>Satureja douglasii</i>	5.9	2.4	10.4
<i>Stachys rigida</i>	1.6	1.4	1.9
Total	123.8	110.2	145.5

along the transect was measured to the nearest 0.5 dm. Additional data recorded for each site were slope, aspect, average vegetation height, and a subjective evaluation of soil moisture conditions (very dry, dry, moist, wet, very wet). Any species not on the transect but occurring nearby was also noted. Since the study was conducted January-March, maximum cover of *Rhus* and some herbs could not be measured. Nomenclature follows Munz (1959) and voucher specimens are deposited in DAV.

#### DISCUSSION AND CONCLUSIONS

Our 15 transect sites ranged in elevation from 50 to 340 m, in slope aspect from 90° (due E) to 350° (NNW), and in steepness of slope from 26 to 80%. Inspection of cover data indicated that slope aspect had the greatest effect on community composition. Table 1 summarizes absolute cover by slope aspect category. "North-facing" here includes all slopes from 270° (due W) to 90° (due E) in orientation, and "south-facing" includes all other orientations.

North-facing slopes were dominated in the overstory by a rather open (26% cover) canopy about 1.5 m tall of *Baccharis pilularis* var. *consanguinea*. The understory, about 0.3 m tall, was dominated by *Polystichum* (45% cover), with *Gaultheria*, *Corylus*, *Pteridium*, *Rubus*, and *Elymus* species accounting for another 27% cover. It was essentially a two-layered community. There was less than 2% bare ground. South-facing

slopes had shared dominance by *Baccharis* (38% cover) and *Rhamnus californica* (40% cover) in an overstory canopy about 1.0 m tall, with an understory dominated by *Mimulus*, *Satureja*, and *Pteridium* species. The southern affinity of this phase is shown by modest cover values for *Artemisia californica* and *Rhus diversiloba*, dominants of coastal sage scrub in the Monterey area (Heady et al. 1977). North-facing slopes exhibited less than 4% cover by deciduous species while south-facing slopes exhibited more than 13%, also illustrating affinity to the predominantly deciduous coastal sage scrub. Species richness was greater on north-facing slopes (total of 20 species encountered) than on south-facing slopes (15 species). There was twice as much bare ground beneath south-facing stands. Only a few species were completely restricted by slope aspect: *Anaphalis margaritacea*, *Corylus cornuta*, *Gaultheria shallon*, *Holodiscus discolor*, *Lupinus arboreus*, and *Picris echioides* were found only on north-facing slopes, and *Artemisia californica* was found only on south-facing slopes.

Additional, stand to stand variation was revealed by ordination. A

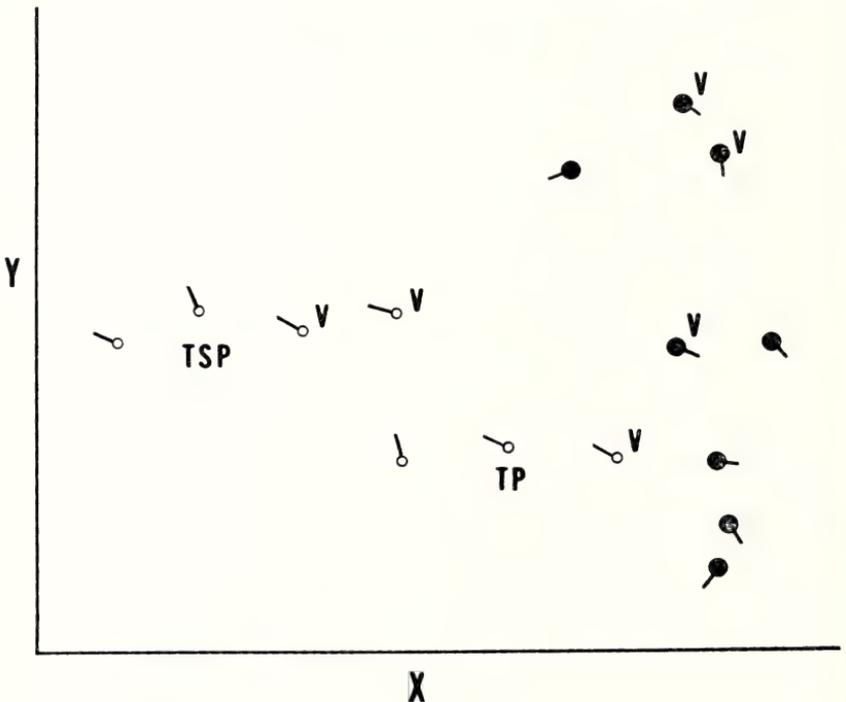


FIG. 2. Ordination of stands. For convenience, "north-facing" stands are indicated as o's, "south-facing" stands as dots. The actual aspect is indicated by the direction of the line away from each dot or o. Stands on Mt. Vision, Tomales Point and Tomales State Park are marked with a V, TP, TSP, respectively. Laguna Ranch sites are unmarked.

similarity index (S) for every pair of stands was calculated as  $S = RC_s/200$ , where  $RC_s$  is the sum of the smaller of the pair of relative cover values for each taxon, for all taxa common to the two stands being compared, and 200 is the sum of relative cover values for all taxa in stands A and B. This equation is Motyka's modification of Sorenson's Index (Mueller-Dombois and Ellenberg, 1974).

The matrix of similarity indices was displayed by a polar ordination method of Bray and Curtis (Cottam et al. 1974), with three mutually orthogonal axes, X, Y, and Z.

The ordination of stands on X and Y axes is shown in Fig. 2 (these two axes accounted for 79% of stand-stand variation, and the Z axis gave very little additional spread of stands). The X axis correlates with our subjective moisture assessments of stands. Relatively mesic, north-facing stands on the left grade into relatively dry, south-facing, lower elevation stands on the right. The Y axis, however, which adds considerable spread to the south-facing stands, does not correlate well with any of the other environmental factors that we recorded (steepness of slope, land-use history, soil type, elevation). Degree of exposure to prevailing winds (a combination of aspect, nearness to the Pacific Ocean, and openness of the site to air movement) accounts for some of the spread on the Y axis. (Subjectively, we noticed that canopy height was lowest on the windiest sites.)

We found no evidence that northern coastal scrub is seral to forest. In the Berkeley Hills, McBride and Heady (1968) and McBride (1974) reported that a *Baccharis* scrub was being invaded by elements of oak or mixed evergreen forest. At Point Reyes National Seashore, Research Biologist Richard M. Brown believes the scrub may be seral to closed-cone pine forest (pers. comm.). Although we did find an occasional tree of *Umbellularia californica*, *Pseudotsuga menziesii*, *Quercus agrifolia*, or *Pinus muricata* in the midst of scrub, we saw no seedlings or saplings.

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STATUS OF *ALLIUM SERRATUM* (LILIACEAE)  
AND DESCRIPTION OF A NEW SPECIES

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In 1871, Watson described "*Allium serratum*" from California. In the protologue he cited ten collections and listed *Allium amplexans* Torr. (1865) as a synonym, indicating that its type (Sonoma, 3 May 185-, *Bigelow s.n.*, NY) "is a very young undeveloped state and the name is inapplicable to the mature plant". Application of the current rules of nomenclature (Arts. 62 and 63) makes "*A. serratum*" superfluous and illegitimate. Later Watson (1879) reconsidered his circumscription of "*A. serratum*". Here he cited *A. amplexans* Torr. as a synonym of *A. attenuifolium* Kell. (1863). (We agree that the types of these names are conspecific; however, the correct name is *A. amplexans* Torr.) "*Allium serratum*" then apparently referred to a taxon represented by the syntypes originally cited in 1871.

During investigation into the taxonomy of the *Allium acuminatum* alliance to which "*A. serratum*" has been referred (Saghir et al., 1966) we studied all but four (*Bolander s.n.*, *Douglas s.n.*, *Kellogg s.n.*, and *Wallace s.n.*) of those ten collections. We believe the six collections studied represent two species. Five (*Hartweg 1991*, GH, NY; *Fremont 469*, GH; *Bridges 345*, NY, US; *Stillman s.n.*, NY; *Rich, s.n.*, NY) correspond closely to Watson's original description and he annotated them "*Allium serratum*". The other specimen (Benecia, 1853-4, *Bigelow s.n.*, GH) does not match the original description and Watson seems to have recognized this since he annotated it "*Allium serratum*, form". This is reinforced by a specimen (*Kellogg 1012*, GH) that he annotated in the same manner but that was not cited among the syntypes. Later authors incorrectly applied the name "*A. serratum*" to these latter specimens disregarding the fact that they do not correspond to Watson's description nor his interpretation of what was "*A. serratum*" and what was a form of this species.

The name *Allium peninsulare* Lemmon ex Greene (1888, Holotype: *Lemmon s.n.* NDG) is the correct name for Watson's typical "A. serratum" and has long been used in this sense. We consider Watson's "A. serratum, form" to represent a distinct species as follows:

**Allium serra** McNeal & Ownbey, sp. nov. (Fig. 1).

Bulbus ovoideus vel subglobosus, 8–12 mm longus, tunico exteriori plerumque brunneo, manifeste celluloso-reticulato, maculis transverse elongatis, deorsum angulatis, regularibus verticalibus ordinibus dispositis, tunicis interioribus albis; folia 2–4, anguste concavo-convexa vel subteretia, scapo aequilonga vel quarta parte breviora; scapus teres, gracilis, 15–30 (50) cm longus; bracteae 2/3, lanceolato-ovatae vel ovatae, acuminatae, 1–2 cm longae; umbella 10–35 (vel pluribus) florus, compacta, pedicellis 6–15 mm longis; pedicelli et flores maturi simul decidui; segmenta perianthii integra rosea, lanceolata vel lanceolato-ovata, acuta, obtusa vel emarginata, erecta, papyracea maturescentibus fructibus et conniventia super capsulam; segmenta perianthii exteriora 8–11 mm longa et 3.0–5.5 mm lata, interiora breviora et angustiora; stamina inclusa, antheris luteis vel rubris, apiculatis; capsula triloba, cristata 3 minutis bilobis processibus circa styli basin; stigma capitatum, trilobum; semina atra, alveolis minute asperis.

TYPE: California, Stanislaus Co., 20.5 mi W of Patterson in Canyon Del Puerto, dry rocky hillside above the road, 11 Apr 1968, *McNeal 397* (Holotype, WS!; isotype, CPH!)

The specific epithet refers to the outer bulb coat which, when broken, has a serrate edge resulting from its typical herringbone reticulation pattern (Fig. 1,f).

Representative specimens (for a complete list of specimens see McNeal, 1970): Alameda Co., Corral Hollow, *Eastwood & Howell 5293* (CAS); Butte Co., Chico, May 1918, *Rixford* (CAS); Colusa Co., Rt. 20, 5 mi E of the Lake Co. line, *Benson 4327* (ND, POM); Contra Costa Co., 2 mi inside the N gate of Mt. Diablo, *Hoffman 2796* (WS); Glenn Co., hills W of Willows, *Eastwood 11149* (CAS); Lake Co., 6 mi N of Lower Lake, *Eastwood & Howell 5583* (CAS, UC, WTU); Merced Co., 10 mi S of Los Banos, *Hoover 2891* (UC, US, WS); Napa Co., 1.3 mi S of Knoxville, *Keck 2374* (CAS, DS, POM, UC); San Joaquin Co., E end of Corral Hollow, *Eastwood & Howell 2094* (CAS); Santa Clara Co., Edenvale, *Thomas 8990* (DS, OSC, RSA); Solano Co., foothills of the Vaca Mts., W of Vacaville, *Heller 15559* (DS, MO, NY, UC, US, WS, WTU); Stanislaus Co., Del Puerto Canyon, 8.3 mi W of Patterson, *McNeal 394* (CPH, WS).

*Allium serra* grows on heavy clay or serpentine soils in the Inner Coast Range of California from Butte Co. south to central Merced Co. at 300–600 m. It is associated with such plants as *Pinus sabiniana*, *Heteromeles arbutifolia*, *Quercus sp.*, *Rhus diversiloba*, *Dodocatheon hendersonii*, and several species of introduced annual grasses common throughout the range.

*Allium serra* belongs to the *A. acuminatum* alliance on the basis of its thick, cellular reticulate bulb coat, which develops from the inner epidermis of the inner leaf base (McNeal and Ownbey, 1973). It appears to be the most closely related to *A. peninsulare* and *A. amplexens*. These are widespread species; *A. peninsulare* occurs south and east of *A. serra* except for two records in the southern part of its range, while *A. amplexens* is sympatric with *A. serra* throughout its range. The resemblances to these two species are in an unrelated combination of morphologic characters. In addition to characteristics in the key below, *A. serra* resembles *A. amplexens* in that the perianth segments, which are erect at anthesis, become papery and connivent over the capsule as it matures. Both species have short pedicels and compact umbels with the pedicel falling as a unit with its flower when the capsules are mature. In *A. peninsulare* the pedicels are comparatively long and the umbels are open with the pedicels and flowers persisting after the capsule matures. In *A. peninsulare* flowers are deep reddish purple while in *A. amplexens* they are white or sometimes flushed with pink; *A. serra* has bright pink flowers.

Chromosome numbers of both *Allium serra* and *A. peninsulare* are  $2n = 14$  while *A. amplexens* has two chromosomal races,  $2n = 3x = 21$  and  $2n = 4x = 28$ , both of which occur in the range of *A. serra* (Table 1).

TABLE 1. CHROMOSOME COUNTS FOR *Allium*. All collections are from California; vouchers are in WS. Our counts were all made during first meiotic metaphase.

\* indicates previously unpublished counts by Dr. Hannah C. Aase.

*Allium serra* McNeal & Ownbey

Alameda Co., Livermore—Tesla Rd., 15.4 mi from Livermore, *Hoffman 2799*, **7 II\***; Colusa Co., above Bear Creek, ca 15 mi N of Rumsey, *Henry s.n.* **7 II**; Lake Co., Hwy. 20, 12 mi E of its jct. with Hwy. 53, *McNeal 408*, **7 II**; Stanislaus Co., Del Puerto Canyon, 20.5 mi W of Patterson, *McNeal 397*, **7 II**; Yolo Co., Cache Creek, 3 mi N of Rumsey, *McNeal 407*, **7 II**.

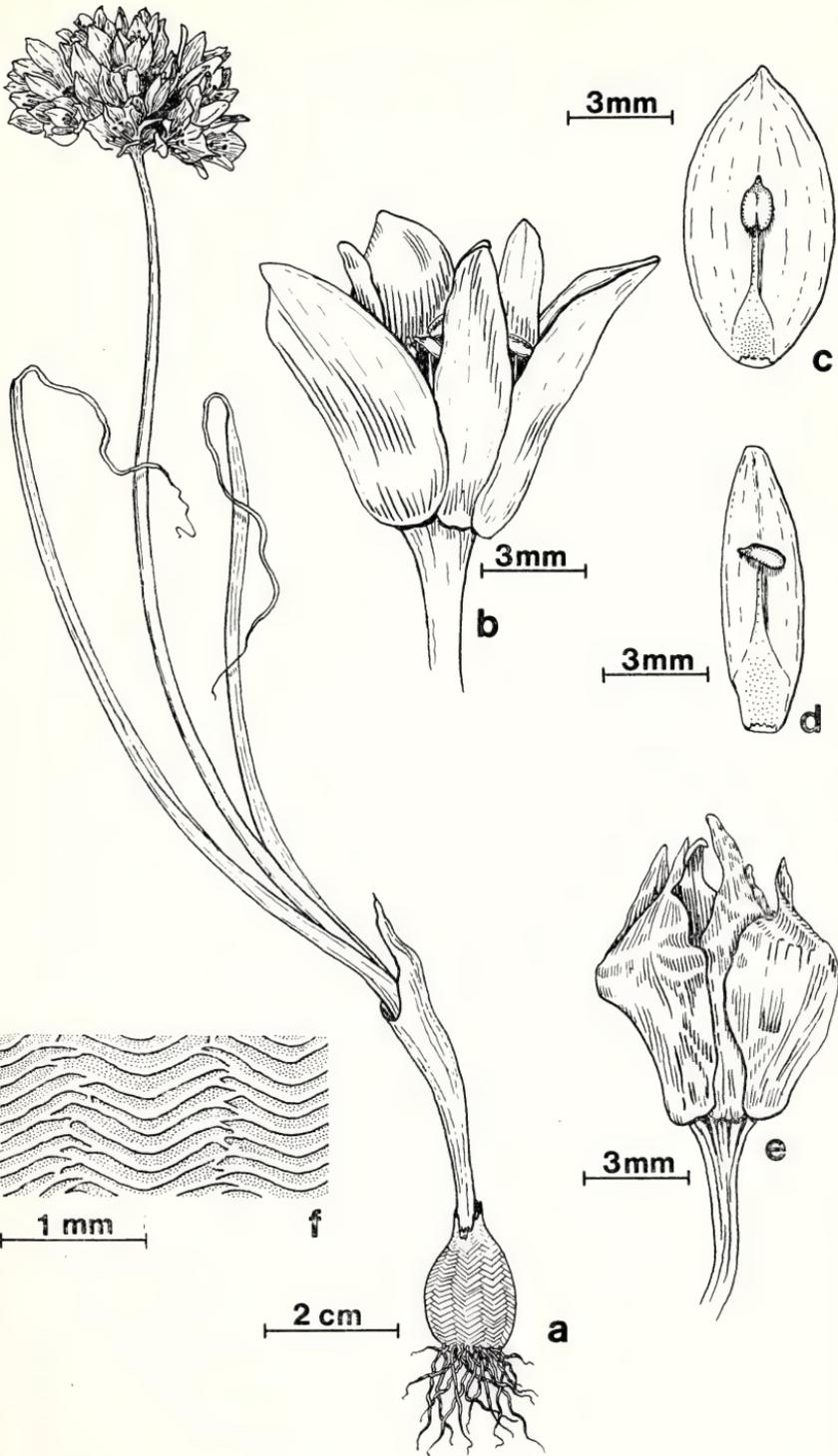
*Allium amplexens* Torr.

Colusa Co., Rt. 20, 21 mi SW of Williams, *Ownbey and Ownbey 2951*, **21 I\*** (Achiasmatic); Lake Co., 6 mi S of Hwy. 20 on Scotts Valley Rd. to Lakeport, *McNeal 409*, **14 II**; 2.8 mi N of Middleton, *Ownbey and Ownbey 2954*, **14 II\***; Marin Co., Big Rock Ridge, 2–3 mi W of Hamilton AFB, *Robbins s.n.*, **21 I\*** (Achiasmatic); San Mateo Co., Jasper Ridge experimental area, edge of Stanford U., *Raven s.n.*, **14 II**; Stanislaus Co., Mt. Hamilton-Livermore Rd., 1.0 mi N of Canyon Del Puerto Rd., *McNeal 575*, **21 I** (Achiasmatic).

*Allium peninsulare* Lemmon ex Greene

Butte Co., Chico-Paradise Rd., 14.8 mi E of Chico, *Hoffman 3774*, **7 II\***; Kern Co., Rt. 178, 1.5 mi E of Onyx, *McNeal 389*, **7 II**.

FIG. 1. *Allium serra*. a, Habit. b, Flower. c, Outer perianth segment with anther in erect position. d, Inner perianth segment with anther in versatile position. e, Older flower with perianth segments connivent over the capsule. f, Portion of outer bulb coat with herringbone reticulation pattern. From 35 mm transparency of living plant and type collection.



The following key distinguishes *Allium serra* from other members of the *A. acuminatum* alliance that have a similar herringbone reticulation pattern on the bulb coats.

- a. Ovary crested with 6 lateral processes; meshes of the reticulum wavy, not in sharply serrate transverse rows, forming a more or less indistinct herringbone pattern, or contorted; inner and outer perianth segments approximately equal in length and breadth. . . . . *Allium amplectens* Torr.
- aa. Ovary crested with 3 minute, 2-lobed central processes; meshes of the reticulum in sharply serrate transverse rows, forming a herringbone pattern; inner perianth segments shorter and narrower than the outer.
  - b. Perianth segments connivent after anthesis, becoming papery; umbel shattering, each flower with its pedicel deciduous as a unit. . . . . *Allium serra* McNeal & Ownbey
  - bb. Perianth segments not connivent after anthesis, texture dull or shiny, never papery; flowers persisting.
    - c. Plants low, fleshy; leaves 3–6, the shorter ones arcuate, the longer tortuous; bracts broadly ovate, abruptly acuminate; umbel compact, pedicels short. Sea cliffs from San Mateo Co. to Mendocino Co., California . . . . *Allium dichlamydeum* Greene
    - cc. Plants taller, slender or stout, not appearing fleshy; leaves 2–4, straight or curved; bracts lanceolate to ovate, acuminate; umbels loose, pedicels spreading. Interior California from Butte Co. south along the Sierra Nevada foothills and Coast Range into Baja California, also in the Santa Cruz Mountains of San Mateo Co.
      - d. Inner perianth segments crisped. . . . *Allium crispum* Greene
      - dd. Inner perianth segments with margins entire or obscurely serrulate, never crisped. . . . . *Allium peninsulare* Lemmon ex Greene

#### ACKNOWLEDGMENTS

We thank curators of herbaria (CAS, DS, GH, JEPS, MO, ND, NY, OSC, POM, RSA, UC, US, WTU) from which material was borrowed during the course of this investigation. We also thank Dr. Robert Smutny of the Classics Department, University of the Pacific, for assistance in preparing the Latin diagnosis of *Allium serra*; Sandra McNett for preparing the drawings; and Dr. Hannah C. Aase for permission to use some of the chromosomal data included in this paper.

Dr. Marion Ownbey died 6 December 1974 without seeing the final drafts of this manuscript. As senior author, I am solely responsible for any errors that appear.

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## RE-ESTABLISHMENT OF THE GENUS HYBRIDELLA (ASTERACEAE:HELIANTHEAE)

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*Hybridella* is a small genus of three herbaceous perennial taxa native to Mexico. It was treated as a subgenus of *Zaluzania* by Robinson and Greenman (1899) and by Sharp (1935), although it was described as a genus by Cassini in 1821. During a study of *Zaluzania* (Olsen, 1977), I became aware that *Hybridella* comprises a cohesive unit phylogenetically remote from *Zaluzania*. Based on morphological, cytological, and ecological data, it should be positioned elsewhere. Table 1 lists major differences between the two genera.

There are only two chromosome counts available for *Hybridella*: *H. globosa* var. *globosa* ( $n = 16$ , Powell and Turner, 1963) and *H. globosa* var. *myriophylla* ( $n = 16$ , Olsen 265, LL, published here). These counts suggest a base number of  $x = 16$  for the genus.

The most likely relationships of *Hybridella* are with *Heliomeris*, a *Viguiera* segregate (Yates, 1967). The base chromosome number of *Heliomeris* is  $x = 8$  (Turner, 1976), presumably one of the ancestral numbers in the Heliantheae (Stuessy, 1976). It is likely that the ancestral base number for *Hybridella* is  $x = 8$ , with stabilization occurring at the tetraploid level. This coupled with the obvious floral similarities between *Hybridella* and *Heliomeris* (Table 1), suggests a close relationship between the two taxa.

TABLE 1. COMPARISON OF *HYBRIDELLA*, *ZALUZANIA*, AND *HELIOMERIS*

<i>HYBRIDELLA</i>	<i>ZALUZANIA</i>	<i>HELIOMERIS</i>
1. Base chromosome number, $x = 16$	Base chromosome number, $x = 18$	Base chromosome number, $x = 8$
2. Leaves pinnatisect	Leaves entire to tripartite, never pinnatisect	Leaves entire or serrate, never pinnatisect
3. Receptacle globose to hemispheric	Receptacle conical	Receptacle hemispheric
4. Tube of disc corolla pubescent with glandular hairs	Tube of disc corolla glabrous or with simple multicellular hairs	Tube of disc corolla may be glandular
5. Ray florets (always present) 15–20, ligule supplied by 5–7 principal veins.	Ray florets (when present) 8–10, ligule supplied by 10–12 principal veins	Ray florets (always present), ca 13, ligule supplied by usually 7 principal veins
6. Ligule of ray floret 2-lobed, usually with 3 basal lobes	Ligule or ray floret (2–)3-lobed, without basal lobes	Ligule of ray floret entire to 2-lobed without basal lobes
7. Plants generally occupying wet habitats; marshy soils; sandy riverbanks, etc.	Plants generally occupying dry habitats; <i>Larrea</i> flats, pine oak forests, etc.	Plants generally occupying dry rocky habitats; exposed mountain slopes, dry plains, etc.

*Hybridella* may also be related to *Viguiera* sect. *Chloracra* series *Pinnatilobatae*. The habit and leaf morphology, especially of *H. anthemidifolia*, resemble that found in *V. stenoloba*, a highly variable taxon with respect to leaf morphology (Butterwick, 1975); however, the absence of a pappus and the presence of fertile ray florets in *Hybridella* serve readily to distinguish the two.

In summary, I consider *Hybridella* to be more closely related to *Heliomeris* and elements of *Viguiera* than to *Zaluzania*; however, it is sufficiently distinct from both to deserve generic status.

#### TAXONOMIC TREATMENT

*HYBRIDELLA* Cass., Dict. Sci. Nat. 22:86. 1821. TYPE: *Anthemis globosa* Ort.

Herbaceous perennials with 1–4 stems arising from a woody caudex. Plants less than 1 m tall, stems striate, usually glabrous at the base, becoming pubescent above. Leaves alternate, sessile, usually obtrullate in outline, pinnatifid, glabrous on upper surface or with a few hairs on the veins, pubescent beneath. Heads one to several; solitary on well developed peduncles. Involucre of 2–3 series; bracts ovate-elliptic to lanceolate; outer series larger than the inner, pubescent with simple multicellular hairs. Receptacle globose or hemispherical. Chaff present,

the pales oblanceolate to linear, herbaceous or subherbaceous. Ray florets pistillate and fertile, 15–20 per head; corollas yellow, glandular along the tube, ligule usually 2-lobed, often with 2 lateral lobes at the base with a smaller central lobe (Fig. 1b). Disc florets numerous, bisexual, fertile; corollas yellow, base of the tube expanded. Ray achenes three-angled in cross section, black, glabrous to sparsely pubescent, epappose. Disc achenes four-angled in cross section, black, glabrous to sparsely pubescent, epappose. Base chromosome number,  $x = 16$ .

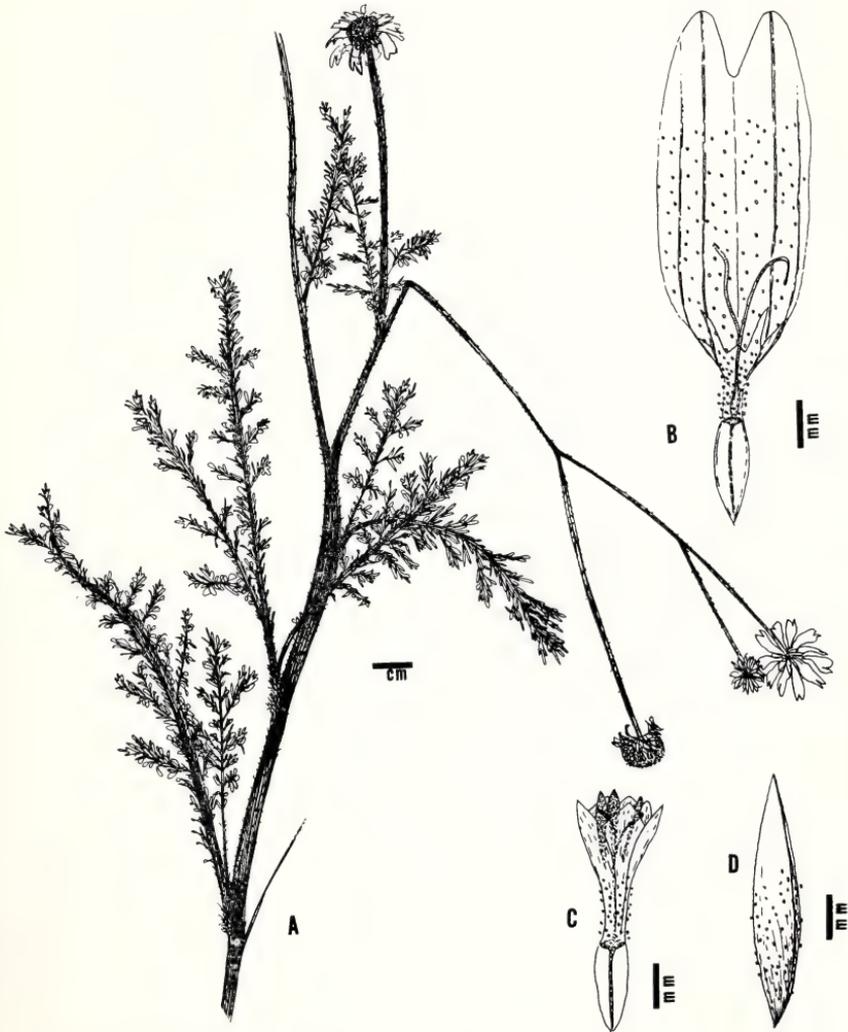


FIG. 1. *Hybridella globosa* var. *myriophylla*. A, habit. B, ray floret illustrating the lateral and basal lobing of the corolla. C, disc floret. D, receptacular chaff. Drawings from Olsen 265, LL.

Key to *Hybridella*

- Plants decumbent; leaves 2-3-pinnatifid, ultimate segments  
 1-2 mm broad. . . . . 1. *H. anthemidifolia*
- Plants erect; leaves 4-pinnatifid, ultimate segments less  
 than 1 mm broad.
- Ultimate leaf segments acute, more than  
 2 mm long. . . . . 2a. *H. globosa* var. *globosa*
- Ultimate leaf segments obtuse or rounded,  
 less than 2 mm long. . . . . 2b. *H. globosa* var. *myriophylla*

1. **Hybridella anthemidifolia** (Rob. & Greenm.) Olsen, comb. nov.  
*Zaluzania anthemidifolia* Rob. & Greenm., Proc. Amer. Acad. 34:531.  
 1899. TYPE: Mexico, Jalisco, wet sandy riverbanks near Guadala-  
 ajara, 23 Sep 1891, *Pringle 5156* (Holotype: GH!).

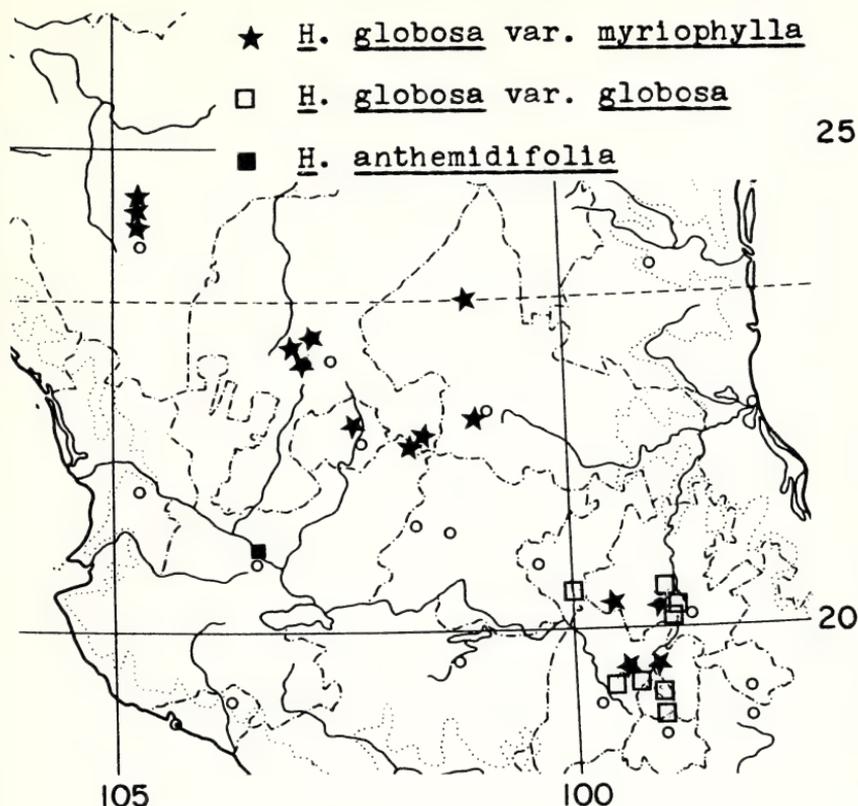
Herbaceous perennials with one to few stems arising from a decumbent woody caudex. Plants to 0.6 m tall; stems striate, glabrous below to sparsely pubescent with simple multicellular hairs above. Leaves sessile, elliptic in outline, 2-3-pinnatifid, ultimate segments 1-2 mm broad. Lower leaves usually absent; upper leaves 4.3-7.0 cm long, 1.8-2.6 cm wide. Upper surface of the leaves glabrous, lower surface with scattered long, thin multi-cellular hairs. Heads 1-3, solitary on peduncles 1.2-4.0 cm long; 2.0-2.6 cm wide including the rays. Involucre of 2-3 series of ovate elliptic bracts; outer series 4.2-7.0 mm long, 2.2-3.1 mm wide; inner series 3.6-3.7 mm long, 1.1-1.7 mm wide. Pales oblanceolate with base wrapped around the base of the disc achenes, 2.9-3.0 mm long, 0.5-0.6 mm wide. Ray florets ca 20 per head; corollas 10.0-11.0 mm long, 2.0-3.8 mm wide, 2- or 3-lobed with no basal lobes present. Disc florets ca 50 per head; corollas 4.1-4.2 mm long, 0.6-0.9 mm wide, glandular. Ray achenes 1.0-1.6 mm long, 0.6-0.7 mm wide, glabrous. Disc achenes 1.5-1.6 mm long, 0.5-0.8 mm wide, glabrous.

Distribution (Fig. 2): Known from only two collections, from barrancas in the Guadalajara region, along Rio Grande de Santiago (*Pringle* in 1891 and 1895). I have looked on two occasions for this taxon, both in the vicinity of the type locality and in the general region of the Rio Grande de Santiago, and have not been able to find it. Neither has *McVaugh* collected this species, even though he has collected extensively in the region. Flowering Sept.-Oct.

Additional specimens examined: JALISCO: wet sandy banks of Rio Grande de Santiago, barranca near Guadalajara, 12 Oct 1895, *Pringle 7367* (F, MO, UC).

2. **HYBRIDELLA GLOBOSA** (Ort.) Cass., Dict. Sci. Nat. 22:86. 1821.

Herbaceous perennials with one to few stems arising from a woody caudex. Plants to 0.6 m tall; stems striate, glabrous below to hispidulous or hirsute above. Leaves sessile, obtrullate in outline, 4-pinnatifid, ulti-

FIG. 2. Distribution of *Hybridella*.

mate segments less than 1 mm broad. Lower leaves 7.4–18.5 cm long, 1.5–6.0 cm wide; upper leaves 1.6–5.3 cm long, 0.5–2.5 cm wide; pubescence of upper surface usually limited to the veins, lower surface hispidulous to strigose. Heads one to several, solitary on peduncles 2.5–13.5 cm long; 1.6–3.2 cm wide including the rays. Involucre of 2–3 series of lanceolate to ovate-lanceolate bracts; outer series 3.8–6.7 mm long, 1.3–2.8 mm wide; inner series 3.3–5.9 mm long, 0.7–2.4 mm wide; both pubescent with simple, multicellular hairs. Pales linear-lanceolate to oblanceolate, 2.0–3.9 mm long, 0.2–0.5 mm wide. Ray florets ca 20 per head; corollas 7.2–11.7 mm long, 1.5–2.8 mm wide, ligules 2-lobed, usually with two small lateral lobes and one central lobe at base, tube glandular. Disc florets ca 100 per head; corollas 2.2–3.1 mm long, 0.4–1.5 mm wide, tube glandular. Ray achenes 0.9–2.2 mm long, 0.4–0.7 mm wide, glabrous to sparsely pubescent along the angles. Disc achenes 1.0–2.4 mm long, 0.4–0.8 mm wide, glabrous to sparsely pubescent. Chromosome number  $n = 16$ .

Distribution (Fig. 2): Mexico, in moist soils from just north of the city of Durango, south and east into the Federal District, Hidalgo, Mexico, and Queretaro. Flowering Jun–Sep.

2a. *HYBRIDELLA GLOBOSA* (Ort.) Cass. var. *GLOBOSA*.—*Anthemis globosa* Ort., Nov. Rar. Plant. 46. 1797.—*Hybridella globosa* (Ort.) Cass., Dict. Sci. Nat. 22:86. 1821.—*Chiliophyllum globosum* (Ort.) DC; Prodr. 5:554. 1821.—*Zaluzania globosa* (Ort.) Sch.-Bip., Flora 44: 564. 1861.—TYPE: not seen, presumably a Sessé collection in MA.

Variety *globosa* is characterized by its glabrous or hispidulous stems, hispidulous to strigose lower leaf surface, acute ultimate leaf segments, more than 2 mm long, linear-lanceolate receptacular pales, and the inner series of involucre bracts, which are pubescent over the entire abaxial surface. This variety is found growing on moist soils of the Federal District, Hidalgo, Mexico, and Queretaro.

Specimens examined: DISTRITO FEDERAL: Valley of Mexico, champs incultes, 12 Jun 1865, *Bourgeau 385* (GH, US); Valley of Mexico, 24 Jun 1887, *Pringle 2925* (GH); low meadows, Valley of Mexico, 27 Jun 1890, *Pringle 3204* (F, GH, LL, MO, NY, UC, US); damp meadows, Valley of Mexico, 7300 ft, 25 Jun 1897, *Pringle 7440* (US); wet meadows, Valley of Mexico, 7300 ft, 7 Jun 1901, *Pringle 9395* (GH, MO, US); near Tlalnepantla, 20 Jun 1901, *Rose & Hay 5247* (US); near Tacuba, 30 Jul 1901, *Rose & Hay 5816* (US). HIDALGO: Real del Monte, Jul 1946, *Martinez 15308* (MO); bosque bajo ladera calcarea, C. de los Pitos, 2690 m, 22 Jul 1951, *Matuda 21494* (NY); swales and ditches, vicinity of Tulancingo on road to Pachuca, 13 May 1947, *Moore 2811* (MICH); ditches and roadsides between Tepetates and Acopinalco on road from Tepeapulco to Apan, 21 Jul 1947, *Moore 3443* (GH); Telles, 21 Sep 1910, *Orcutt 4139* (F, GH, MO); along rt. 85 ca 20 mi N of road to the pyramids (Rt. 30), 10 Aug 1961, *Powell & Edmondson 597* (F, LL); Pachuca, Jul 1903, *Purpus 77* (MO, UC, US); Sierra de Alcaparrosa, 5 km al NW de Tepozolan, 29 Jul 1971, *Rzedowski 28247* (LL, NY, US); 2 mi W of Tulancingo, 29 Aug 1965, *Torres 1709* (MICH); N shore of Laguna de Apan, 4 km NW of Apan, 19 Jul 1966, *West R-12* (MICH). MEXICO: near Tlalnepantla, 6 Jul 1905, *Rose et al. 8417* (US); Mexico, *Schmitz 2246* (GH). QUERETARO: 10 mi E of Palmillas on Mexico 45, 14 Jul 1971, *Sanderson 258* (LL).

2b. *Hybridella globosa* (Ort.) Cass. var. *myriophylla* (Sch.-Bip.) Olsen, comb. nov.—*Zaluzania myriophylla* Sch.-Bip., Flora 44:565. 1861.—*Zaluzania globosa* var. *myriophylla* (Sch.-Bip.) W. M. Sharp, Ann. Missouri Bot. Gard. 22:103. 1935. TYPE: Mexico, Aguascalientes, low places, *Hartweg 111* (Isotype: GH!).

Variety *myriophylla* (Fig. 1 a-d) is characterized by hirsute stems, hispid lower leaf surfaces, rounded or obtuse ultimate leaf segments less than 2 mm long, oblanceolate receptacular pales, and the inner series of involucral bracts, which are pubescent only along the margins. This variety is a more northern element, being sympatric with variety *globosa* only in Hidalgo and the Federal District. Where sympatric, the two varieties remain distinct with no mixed populations found and no evidence of hybridization.

Specimens examined: AGUASCALIENTES: 31 mi N of Aguascalientes, 24 Aug 1953, *Manning & Manning 531252* (GH). DURANGO: in moist low soil about 16 mi NE of Durango, rt 31, 25 Jul 1958, *Correll & Johnston 20163* (LL); 8-9 mi NE of Ciudad Durango near Rio Mesquital, 1 Oct 1948, *Gentry 8568* (GH, MICH, UC); in the vicinity of Durango, Apr-Nov 1896, *Palmer 307* (F, GH, MO, NY, UC, US); in grassland 5 mi SE of Victoria, 26 Aug 1939, *Shreve 9172* (ARIZ, GH). HIDALGO: 3 km W of Tezontepec, 14 Jun 1963, *Rzedowski 16718* (MICH, US). JALISCO: near km 57, just E of the Aguascalientes state line, road from Ojuelos, ca 13 mi W of Paso de la Troje, 16 Aug 1958, *McVaugh 17053* (LL, MICH, NY, US). MEXICO: Tlalnepantla, 15 May 1904, *Pringle 13092* (ARIZ, F, LL, MO, US); San Juan Teotihuacan, 1 Jun 1973, *Rzedowski 30174* (MICH). SAN LUIS POTOSI: region of San Luis Potosi, 1878, *Parry & Palmer 527* (F, GH, MO, NY, US); Laguna Seca, km 20 carretera San Luis Potosi-Antigua Morelos, 30 Aug 1955, *Rzedowski 6302* (LL); San Miguelita, Sep 1876, *Schaffner 345 & 770* (GH, NY, US). ZACATECAS: 2 mi SW of Zacatecas-San Luis Potosi state line along hwy 80, 23 Jul 1969, *Biernier & Turner 116* (LL, NY); 6 mi W of Ojo Caliente, 6-8 Sep 1938, *Johnston 7454* (GH); 9 mi S of Fresnillo, 20 Aug 1956, *Linsdale 56-F1* (UC); 9 mi S of Fresnillo, 9 Aug 1954, *Linsley, MacSwain, & Smith 1* (LL, UC); 15 mi N of Zacatecas on hwy 45, in La Joya, 3 Sep 1975, *Olsen 265* (LL); Frio, 23 Aug 1934, *Pennell 18115* (US); damp hollow plains of Calera Station, 1 Sep 1904, *Pringle 8914* (F, GH, LL, MO, NMC, NY, UC, US).

#### ACKNOWLEDGMENTS

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## A REVISION OF LINANTHUS SECT. SIPHONELLA (POLEMONIACEAE)

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*Linanthus* comprises nearly 40 species and is one of the larger genera in the Polemoniaceae. Four species are suffrutescent perennials, and the rest are annuals. The genus is distributed throughout much of western North America, with one annual species indigenous to Chile. In spite of the size and relatively widespread distribution of the genus, it is one of the least examined in the family from a taxonomic viewpoint.

The four perennials constitute one of the least understood groups in *Linanthus*. These plants were first described by Gray (1870) as two species, *Gilia nuttallii* and *G. floribunda*. Milliken (1904) recognized these two taxa as members of *Linanthus* on the basis of their palmately-lobed leaves. A number of subsequent authors (McMinn, 1939; Munz, 1958; Grant, 1959) were basically in accord with Milliken, while others regarded this complex as belonging in related genera such as *Leptodactylon* (Rydberg, 1906; Jepson, 1925; Tidestrom, 1935) *Navarretia* (Kuntze, 1891), *Siphonella* (Heller, 1912; Jepson, 1943), and *Linanthastrum* (Ewan, 1942; Wherry, 1945) or retained it in its original genus, *Gilia* (Brand, 1907). In addition to these varied generic interpretations, a number of species, subspecies, varieties, and forms have been recognized and named. These will be considered in greater detail in the taxonomic treatment that follows.

The perennial species of *Linanthus* grow predominantly in montane and subalpine localities in many areas in the western United States and northern Mexico (Fig. 1). The distribution of these species is a series of geographically isolated populations corresponding roughly to the mountain ranges. The perennials are characterized morphologically by a suffrutescent habit, opposite, palmately-lobed leaves, calyces with a narrow hyaline membrane between the lobes, and funnelform corollas with stout tubes. They exhibit little morphological variation within any population, but there are populations that differ significantly from each other in one or more characteristics, such as leaf pubescence, calyx pubescence (Fig. 2 a-c), leaf lobe shape (Fig. 2 d-f), number of lobes per leaf, pollen grain diameter, and seed size. In addition, some populations consist only of tetraploids, while others consist only of diploids.

*Linanthus laxus* (Vasey & Rose) Wherry, an annual, is closely related to the perennials and is characterized by the same calyx and corolla morphology. It is a poorly known species and very few specimens are present in herbaria. Its geographical range is restricted to the coastal canyons near San Quintín, Baja California (Fig. 1). It does not present the same kinds of taxonomic problems that are found in the perennial species; however, it is included in this treatment because of its close relationship to the perennials.

Grant (1959) placed the perennial species of *Linanthus*, plus *L. laxus*, in sect. *Siphonella* (A. Gray) V. Grant, but no attempt to elucidate the relationships of the taxa within the section was made. A revision of sect. *Siphonella* is presented here. It is based on the examination of specimens in the field and over 2400 herbarium specimens. Particular attention was paid to characters whose expressions vary from population to population.

Representatives of each morpho-geographical group were grown in the greenhouse to establish whether a genetic basis exists for the character differences used to distinguish taxa, especially leaf and calyx pubescence and leaf lobe shape. Each of the diagnostic characters examined was retained by each taxon when grown under uniform conditions for at least two growing seasons, and progeny obtained from self-fertilizations maintained these parental features.

Chromosome numbers were counted for eight of the nine taxa considered in this treatment. Six were diploid with a somatic number of  $2n = 18$ , two were tetraploid,  $2n = 36$ . Cytological material for *L. floribundus* subsp. *hallii* was not available. Voucher specimens are cited in Table 1 and deposited at UCSB.

Pollen grain diameters were measured for all nine taxa; they range from 23 to 28  $\mu\text{m}$  in diploids, and from 33 to 38  $\mu\text{m}$  in tetraploids. The diameter of pollen grains was used to estimate the chromosome number of specimens from regions where live material was unavailable. On this basis, *L. floribundus* subsp. *hallii* is considered to be diploid.

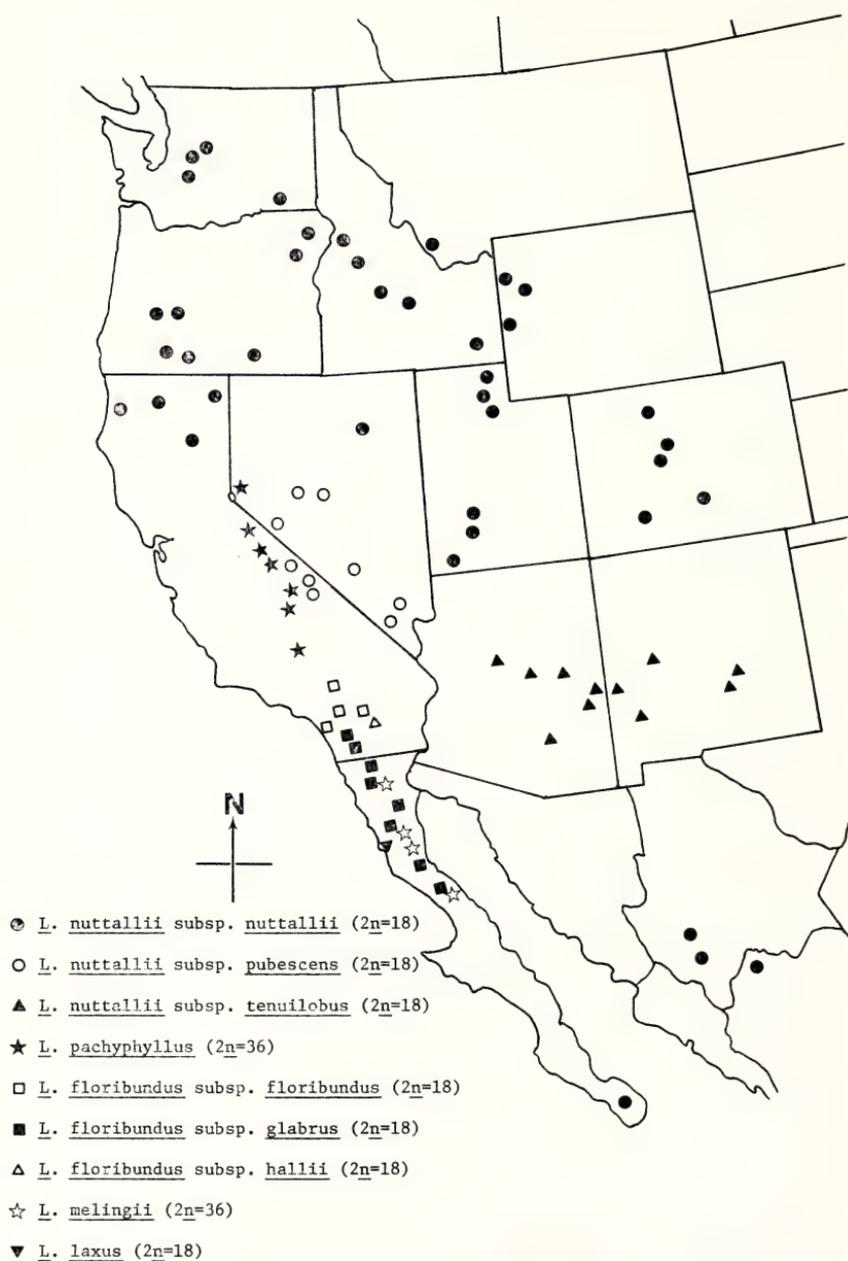


FIG. 1. Geographical distribution of *Linanthus* sect. *Siphonella*.

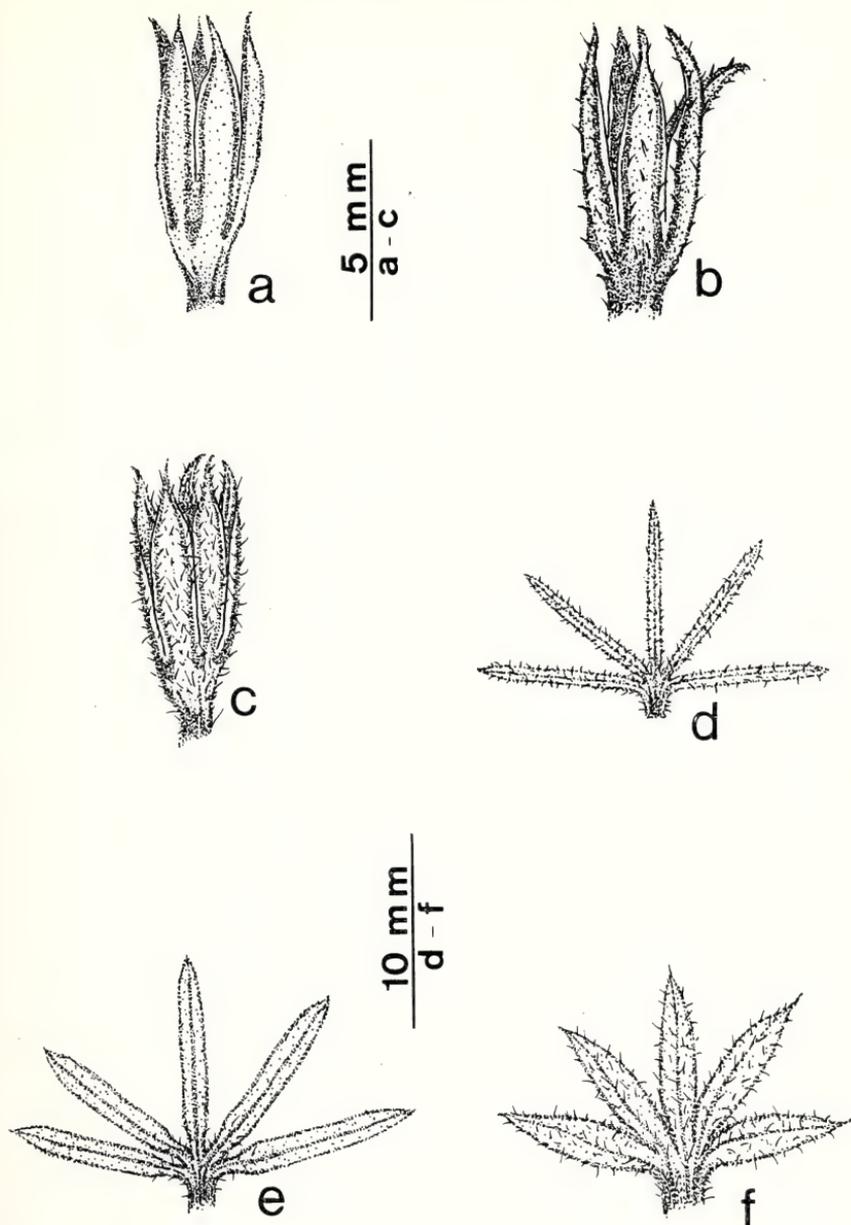


FIG. 2. a-c. Calyx pubescence in *Linanthus* sect. *Siphonella*. a, *L. floribundus* subsp. *glabrus* (Patterson 1021) showing glabrous calyx. b, *L. nuttallii* subsp. *nuttallii* (Patterson 1032) showing lightly pubescent calyx. c, *L. nuttallii* subsp. *pubescens* (Patterson 1012) showing densely pubescent calyx. d-f, Variation in leaf lobe shape in sect. *Siphonella*. d, *L. nuttallii* subsp. *tenuilobus* (Patterson 1009). e, *L. nuttallii* subsp. *nuttallii* (Patterson 1030). f, *L. pachyphyllus* (Patterson 1001), also found in *L. melingii*. Drawings by B. Tanowitz.

TABLE 1. CHROMOSOME COUNTS FOR LINANTHUS SECT. SIPHONELLA.

- L. nuttallii* (A. Gray) Greene ex Milliken subsp. *nuttallii*;  $2n = 18$ .  
 COLORADO: Eagle Co.: Tennessee Pass, *Patterson 1031*. Lake Co.: 3 mi SW of Climax, *Patterson 1030*.  
 IDAHO: Blaine Co.: Trail Creek Summit, *Patterson 1033*.  
 WYOMING: Lincoln Co.: Allred Springs Campground, *Patterson 1032*.
- L. nuttallii* (A. Gray) Greene ex Milliken subsp. *pubescens* R. Patterson;  $2n = 18$ .  
 CALIFORNIA: Mono Co.: Junction of White Mountain and Silver Canyon Roads, *Patterson 1013*.  
 NEVADA: Clark Co.: Mary Jane Falls Campground, *Patterson 1012*.
- L. nuttallii* (A. Gray) Greene ex Milliken subsp. *tenuilobus* R. Patterson;  $2n = 18$ .  
 ARIZONA: Gila Co.: Camp Verde-Strawberry Road, one mi W of Strawberry, *Patterson 1009*.
- L. pachyphyllus* R. Patterson;  $2n = 36$ .  
 CALIFORNIA: Inyo Co.: Bishop Creek near South Lake Road, *Patterson 1001*; two mi E of Onion Valley, on Independence Road, *Patterson 1002*.  
 Kern Co.: one mi SW of Piute Mountain, *Smith s.n.* Mono Co.: Lee Vining Creek, just S of ranger station, *Patterson 1000*; Rock Creek, *Meyers s.n.*
- L. floribundus* (A. Gray) Greene ex Milliken subsp. *glabrus* R. Patterson;  $2n = 18$ .  
 CALIFORNIA: Riverside Co.: Santa Rosa Mountains, *Meyers s.n.* San Diego Co.: Four mi S of Tenaja Campground, on road to Fallbrook, *Patterson 1020*.
- L. floribundus* (A. Gray) Greene ex Milliken subsp. *glabrus* R. Patterson;  $2n = 18$ .  
 CALIFORNIA: San Diego Co.: nine mi NE of U.S. Highway 80, on county road S-1, *Patterson 1011*.
- L. melingii* (Wiggins) V. Grant;  $2n = 36$ .  
 BAJA CALIFORNIA: The observatory, Sierra San Pedro Mártir, *Haller s.n.*
- L. laxus* (Vasey & Rose) Wherry;  $2n = 18$ .  
 BAJA CALIFORNIA: Arroyo Socorro, *Moran 19330*, *Moran & Reveal 20281*, *Moran 20593*.

## TAXONOMY

LINANTHUS Benth. sect. SIPHONELLA (A. Gray) V. Grant, Natural history of the *Phlox* family 106. 1959.—*Gilia* sect. *Siphonella* A. Gray, Proc. Amer. Acad. Arts 8:266. 1870 (Based on a generic name in Nuttall's herbarium).—*Siphonella* (A. Gray) Heller, Muhlenbergia 8:57. 1912.—TYPE: *Linanthus nuttallii* (A. Gray) Greene ex Milliken. Suffrutescent perennials and one annual; leaves opposite, mostly palmately lobed; inflorescence ranging from dense, subcapitate clusters to sub-panicles, rarely solitary; pedicels present or absent; calyx herbaceous with narrow hyaline membrane connecting the lobes to about one-half their length; corolla funnelform, tube stout, equalling to twice as long as the calyx; stamens inserted on corolla throat; pollen grains 23–38  $\mu\text{m}$  in diameter, yellow; style divided into three lobes, each as long as the united style body, the point of trifurcation stigmatic; fruit a three-parted septicidal capsule; seeds smooth, light to dark brown, non-mucilaginous.

Key to *Linanthus* sect. *Siphonella*

Plants suffrutescent perennials; mostly montane or subalpine, seldom below 500 m.

Leaves palmately-lobed.

Leaves predominantly 5-lobed.

Leaf lobes linear to linear-lanceolate.

Leaf lobes linear; corolla tube equalling calyx; seeds 1.5–2.0 mm long.

Leaf lobes and calyces subglabrous to lightly pubescent, never densely so; wide ranging in Rocky Mountains, eastern Great Basin ranges, ranges of Washington, Oregon, and northern California, and the Sierra Madre Occidental of Mexico. 1a. *L. nuttallii* subsp. *nuttallii*

Leaf lobes and calyces densely hirtellous; dry mountain ranges of Nevada and eastern California. . . . .

. . . . . 1b. *L. nuttallii* subsp. *pubescens*

Leaf lobes linear-lanceolate; corolla tube often exceeding the calyx; seeds 2.5–3.5 mm long; Sierra Nevada. . . . .

. . . . . 2. *L. pachyphyllus*

Leaf lobes nearly filiform; mountains of central Arizona and New Mexico. . . . . 1c. *L. nuttallii* subsp. *tenuilobus*

Leaves predominantly 3-lobed.

Leaves and calyces glabrous to moderately pubescent; plants usually robust, to over 3 dm high; mountain ranges of southern California and Baja California.

Leaves and/or calyces subglabrous to moderately pubescent. . . . . 3a. *L. floribundus* subsp. *floribundus*

Leaves and calyces glabrous. 3b. *L. floribundus* subsp. *glabrus*

Leaves and calyces densely hirtellous; plants compact, often matted; higher elevations of the Sierra Juarez, Sierra San Pedro Mártir, and Sierra San Borja, Baja California. . . . .

. . . . . 4. *L. melingii*

Leaves mostly entire; dry eastern slopes of coast ranges of southern California and Baja California. 3c. *L. floribundus* subsp. *hallii*

Plants annual; occurring below 100 m; coastal areas near San Quintín, Baja California. . . . . 5. *L. laxis*

1a. LINANTHUS NUTTALLII (A. Gray) Greene ex Milliken subsp. NUTTALLII, Univ. Calif. Publ. Bot. 2:54. 1904.—*Gilia nuttallii* A. Gray, Proc. Amer. Acad. Arts 8:267. 1870.—*Navarretia nuttallii* (A. Gray) Kuntze, Revisio generum plantarum 2:432. 1891.—*Leptodactylon nuttallii* (A. Gray) Rydberg, Bull. Torrey Bot. Club 33:149. 1906.—*Siphonella nuttallii* (A. Gray) Heller, Muhlenbergia 8:57. 1912.—

- Linanthastrum nuttallii* (A. Gray) Ewan, J. Wash. Acad. Sci. 32:139. 1942.—LECTOTYPE (here designated): R. Mts. Bear R. Hills, *Nuttall s.n.* (PH, seen only as photograph; isolectotype: GH!).
- Gilia nuttallii* A. Gray var. *montana* Brand, Pflanzenreich 4(250):125. 1907.—SYNTYPES: *Allen 119*, *Hall 941*, *Parish 3686*, and *Purpus 1443*.
- Gilia nuttallii* A. Gray var. *parviflora* Brand, Pflanzenreich 4(250):125. 1907.—SYNTYPES: *Baker 1053*, *Cusick 255*, and *Jones 1106*.

Perennial herb from woody base, stems erect, 1–4 dm high, slightly puberulent; leaves mostly 5-partite into linear lobes, 6–32 mm long, subglabrous to moderately pubescent; flowers mostly sessile in upper axils, in dense subcapitate clusters; calyx narrow-campanulate, 8–10 mm long, tube 2–4 mm long, lobes lance-subulate, slightly pubescent; corolla 12–16 mm long, tube 8–10 mm long, white, pubescent on outer surface, throat short, yellow, lobes 5–8 mm long, oval to oblanceolate; stamens inserted at base of throat or just below, glabrous, barely exerted to included; pollen 23–28  $\mu$ m in diameter; chromosome number  $2n = 18$ .

Distribution (Fig. 1) and phenology: Cascade range from central Washington to northern California; high ranges of eastern Washington, Oregon, and northeastern California; Rocky Mountains from central Idaho to southern Colorado; higher ranges of Utah; Sierra Madre Occidental of Chihuahua and Durango; Sierra de la Victoria, Baja California. Flowering July to August (June to September). The populations of *L. nuttallii* subsp. *nuttallii* from the Sierra Madre Occidental and the Sierra de la Victoria present an interesting disjunction from the majority of populations of this subspecies. The nearest population of subsp. *nuttallii* is in southern Colorado. The Mexican populations are poorly represented in herbarium collections, but the regions within the area of disjunction (e.g., Arizona and New Mexico) are well known botanically; hence, the disjunction is not simply the result of insufficient collecting. Future studies on the nature and significance of this disjunction should be rewarding from a systematic viewpoint after the range of *L. nuttallii* subsp. *nuttallii* in Mexico is better known.

Representative specimens: CALIFORNIA: Little Lily Lake, *Wheeler 3789* (GH, NY, UC, US, UTC). COLORADO: Tennessee Pass, *Clokey 3549* (CAS, DS, GH, MICH, NY, POM, TEX, US, UTC, WSU); Rabbit Ears Pass, *Gooding 1540* (COLO, DS, GH, MO, NY, RM, UC, US). IDAHO: Squaw Valley, *Macbride & Payson 3388* (CAS, DS, GH, MO, NY, POM, RM, UC, US); 3.5 mi SW Stanley Lake, *Hitchcock & Muhlick 9635* (NY, RM, UC, UTC, WSU, WTU); Trinity Lake region, *Macbride 691* (DS, GH, MO, NY, RM, UC, US, WSU, WTU). NEVADA: Lamoille Terrace Ranger Station, *Maguire & Holmgren 22166* (GH, NY, UC, UTC). OREGON: near Cornucopia, *Thompson 13353* (CAS, COLO, GH, MO, NY, RSA, UC, UTC, WSU); along Musick Mine Road,

*Dennis 2313* (ASU, CAS, DS, ID, NY, OSU, RSA, US, UTC, WSU, WTU). UTAH: *Alta, Jones 1106* (ARIZ, GH, MICH, NY, OSU, RSA, US, UTC, WSU). WASHINGTON: alpine slopes of Mt. Wow, *Thompson 12585* (CAS, DS, GH, MO, NY, POM, UC, US, WSU, WTU); Blue Mountains, *Piper 2419* (GH, WSU). WYOMING: Teton Pass, *Cronquist 831* (ID, UC, UTC). BAJA CALIFORNIA: La Laguna, *Gentry 4372* (ARIZ, DS, MO, UC, US). CHIHUAHUA: SW Chihuahua, *Palmer 398* (MO, NY, US).

1b. *Linanthus nuttallii* (A. Gray) Greene ex Milliken subsp. **pubescens**

R. Patterson, subsp. nov.—TYPE: California, Inyo County, White Mountains, junction of White Mountain and Silver Canyon Roads, 3100 m, 2 Aug 1970, *Patterson 1009* (Holotype: UC!; isotypes: NY!, UCSB!).

Herba perennis, 1–4 dm alta; folia plerumque 5-partita, moderate vel dense pubescentia, lobis linearis; flores sessiles racemis subcapitatis; calyces moderate vel dense pubescentes; chromosomatum numerus  $2n = 18$ .

Distribution (Fig. 1) and phenology: Dry mountain ranges of central and southern Nevada and the White and Inyo Ranges of California, mostly above 2800 m. Flowering July to August (June to September).

Representative specimens: CALIFORNIA: Wyman Creek, *Duran 3048* (ARIZ, CAS, DS, GH, MICH, MO, NY, POM, RM, SD, UC, US, UTC); 1.5 mi N of New York Butte, *Alexander & Kellogg 3083* (ARIZ, DS, MO, UC, US, UTC). NEVADA: Charleston Park, *Clokey 7253* (ARIZ, CAS, COLO, DS, GH, ID, MICH, MO, NY, OSU, POM, RM, TEX, UC, US, UTC, WSU); 2 mi N of Toiyabe Dome, *Hitchcock & Martin 5598* (DS, POM, UC, UTC, WSU).

1c. *Linanthus nuttallii* (A. Gray) Greene ex Milligen subsp. **tenui-**

**lobus** R. Patterson, subsp. nov.—TYPE: Arizona, Gila County, one mile east of Strawberry on Camp Verde-Strawberry Road, 1700 m, 22 Aug 1970, *Patterson 1013* (Holotype: UC!; isotypes: NY!, UCSB!).

Herba perennis, 1–4 dm alta; folia plerumque 5-partita, parce pubescentia, lobis tenuibus; flores sessiles racemis subcapitatis; calyces parce vel moderate pubescentes; chromosomatum numerus  $2n = 18$ .

Distribution (Fig. 1) and phenology: Mountain ranges of central Arizona and New Mexico, and in the Santa Catalina Mountains of southern Arizona, mostly above 1500 m. Flowering July to August (June to September).

Representative specimens: ARIZONA: Strawberry Valley, *Toumey 201* (ARIZ, DS, GH, POM, US); 3 mi S of Stray Horse Camp, *Parker & McClintock 7662* (ARIZ, CAS, COLO, MO, RSA, UC). NEW MEXICO: Mogollon Mountains, *Rusby 272* (MICH, MO, NY); White Mountains, *Wootton 205* (DS, GH, MO, NY, POM, RM, UC, US).

2. *Linanthus pachyphyllus* R. Patterson, sp. nov.—TYPE: California, Mono County, Lee Vining Grade, 9000 ft, 30 Jun 1934, *Keck, Abrams, & Blake 2872* (Holotype: UC!; isotypes: CAS!, DS!, GH!, POM!, US!).

Herba perennis e basi lignea; caules erecti, 1–4 dm alta, moderate vel dense pubescentes; folia plerumque 5-partita, moderate vel dense pubescentia, lobis lineari-oblongatis, 3–30 mm longa; flores sessiles in axiles superioribus ramorum fascientes racemos dense subcapitados; calyx superioribus ramorum fascientes racemos dense subcapitados; calyx tenui-campanulatus, 8–10 mm longus, dense pubescens, tubo 3–5 mm longo, lobis lanci-subulatis; corolla 12–18 mm longa, tubo 8–12 mm longo, albo, externe pubescente, fauce brevi, flavo, lobae 5–8 mm longi, albi, ovali-oblongati; stamina basi faucis vel modo infra inserta, glabrata, vix-moderate exserta; pollinis granula 33–38  $\mu\text{m}$  diametro; semina fulva, 2.5–3.5 mm longa; chromosomatum numerus  $2n = 36$ .

Distribution (Fig. 1) and phenology: *Linanthus pachyphyllus* is restricted to the Sierra Nevada of California and western Nevada. Its southernmost limit is near Piute Mountain in Kern County, California, and its northernmost limit is near Mt. Rose in Washoe County, Nevada. Flowering June to July (May to September).

Representative specimens: CALIFORNIA: Lee Vining, *Benson 3767* (NY, POM, RM, UC, US); Sabrina Lake, *Jones s.n.* (CAS, DS, GH); Farewell Gap, *Baker 4536* (CAS, DS, GH, MO, NY, POM, US). NEVADA: Zephyr Point, *Mason 12161* (ARIZ, CAS, COLO, DS, GH, ID, MICH, MO, NY, POM, RM, UC, US, UTC, WSU).

- 3a. LINANTHUS FLORIBUNDUS (A. Gray) Greene ex Milliken subsp. FLORIBUNDUS, Univ. Calif. Publ. Bot. 2:55. 1904.—*Gilia floribunda* A. Gray, Proc. Amer. Acad. Arts 8:267. 1870.—*Linanthus nuttallii* (A. Gray) Greene ex Milliken var. *parviflora* Brand subvar. *floribunda* (A. Gray) Brand, Pflanzenreich 4(250):125. 1907.—*Leptodactylon nuttallii* (A. Gray) Rydberg var. *floribundum* (A. Gray) Jepson, Manual of the flowering plants of California 808. 1925.—*Leptodactylon floribundum* (A. Gray) Tidestrom, Proc. Biol. Soc. Wash. 48:42. 1935.—*Linanthus nuttallii* (A. Gray) Greene ex Milliken var. *floribundus* (A. Gray) McMinn, Illustrated manual of California shrubs 446. 1939.—*Linanthastrum nuttallii* (A. Gray) Ewan subsp. *floribundum* (A. Gray) Ewan, J. Wash. Acad. Sci. 32:139. 1942.—*Siphonella floribunda* (A. Gray) Jepson, A flora of California 3:218. 1943.—*Linanthastrum floribundum* (A. Gray) Wherry, Amer. Midl. Naturalist 34:218. 1945.—*Linanthus nuttallii* (A. Gray) Greene ex Milliken subsp. *floribundus* (A. Gray) Munz, Aliso 4:96. 1958.—LECTOTYPE (here designated): California, *Coulter 454* (GH!).
- Linanthus saxiphilus* A. Davidson, Bull. S. Calif. Acad. Sci. 19:10. 1920.—*Linanthastrum floribundum* (A. Gray) Wherry forma *saxiphilum*

(A. Davidson) Wherry, Amer. Midl. Naturalist 34:386. 1945.—TYPE: California, San Bernardino County, Seven Oaks, Jul 1901, *Davidson 2242* (Holotype: US!).

Suffrutescent perennial, 1–4 dm high; leaves mostly 3-partite, lobes linear, 6–24 mm long; inflorescence an open subcapitate panicle to nearly solitary; flowers mostly pedicellate with pedicels 1–6 mm long; calyx puberulent, narrow-campanulate, 8–9 mm long, lobes lance-subulate; pollen grains 23–28  $\mu\text{m}$  in diameter; chromosome number  $2n = 18$ .

Distribution (Fig. 1) and phenology: San Bernardino, Santa Margarita, and Santa Rosa Mountains of southern California, rarely in adjacent ranges. Flowering April to June (March to August).

Representative specimens: BAJA CALIFORNIA: Cerro el Sauco, *Moran 8090* (ARIZ, RSA, SD). CALIFORNIA: near Seven Oaks, *Parish 3686* (ARIZ, CAS, DS, GH, NY, UC, US); Laguna Mountains, *Spencer 958* (GH, NY, POM).

3b. *Linanthus floribundus* (A. Gray) Greene ex Milliken subsp. **glabrus** R. Patterson, subsp. nov.—TYPE: California, San Diego County, 9 mi NE of U.S. highway 80 on county road S-1, 1700 m, 3 Apr 1971, *Patterson 1011* (Holotype: UC! isotypes: NY!, UCSB!).

Herba perennis, 1–4 dm alta; caules glabrati vel leviter puberuli; folia plerumque 3-partita, glabrata, lobis linearis vel filiformibus; calyx glabratus; chromosomatum numerus  $2n = 18$ .

Distribution (Fig. 1) and phenology: Most of the high mountain ranges of southern California excluding the San Bernardino Mountains; the higher ranges of northern Baja California, mostly below 200 m. Flowering April to June (March to July).

Representative specimens: BAJA CALIFORNIA: Rancho El Barril, *Moran 13840* (ARIZ, RSA, SD, UC). CALIFORNIA: Descanso, *Epling s.n.* (COLO, DS, MO, NY, RSA, UC).

3c. LINANTHUS FLORIBUNDUS (A. Gray) Greene ex Milliken subsp. **HALLII** (Jepson) H. L. Mason, in Abrams, Ill. Fl. Pacific States 3:431. 1961.—*Siphonella floribunda* (A. Gray) Jepson var. *hallii* Jepson, Flora of California 3:218. 1943.—*Linanthastrum floribundum* (A. Gray) Wherry forma *hallii* (Jepson) Wherry, Amer. Midl. Naturalist 34:386. 1945.—TYPE: California, San Diego County, Coyote Canyon, in the lower Sonoran zone, 600 ft, Apr 1902, *Hall 2767a* (Holotype: JEPS!; isotype: UC!).

Perennial herb, 1–4 dm high; stems slightly puberulent; leaves entire, linear, rarely 3-partite on lower branches, glabrous; calyx moderately pubescent to glabrous; pollen grain diameter 23–28  $\mu\text{m}$ .

Distribution (Fig. 1) and phenology: Dry washes below 700 m in southern Santa Rosa Mountains, Riverside and San Diego Counties, California. Flowering late March and May.

Representative specimens: CALIFORNIA: Rockhouse Canyon, *Jaeger 1088* (DS, POM); Martinez Canyon, *Davidson s.n.* (UC); Thermal, *Davidson s.n.* (DS); Elder Canyon, *Woglum 3041* (RSA); canyon east of Clark Dry Lake, *Buechner 694* (RSA); Palm Canyon, *Gander 1277* (SD).

4. *LINANTHUS MELINGII* (Wiggins) V. Grant, Natural history of the *Phlox* family 107. 1959.—*Leptodactylon melingii* Wiggins, Contr. Dudley Herb. 1:173. 1933.—*Linanthastrum melingii* (Wiggins) Wherry, Amer. Midl. Naturalist 34:386. 1945.—TYPE: Baja California, in gravelly soil along the margins of an open meadow at La Encantada, Sierra San Pedro Mártir, 2100 m, 18 Sep 1930, *Wiggins & Demaree 4884* (Holotype: DS! isotype: UC!).

Low suffrutescent perennial, branches 3–15 cm long, often forming dense mats to 3 dm in diameter; leaves 3-partite, lobes 3–6 mm long, linear-lanceolate, densely hirtellous; flowers sessile in subcapitate clusters, rarely solitary; calyx narrow campanulate, 4–5 mm long, hirtellous, tube 1 mm long, lobes 3–4 mm long; corolla white with yellow throat, often tinged with purple, tube 4–5 mm long, lobes 4–5 mm long, ovate; stamens inserted in throat, barely exerted; pollen grains 33–38  $\mu$ m in diameter; chromosome number  $2n = 36$ .

Distribution (Fig. 1) and phenology: High elevations (above 2000 m) in the Sierra Juárez, Sierra San Pedro Mártir, and Sierra San Borja, Baja California. Flowering July to August (June to September).

In Wiggins' original description of *Leptodactylon melingii*, he characterized this species in part as having wingless seeds in differentiating it from *Leptodactylon nuttallii*; however, the examination of numerous herbarium specimens indicates that none of the members of sect. *Siphonella* possess winged seeds (Patterson, 1975).

Munz (1959) cited *Linanthus melingii* as occurring in the White Mountains of California and Nevada, and in the Toiyabe Mountains of Nevada. There are plants that have the same habit as *L. melingii* in these localities; however, these individuals are characterized by 5-partite leaves and are recognized herein as *L. nuttallii* subsp. *pubescens*. In addition, pollen grain diameters of the Toiyabe and White Mountains specimens vary between 23–28  $\mu$ m, indicating that they are diploids.

Representative specimens: BAJA CALIFORNIA: 8 mi N of Vallecitos, *Breedlove 16306* (CAS, MICH); Hansen's Ranch, *Orcutt 128* (UC, US).

5. *LINANTHUS LAXUS* (Vasey & Rose) Wherry, Amer. Midl. Naturalist 34:386. 1945.—*Gilia laxa* Vasey & Rose, Proc. U. S. Natl. Mus. 11: 531. 1889.—TYPE: Baja California, San Quintín Bay, Jan 1889, *Palmer 650* (Holotype: US!; isotype: UC!).

*Linanthus wigginsii* Mason, Madroño 6:203. 1942.—TYPE: Baja California, southern end of Santa María Plains, 5 Feb 1935, *Wiggins 7557*

(Holotype: DS!; isotype: UC!)

Slender annual, 3–15 cm high; stems erect, glabrous to slightly pubescent; leaves 3-partite (rarely 5-partite), lobes 5–20 mm long, linear, glabrous to slightly pubescent; inflorescence solitary to subpaniculate, pedicels 2–16 mm long; calyx narrow-campanulate, 4–5 mm long, tube 1 mm long, lobes 3–4 mm long, glabrous to moderately pubescent; corolla tube equal to or slightly exceeding the calyx, white with yellow throat, lobes 5 mm long, white, obovate; stamens inserted below throat, 1.5–2.0 mm long, barely exserted; pollen grains 23–28  $\mu\text{m}$  in diameter; chromosome number  $2n = 18$ .

Distribution (Fig. 1) and phenology: Coastal canyons and plains, Río Santa María, San Quintín, and Arroyo Socorro, Baja California. Flowering January to April.

Representative specimens: BAJA CALIFORNIA: Arroyo Socorro, *Moran 19330* (SD, UCSB), *Moran & Reveal 20281* (SD, UCSB), *Moran 20593* (SD, UCSB); Santa María, *Orcutt s.n.* (MO); north of San Quintín Bay, *Raven 12370* (UC).

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## A NEW SUBSPECIES OF *HULSEA VESTITA* (ASTERACEAE)

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The *Hulsea vestita* complex of California and Nevada comprises five currently recognized subspecies of self-incompatible, densely lanate, caespitose, herbaceous perennials with a dimorphic, quadripartite, pale-aceous pappus and a uniform diploid complement of 38 chromosomes (Wilken, 1975). Of particular interest within this complex is the occurrence in the western Transverse Ranges of southern California of populations that have been variously treated in several floristic works. Specific epithets applied to these populations include *H. callicarpha* (Hall) Rydberg, *H. parryi* A. Gray, and *H. vestita* A. Gray (Rydberg, 1914; Jepson, 1951; Keck, 1959; Ferris, 1960; Munz, 1974). Recently, I postulated (Wilken, 1975) that these populations represent an intergrading complex involving ssp. *vestita* and ssp. *parryi*. This hypothesis was based on observations of leaf morphology and ray flower number. Further study has revealed, however, that populations from the western Transverse Ranges, particularly the San Gabriel Mountains, display discordant variation with respect to presently circumscribed taxa. It is the purpose of this paper to discuss the relationships and status of these problematical populations by a numerical analysis of morphological variation and studies of synthetic hybrids.

### MATERIALS AND METHODS

Field studies were begun in 1970 and seeds were collected to serve as a source of parental strains for an extensive crossing program. Methods with respect to crossing attempts and studies of meiosis and hybrid fertility (= pollen stainability and seed set) were as described elsewhere (Wilken, 1975). During the spring and summer of 1972, a series of populations, derived from 18 natural populations, were grown from seed to flowering maturity in a common garden at Occidental College, Los Angeles, California. These garden populations represented all recognized subspecies of *Hulsea vestita* and six populations from widely sepa-

rated sites in the San Gabriel Mts. (Table 1). Each of the garden populations comprised 10–18 plants and represented progenies of at least five randomly selected plants in each of the natural populations. Twenty vegetative and floral characters were chosen for measurement (Table 2). These characters have been shown to be the most useful in delimiting taxa within the complex (Wilken, 1973). The data were standardized by range and an unweighted analysis was performed, using Gower's Correlation Coefficient (Sneath and Sokal, 1973) and a program written for the CDC 6400 computer. Each of the 18 garden populations was treated as an OTU in the numerical analysis. A phenogram was constructed by using single-linkage clustering. Although variation of leaf shape and blade margin was valuable in assessing relationships, quantification of these characters for the numerical analysis was not done. Variation of leaves among garden populations is illustrated in Figure 1. Additional morphological studies were made of natural population samples, synthetic hybrids, and specimens borrowed from several herbaria (CAS, GH, JEPS, MO, NY, POM, RM, RSA, UC, UTC, WTU). Common garden and greenhouse populations were assigned the number corresponding to vouchers of natural population samples.

### RESULTS

A phenogram of relationships (Fig. 2) reveals the distinctiveness of San Gabriel Mt. populations and supports the delimitation of accepted infraspecific taxa of the *Hulsea vestita* complex. The lowest level of similarity between OTUs representing a recognized taxon is 0.889 for ssp. *inyoensis*, whereas the highest level is 0.945 between OTUs and 8200

TABLE 1. LOCATIONS OF NATURAL POPULATIONS USED AS SEED SOURCES FOR THE CROSSING PROGRAM AND GARDEN POPULATIONS. Plants of all 18 populations were examined for chromosome number, which was uniformly  $2n = 38$ . All collections, with the exception of ssp. *inyoensis*, are those of the author (cited *W*). The two collections of ssp. *inyoensis* were provided by J. Beatley. Vouchers are deposited at CS.

California, Inyo Co., Cottonwood Meadows at head of Cottonwood Creek, *W* 4255. Los Angeles Co., Devil's Backbone, S slope of Mt. San Antonio, *W* 11891; E slope of Mt. Williamson, *W* 11890; 3 mi E of Chilao, *W* 11880; upper Tujung Canyon, 1.5 mi W of Highway 2, *W* 11879; along road to Mt. Pacifico, 2 mi E of Mill Creek Summit, *W* 11878; near summit of Mt. Gleason, 5 mi W of Mill Creek Summit, *W* 7946. Madera Co., near Rainbow Falls, Devil's Postpile N. M., *W* 8202. Mono Co., along Highway 120, 6.9 mi E of Highway 295, *W* 8200. Riverside Co., road to Toro Pk., 5.9 mi S of Highway 74, Santa Rosa Mts., *W* 7896; County Road R1, 8.6 mi NW of Idyllwild, San Jacinto Mts., *W* 7844; County Road R1, 1 mi S of Idyllwild, San Jacinto Mts., *W* 7858. San Bernardino Co., summit of Mt. San Gorgonio, *W* 8703; ridge between Fish Creek and Big Meadows, San Bernardino Mts., *W* 8703; Coon Creek, 3 mi SE of Highway 38, San Bernardino Mts., *W* 3047; along Highway 38, 2 mi E of Heart Bar Park, San Bernardino Mts., *W* 3048.

Nevada, Nye Co., SW face of Rainier Mesa, Belted Range, *Beatley* 9376; top of Rainier Mesa, *Beatley* 8836.

TABLE 2. CHARACTERS USED IN THE NUMERICAL ANALYSIS. Actual values were measured, recorded, and coded. Leaf and pubescence data were taken from the tenth leaf of the basal rosette. Pubescence density was determined by counting the trichomes within a 1 cm<sup>2</sup> square placed over the midrib at the center of the blade. Bract data were taken from the lowermost bract of the inflorescence. All capitulum and floral data were taken from the first mature capitulum.

Plant height (cm); Leaf length (mm); Leaf width (mm); Bract length (mm); Bract width (mm); Abaxial nonglandular pubescence density (number of trichomes per cm<sup>2</sup>); Peduncle length (cm); Number capitula per plant; Number of phyllaries per capitulum; Phyllary length (mm); Phyllary width (mm); Number of ray flowers; Ray corolla length (mm); Number disc flowers; Disc corolla length (mm); Achene length (mm); Narrow pappus pair length (mm); Broad pappus pair length (mm); Achene pubescence length (mm).

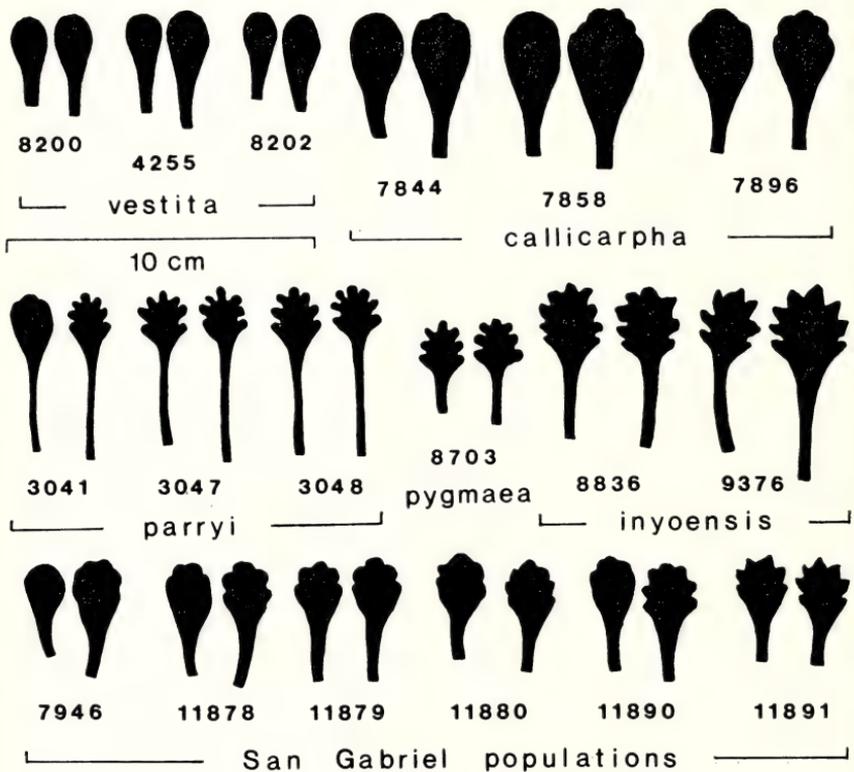


FIG. 1. Basal leaf silhouettes depicting range in size. Silhouettes were drawn from the tenth leaf of the basal rosette of common garden plants. Each pair represents the largest and smallest tenth leaf observed within each of the garden populations. Each number refers to the voucher of the natural population (= seed source).

and 8202 of *ssp. vestita*. The lowest level of similarity between the six problematical OTUs is 0.906, which is the overall similarity between OTU 11891 and the other five OTUs.

Phenetic relationships of the six San Gabriel OTUs indicate an alliance with *ssp. callicarpha*. Variation in garden populations of both groups overlapped with respect to a number of characters, including plant height, peduncle length, achene length, pappus length, and the number of phyllaries, ray flowers, and disc flowers. Basal leaf shape and size in San Gabriel populations are intermediate to those of *ssp. vestita* and *ssp. parryi*, but blade margin approximates that of *ssp. parryi* or *ssp. inyoensis*. There is a tendency toward subentire leaves in western populations in the San Gabriel Mt. (7936, 11878) and crenate to slightly

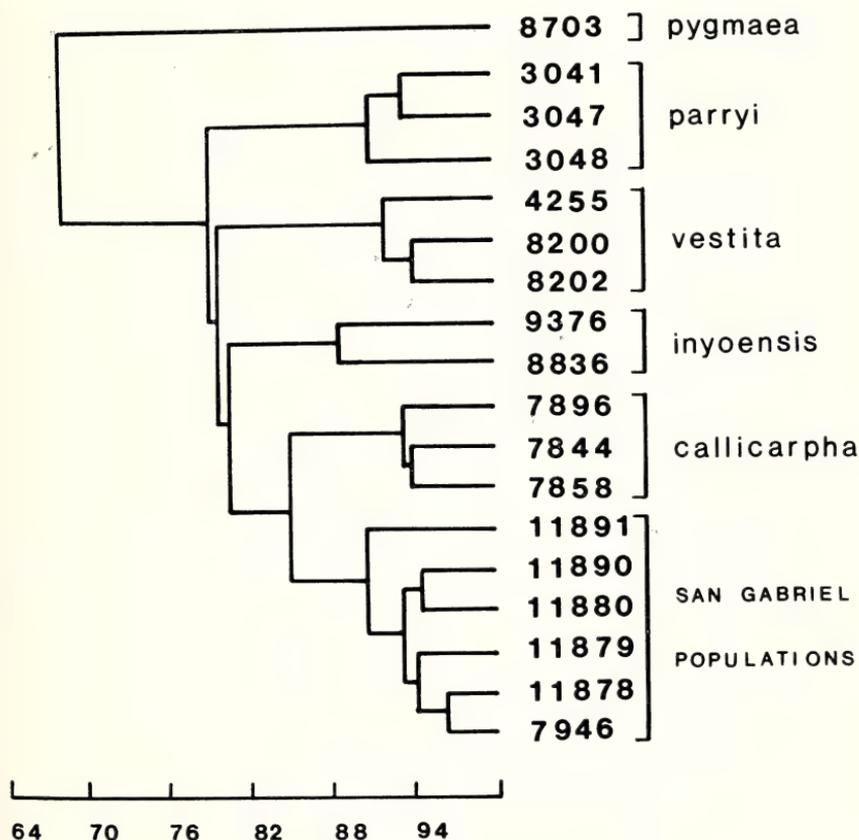


FIG. 2. Cluster diagram of 18 populations representing all infraspecific taxa within *Hulsea vestita* A. Gray. The phenogram was constructed using single-linkage clustering. The horizontal axis represents the correlation coefficient used in this study. Each number refers to the voucher of the natural population (= seed source).



subspecific) were not statistically significant. Germination ranged from 3 to 100% (ave. = 37), but no significant correlations with kinds of combinations were observed. Hybrids of all 18 intrapopulation and 91 interpopulation combinations were grown to flowering maturity and examined for meiosis and pollen stainability (Fig. 3). Nearly all hybrids, regardless of combination, were vigorous under garden and greenhouse cultivation. Normal meiosis and high pollen stainabilities characterized most hybrids. The lowest pollen stainabilities were in  $F_1$  hybrids involving ssp. *pygmaea* as one parent. Observations of meiosis in these hybrids revealed the presence of either 17 bivalents and a chain of 4 chromosomes or 17 bivalents, a chain of 3, and 1 univalent. Most interspecific  $F_1$  hybrids resembled the maternal parent with respect to peduncle length and plant height but were intermediate to both parental strains with respect to most other morphological characters.

#### DISCUSSION

Contrary to my earlier assessment that western Transverse Range populations represent an intergrading complex involving ssp. *vestita* and ssp. *parryi* (Wilken, 1975), the numerical analysis and review of morphological variation indicate that these populations possess a combination of characters unique within *Hulsea vestita*. These characters include subentire to crenate, spatulate leaves with relatively broad petioles, reddish-tinged, lanceolate to broadly obovate phyllaries, reddish-tinged corollas, and peduncles from 11–47 cm long. Most plants of natural populations may be distinguished by these characters. Furthermore, the use of data based on common garden plants suggests the genetic similarity of these populations. This distinctive morphology, combined with an allopatric distribution, leads to the conclusion that these populations represent a discrete taxon. Accordingly, I propose the following name:

***Hulsea vestita* ssp. *gabrielensis* Wilken, ssp. nov.**

Herbae perennes scaposae, 17–38 cm altae. Folia basalia spatulata, ca. 3–6 cm longa, ca. 1.0–2.5 cm lata, utrinque glandulosa et laxe lanata, margine integra vel crenulata vel rare crenata. Capitula plerumque numerosa, vel in plantis minoribus tantum 1–3, pedunculis 11–47 cm longis. Involucrum subcylindricum usque hemisphericum, ca. 2 cm latum, ca. 1 cm altum, phyllariis 3–4-seriatis, interiores oblongis vel anguste lanceolatis, exteriores lanceolatis vel late obovatis ex rubreo viridis. Flores radii 16–23, ex rubreo pallide flava. Flores disci 41–91, corolla ca. 6 mm longa, tubo gracili, lobis ex rubreo flavis, parce glanduloso, faucibus late cylindricis. Achaenia compresso-quadrangulata, ca. 5 mm longa, supra 1 mm lata, nigra, strigosa. Pappus ex 4 paleis, subequalis. Chromosomatum numerus:  $n = 19$ .

TYPE: California, Los Angeles Co., Angeles Crest Highway, 3 mi E of Chilao, San Gabriel Mts., 6000 ft., 1 Jun 1973, *D. H. Wilken 11880* (Holotype: RSA!; isotype: CS!, others to be distributed).

Distribution: Known from open, gravelly or disturbed sites within or marginal to the coniferous forest of the western Transverse Ranges of southern California from Frazier Mt., Ventura Co., east to Mt. San Antonio, Los Angeles Co.

Representative specimens: CALIFORNIA: Los Angeles Co.: *Anderson 132* (WTU), *Bacigalupi 4201* (CAS, JEPS, RM, UTC), *Bacigalupi & Alava 6426* (JEPS), *Elmer 3700* (DS, GH, MO, POM, US, WTU), *Ewan 7216* (POM), *Goodman & Hitchcock 1722* (MO, NY, RM), *Pierson 2440* (JEPS, RSA). Ventura Co.: *Hall 6598* (DS, UC, US).

Affinities of ssp. *gabriellensis* and evolutionary relationships of infraspecific taxa within *Hulsea vestita* remain unclear. These taxa are primarily separated by combinations of morphological characters that vary in a quantitative but discontinuous fashion. Intersubspecific hybrids were produced with relative ease and, with the exception of hybrids involving ssp. *pygmaea*, were characterized by normal meiosis and comparatively high pollen fertility. These data suggest that evolution within the complex has not been accompanied by selection from genetic barriers to cross-compatibility nor by major chromosomal reorganization. Distribution of the several subspecies is largely allopatric. Although sympatric with ssp. *vestita* in the Sierra Nevada and with ssp. *parryi* in the San Bernardino Mts., ssp. *pygmaea* is restricted to alpine or subalpine sites while the former taxa are associated with coniferous forest at lower elevations. It is likely, then, that differentiation has primarily been associated with geographical and ecological isolation. Maximum isolation of populations probably was last achieved during the Xerothermic period, some 8500 to 3000 years ago (Heusser, 1960). During this period, the distribution of coniferous forest was probably restricted to only the highest elevations in the mountains of southern California (Axelrod, 1966). Earlier glacial-interglacial cycles also contributed to fluctuations in elevational distribution of coniferous forest. As suggested by Axelrod, such conditions favored population instability and local isolation. I suggest that these conditions also contributed to differentiation within *Hulsea vestita*, as is indicated by the strongly insular patterns of morphological variations within the complex.

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## AN INTERSECTIONAL HYBRID IN HEMIZONIA (COMPOSITAE: MADIINAE)

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The tarweed genus *Hemizonia* consists of 25 annual and six perennial species that bloom in late spring, summer, and fall. They occur throughout the Coast Ranges and valleys of California, northern Baja California, and the adjacent offshore islands. Two of the annual species found in the Southern Coast Ranges are *Hemizonia australis* (Keck) Keck (sect. *Centromadia*,  $n = 11$ ) and *H. ramosissima* Benth. (sect. '*Deinandron*' sensu Keck,  $n = 12$ ). [Apparently Keck (1935, 1958, 1959) did not formally establish this section; it will probably be designated as sect. *Hartmannia* (Gray) Gray (1874, 1876; Tanowitz, ined.)]. Distributions of these two species overlap in the low-lying coastal regions of Santa Barbara County where six intersectional hybrids were discovered. This hybrid combination is apparently rare.

Intersectional hybrids have been described in a number of genera such as *Ceanothus* (Nobs, 1963; Hannan, 1974), *Crepis* (Babcock and Stebbins, 1938), *Ribes* (Keep, 1962), *Helianthus* (Heiser et al., 1962), and *Perityle* (Powell, 1970). A number of intersectional hybrid attempts in *Hemizonia* were made by Clausen (1951). All were highly sterile except for a quite fertile one between *H. pungens* (H. & A.) T. & G. (sect. *Centromadia*,  $n = 9$ ) and *H. ramosissima*. *Hemizonia pungens*, although well differentiated from other members of its section, clearly

belongs in sect. *Centromadia* (Kyhos, pers. comm.). Hybrids at this taxonomic level, however, are rare in nature and can be produced experimentally only with difficulty (Grant, 1963, 1970). It was interesting then to carry out morphological and cytological studies to aid in determining possible phylogenetic relationships between the sections.

TABLE 1. MORPHOLOGICAL COMPARISON OF *HEMIZONIA AUSTRALIS*, *H. RAMOSISSIMA*, AND PUTATIVE HYBRIDS.

Character	<i>H. australis</i>	Hybrids	<i>H. ramosissima</i>
Shape of leaf tip	apiculate	acute-obtuse	obtuse
Peduncle length:			
maximum (mm)	9.0(3.8-15.0)	10.7(6.0-16.8)	12.5(6.5-22.0)
minimum (mm)	0.0	2.9(0.5- 6.5)	4.0(0.5-12.5)
max/min	0.0	<sup>a</sup> 5.3(1.4-13.5)	4.0(1.7-16.0)
Number of heads on ultimate branches	4.9(3-8)	8.7(5-13)	10.4(7-18)
Shape of phyllary tip	apiculate	acute-obtuse	obtuse
Phyllary:			
length (mm)	4.3(3.5-5.5)	<sup>a</sup> 4.9(3.5-6.2)	4.2(3.5-5.5)
width (mm)	5.9(5.0-6.5)	4.5(3.0-6.0)	3.1(2.2-4.5)
l/w	0.7(0.5-0.8)	1.1(0.8-1.4)	1.5(0.7-1.9)
Number of ray flowers/head	19(16-22)	8.9(8-10)	5
Number of disc flowers/head	40(33-48)	13.6(9-16)	6
Receptacular bract:			
length (mm)	4.6(4.2-5.0)	<sup>a</sup> 5.3(4.5-5.8)	4.9(4.0-6.2)
width (mm)	1.0(0.9-1.1)	<sup>a</sup> 1.6(1.5-2.0)	1.4(1.2-1.8)
l/w	2.2(2.0-2.4)	0.4(0.3-0.5)	0.3(0.2-0.4)
Ray corolla:			
length (mm)	5.1(4.5-6.0)	<sup>a</sup> 5.5(4.5-6.0)	5.2(3.0-7.0)
width (mm)	1.6(1.2-2.0)	2.2(1.5-2.8)	3.6(3.0-5.0)
l/w	3.2(3.0-4.0)	2.2(2.0-3.5)	1.5(1.0-1.8)
lobe number	2	2 or 3	3
Ray achene:			
length (mm)	1.9(1.5-2.5)	<sup>a</sup> 2.2(2.0-2.5)	2.0(1.8-2.5)
width (mm)	1.1(1.0-1.2)	1.0(0.8-1.2)	1.1(1.0-1.5)
l/w	1.6(1.4-1.8)	<sup>a</sup> 2.2(1.8-2.7)	1.9(1.2-2.2)
Disc achene length (mm)	1.2(1.5-2.5)	1.4(1.2-1.8)	1.9(1.5-2.5)
Number of pappus paleae/disc flower	3(3-4)	6(5-7)	7.6(7-10)
Length of pappus paleae/disc flower:			
maximum (mm)	2.9(2.2-3.0)	2.4(1.8-3.0)	1.4(1.0-1.8)
minimum (mm)	2.6(2.0-3.2)	1.2(1.0-1.5)	1.1(1.0-1.5)
max/min	1.1(1.0-1.2)	<sup>a</sup> 2.0(1.3-2.7)	1.3(1.0-1.5)

<sup>a</sup> Numerical values represent the mean of 10 measurements on each of 5 individuals from 20 populations for each of the parents and 20 measurements on each of the 6 hybrids. Note that for some characters the hybrids exceed either of the parental types.

## MATERIALS AND METHODS

Comparisons of hybrids and parental taxa for 26 characters are given in Table 1. These were selected for ease of measurement and represent some of the most striking differences in character states. Vouchers of specimens from populations used in this study are listed in Table 2 and are deposited at UCSB.

Meiotic figures in PMC's were obtained from flower buds fixed in a solution of either Newcomer's fixative or modified Carnoy's (ethanol:chloroform:acetic acid, 6:3:2, v/v). Buds were transferred to 70% ethanol for storage. Cells were stained in iron acetocarmine and slides were made permanent following Beeks' method (1955). Pollen was stained in 1% aniline blue in lactophenol for at least 24 hr. Five hundred pollen grains for 20 specimens of *H. australis* and 20 specimens of *H. ramosissima* were scored. Twenty flower buds were sampled from each of the six putative hybrids. Pollen grains that stained evenly were considered viable; unstained or unevenly stained grains were considered inviable.

## RESULTS

*Meiosis in the parents.* *Hemizonia australis* ( $2n = 22$ ; Venkatesh, 1956; Table 2) exhibits regular meiosis with 11 pairs of morphologically similar chromosomes. There are normally 2 chiasmata per bivalent, one in each arm. There is occasionally an interstitial chiasma formed in one of the arms. This species showed an average of 94.6% stainable pollen, ranging from 86.0 to 99.8% for all populations. *Hemizonia ramosissima* ( $2n = 24$ ; Johansen, 1936; Table 2) also exhibits regular meiotic divisions with 12 bivalents. These chromosomes are morphologically similar as well. The chiasma frequency is approximately two per bivalent with one chiasma per arm. This species showed 98.2% stainable pollen, ranging from 93.6 to 100% for all populations.

*Meiosis in the hybrids.* Pachytene chromosomes were normally unanalyzable. Late diakinesis and metaphase cells were analyzed in four of the six hybrid plants. Configurations ranged from univalents to hexavalents. Most cells, however, contained only univalents, bivalents, and trivalents (Table 3 and Fig. 1). Bivalents were generally rod-shaped, while trivalents were predominantly forked (Figs. 1,4). Bivalents and trivalents were generally oriented on the equator; univalents were scattered through the cell (Fig. 2). Diakinesis and metaphase cells were often difficult to analyze thoroughly due to the large number of chromosomes, the tendency for the chromosomes to be "sticky", and the reduced pairing. Numbers of other cells were observed in which the complete complement could not be clearly discerned; many of these cells seemingly contained univalents, bivalents, and occasionally a trivalent.

TABLE 2. CHROMOSOME NUMBERS OF *HEMIZONIA AUSTRALIS*, *H. RAMOSISSIMA*, AND HYBRIDS USED FOR ANALYSIS IN THIS STUDY. All collections are from Santa Barbara County, California. Collection numbers without name refer to Tanowitz collections.

*H. australis* (Keck) Keck;  $n = 11$ .

Field S of Storke and Hollister Rds, 899-1B, 899-R, 1573-A, 1573-B, 1573-L; field E of Los Carneros and El Colegio Rds, 1576-A, 1576-B, 1576-C, 1576-D; lagoon on campus UCSB, Tanowitz & Varney 1583; slough E of Los Carneros and Hollister Rds, Tanowitz & Zalin 1725-A.

*H. ramosissima* Benth;  $n = 12$ .

Road cut off Hwy 101 at Gaviota, 465-1C, 1218; San Antonio Creek Trail near San Marcos Pass Bridge, 747, 1523; Modoc Rd. at entrance to La Cumbre Country Club, 1525; 0.4 mi W of Bailard Av. on Carpenteria Av., 1532-A, 1532-H; along Arroyo Paredo Creek intersecting Hwy. 192, 1534-B; field S of Storke and Hollister Rds., 1537-A, 1537-B, 1537-C, 1537-D, 1537-M; El Cielito Rd. and Stanwood Dr., 0.2 mi from Sheffield Reservoir, Tanowitz & Cowan 1589; W side of campus lagoon, 1507; along Casitas Pass Rd., at intersection with Livingston Canyon Rd., 2428.

*H. australis*  $\times$  *H. ramosissima*;  $2n = 23$ .

W side of campus lagoon, UCSB 1299; field on UCSB campus near Pardall Rd., Tanowitz & Smith 1300-E; field E of Storke and Hollister Rds., Tanowitz & Zalin 1517; W side of campus lagoon UCSB, 1524; field E of Storke and Hollister Rds., near University Village, 1538; field near ocean bluff and San Rafael Dormitory, UCSB campus, 1568.

TABLE 3. FREQUENCIES AND MEANS OF SYNAPTIC CONFIGURATIONS IN POLLEN MOTHER CELLS (PMC) OF *HEMIZONIA AUSTRALIS*  $\times$  *H. RAMOSISSIMA*. Data derived from diakinesis or first metaphase in 155 PMC's from 4 plants.

Type	Frequency/PMC											Mean/cell	
	0	1	2	3	4	5	6	7	8	9	10		11
I	11	13	25	33	28	22	12	6	3	1	—	1	3.49
II	—	2	4	10	28	36	35	25	9	6	—	—	5.47
III	12	50	61	25	7	—	—	—	—	—	—	—	1.77
IV	74	69	11	1	—	—	—	—	—	—	—	—	0.61
V	136	19	—	—	—	—	—	—	—	—	—	—	0.12
VI	149	6	—	—	—	—	—	—	—	—	—	—	0.04

Chiasma frequency is low (approximately 14 per cell) but all chiasmata appear to terminalize fully. Most bivalents had only one chiasma. The modal frequency of ring bivalents was only two per cell. Only three bivalents in all the cells analyzed contained three chiasmata. All forked trivalents had three chiasmata, while chains of three contained only two. All but four quadrivalents had three chiasmata. Pentavalents had four; hexavalents, five. Very few cells contained fragments at metaphase.

Forty-eight anaphase cells were analyzed. In every instance laggards were observed. Occasionally, univalents were left on the metaphase plate (Fig. 3) or there was precocious separation of univalents (Fig. 4). There was a very low frequency of bridges or fragments evident at this stage. Two cells had a large amount of fragmentation, giving them an appearance of being "shattered". Such spontaneous breakage has been

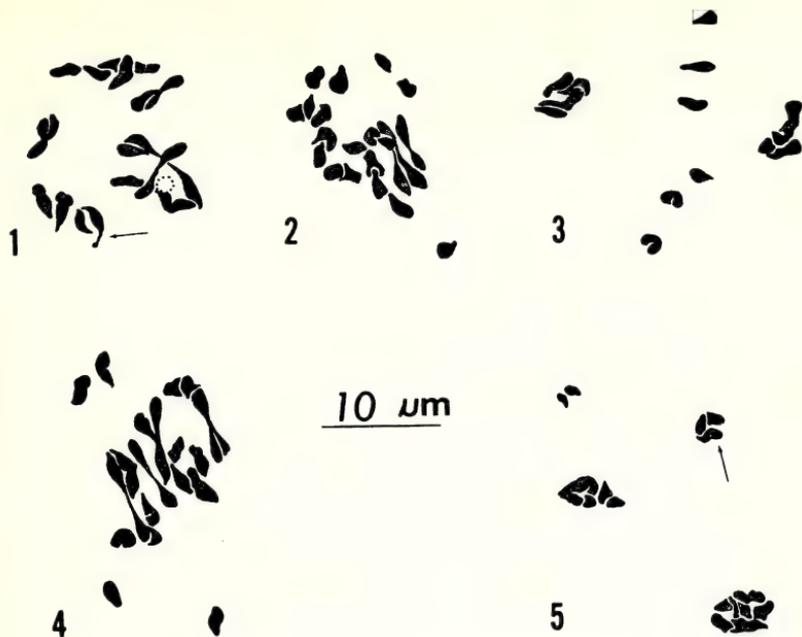


FIG. 1-5. Camera lucida drawings of meiotic chromosomes of *Hemizonia australis*  $\times$  *H. ramosissima*. 1. Late diakinesis; note forked trivalents and heteromorphic pair (arrow),  $2_I + 6_{II} + 3_{III}$ ; *Tanowitz 1568-B*. 2. metaphase I; univalents scattered throughout cell; *Tanowitz 1538-A*. 3. Telophase I; univalents remaining on the metaphase plate; *Tanowitz 1568-B*. 4. Early anaphase I; note precocious separation of univalents  $4_I + 4_{II} + 2_{III} + 1_V$ ; *Tanowitz 1524-F*. 5. Telophase I with two micronuclei; note association of 3 chromosomes (arrow); *Tanowitz 1529-B*.

described in a number of other plants (Darlington and Upcott, 1941; Walters, 1956; Burns and Gerstel, 1969). The fragments appeared to be paired and of more or less equal size.

First telophase exhibited lagging chromosomes and micronuclei. There often appeared to be an association of three chromosomes forming a micronucleus at this stage (Fig. 5). Bridge-fragment formation was as infrequent in the second division as it was in the first. Sporads of these hybrids display a great deal of variation. The range was from four to eight cells, with an average of six cells per sporad. The number of microspores per sporad ranged from one to five, with an average of three per sporad. Pollen stainability was quite low, averaging 7.2% and ranging from 0.4 to 17.2%.

## DISCUSSION

Generic sections are constructed in order either to reflect the distinctiveness between any two or more species groups or to indicate the affiliation of a group of species. Sections are generally circumscribed on the basis of morphological characters, although cytogenetic, chemical, geographical, or ecological characters are sometimes used. Sections of *Hemizonia* are morphologically circumscribed and there are numerous striking character differences between the sections. Yet earlier investigations (Clausen, 1951; Venkatesh, 1958) suggested a lower degree of divergence when the genomic make-up of the species belonging to sections *Centromadia* and '*Deinandra*' was compared.

Although the frequency of hybridization in *Hemizonia* appears to be low, it may have been more common in the earlier stages of divergence of the genus. Venkatesh (1958) suggested that the aneuploid series in sect. *Centromadia* ( $n = 9, 11, 12, 13$ ; Johansen, 1936; Venkatesh, 1958; Table 2) may have resulted from crosses between species with disparate chromosome numbers, possibly of different sections. It is also possible that the series in sect. '*Deinandra*' ( $n = 9, 10, 11, 12, 13$ ; Johansen, 1936; Table 2) may have resulted in this manner. Intra- as well as inter-sectional hybrids appear reasonable sources for speciation. Hybrids of intra- and inter-sectional origin were suggested for the origin of some *Clarkia* species (Lewis and Roberts, 1956). Nevertheless, inter-sectional hybridization in *Hemizonia* does not appear to be widespread now.

Species may have significant barriers to gene exchange maintained by both pre- and postmating isolating mechanisms (see Levin, 1971). Observations in the field suggest that both kinds of barriers occur between *H. australis* and *H. ramosissima*. Weak seasonal isolation is maintained throughout the respective ranges. *Hemizonia ramosissima* blooms earlier than *H. australis*; however, the period of overlap is significant. Microhabitat differences are found: *H. australis* occupies more saline regions than *H. ramosissima* and the hybrids are found in the intermediate areas. Pollinator constancy is quite strong where the species are in close contact (Tanowitz, ined.). Hybrid sterility is certainly evident from the data. Chromosomal differences are demonstrated clearly by the meiotic configurations in the hybrids (Figs. 1-5, Table 3) exhibiting univalents and multivalents, heteromorphic bivalents, and occasional bridges and fragments. Presumably, these meiotic irregularities contribute greatly to the sterility of the hybrids and reflect the occurrence of translocations, paracentric inversions, and perhaps other chromosomal reorganizations. None of these chromosomal differences per se necessarily preclude crossing between the species and thus many more hybrid individuals might be expected to occur; however, it is presumed that reproductive barriers, about which nothing is now known, must occur in combination with chromosomal disparity, since there is a paucity of hybrids in the field.

The hybrid plants are highly sterile annuals and obligate outcrossers (Keck, 1959; Tanowitz, ined.; Kyhos, pers. comm.). There is no evi-

dence of introgression; only putative  $F_1$ 's have been found in the sympatric populations. This suggests that gene flow is non-existent or rare and that these sharply distinctive species seemingly maintain their integrity completely. The morphological and cytogenetical evidence supports their assignment to separate sections.

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## NOTES AND NEWS

CHROMOSOME NUMBERS AND RELATIONSHIPS OF *CLAYTONIA SAXOSA* AND *C. ARENICOLA* (PORTULACACEAE).—*Claytonia saxosa* Brandegee and *C. arenicola* Henderson are rather uncommon and poorly understood taxa of western North America. Their chromosome numbers, reported here for the first time, as well as morphological observations, provide evidence for suggestions on possible relationships with other species of *Claytonia* sect. *Limnia*. Current studies of the *C. perfoliata* Donn and *C. spathulata* Hook. complexes of sect. *Limnia* reveal parallel variation in a number of the vegetative morphological features traditionally used to define these species (Miller, Syst. Bot. 1:20–34. 1976; Fellows, Madroño 23: 296–297. 1976). This work suggests that relationships are better expressed by chromosome base number and floral features, especially the surface of the seed coat. Our purpose is to report the chromosome numbers of *C. arenicola* and *C. saxosa* and to suggest, from correlations with seed morphology and other traits, how the relationships shown by previous studies may be revised.

Two recent reviewers of infrageneric relationships in *Claytonia* (Swanson, Brittonia 18:299–241. 1966; McNeill, Canad. J. Bot. 53:789–809. 1975) have placed *C. saxosa* and *C. arenicola* in sect. *Limnia*, together with the other annual species *C. perfoliata*, *C. spathulata*, and *C. gypsophiloides* F. & M. McNeill put in sect. *Limnia* the perennials *C. sibirica* L. and *C. heterophylla* (T. & G.) Swanson, whereas Swanson assigned these taxa to two other sections. Most of the clustering methods used by McNeill in his numerical taxonomic analysis placed *C. sibirica* and *C. heterophylla* as a closely allied pair, adjacent to—but somewhat removed from—the cluster formed by the five other species mentioned above. In the several dendrograms presented by McNeill, *C. arenicola* links directly to the pair formed by *C. spathulata* and *C. gypsophiloides*. A close morphological tie between these three is also evident in McNeill's plot (his fig. 8) of the first two axes in a principal-coordinates analysis of sects. *Limnia* and *Rhizomatosae*. On this plot, *C. sibirica* and *C. heterophylla* are in a more distant position, intermediate toward sect. *Rhizomatosae*. *Claytonia saxosa* links directly to *C. perfoliata* in several of McNeill's dendrograms but in the plot just cited, it stands alone, about equidistant from *C. perfoliata* and *C. spathulata*.

Our studies show that *Claytonia arenicola* is diploid, with  $x = 6$  ( $2n = 12$ ; ID, Adams Co., Hells Canyon, 13.4 km upriver from Hells Canyon Dam, Miller 496; OR, Wallowa Co., Hells Canyon, 1.5 km below Hells Canyon Dam, Miller 499; WA, Asotin Co., Clarkston, 6 km W on S side of the Snake R., Miller 493). This is the same as the base number found in *C. sibirica* (Lewis, Bot. Rev. 33:105–115. 1975). The flowers of *C. arenicola* are virtually indistinguishable from those of *C. sibirica*, being protandrous with a showy corolla of “candy-striped” white or pinkish petals 5–10 mm long. Its breeding system, like that of *C. sibirica* (Swanson, Ph.D. Dissertation, Univ. California, Berkeley, p. 59. 1964), appears to be one of obligate outcrossing, since plants that flowered in an insect-free greenhouse set no seeds spontaneously. The inflorescence of *C. arenicola* resembles that of *C. sibirica* in having a bract by each pedicel of the raceme. Mature seeds of the species have a low-tubercled surface similar to that of *C. sibirica* but distinctly different from the more prominently tubercled seeds of *C. spathulata* and *C. gypsophiloides*. Unlike the dull-surfaced seeds of *C. gypsophiloides* and *C. spathulata*, the seeds of *C. sibirica*, *C. arenicola*, and *C. perfoliata* show a “shiny highlight” when illuminated. Therefore, *C. arenicola* differs significantly from *C. spathulata* and *C. gypsophiloides*, which have a base chromosome number of  $x = 8$  (Fellows, loc. cit.; Lewis, Ann. Missouri Bot. Gard. 54:180. 1967; Nilsson, Bot. Not. 119:464–468. 1966), and in which the racemes have only a single bract at the base. *Claytonia perfoliata* has a chromosome base number of  $x = 6$  (Fellows, loc. cit.; Miller, loc. cit.; Swanson, op. cit.) but it varies from *C. arenicola* in its consistently small, self-pollinating flowers and its racemes, which are bracteate only at the base. If special weight is

given to the above characteristics, therefore, *C. arenicola* appears to be more closely related to *C. sibirica* than to either the *C. perfoliata* or the *C. spathulata-gypsophiloides* complexes.

*Claytonia saxosa* is diploid with  $x = 8$  ( $2n = 16$ ; CA, Siskiyou Co., Scott Valley, mouth of Heartstrand Gulch, Miller 488). Its corollas are showy, with pink petals 6–8 mm long, and the species is putatively outcrossing, as one would also suspect of the large-flowered, diploid *C. gypsophiloides*. In the material of *C. saxosa* we have examined, the racemes are completely ebracteate (contrary to a statement in the key by McNeill, op. cit., p. 801). The seed coat of *C. saxosa* is prominently tubercled and dull-surfaced as in *C. spathulata* and *C. gypsophiloides*, although the shape of the tubercles is slightly different. Although paired with *C. perfoliata* in some of the numerical analyses reported by McNeill (op. cit.), *C. saxosa* seems to be relatively more distant from that species than it is from *C. gypsophiloides* and *C. spathulata*, if one assumes that chromosome number and seed coat morphology are conservative indicators of genetic relationship.

Voucher specimens and permanent microslides for the chromosome counts reported in this study are deposited in OSC. —JOHN M. MILLER and KENTON L. CHAMBERS, Department of Botany and Plant Pathology, Oregon State University, Corvallis 97331.

ON THE RELATIONSHIPS OF CHENOPODIUM FLABELLIFOLIUM AND *C. INAMOENUM*.—Taxonomists have disagreed on the treatment of *C. inamoenum* Standley (North Amer. Flora 21:1–93, 1916; type: Arizona-Mexico border near Douglas, Mearns 2286, US) and *C. flabellifolium* Standley (op. cit.; type: Baja California, San Martín Island, 1897, T. S. Brandegee s.n., UC 116454).

Standley placed *C. inamoenum* in "group" Leptophylla together with several other species. One of the species was *C. hians* Standley (op. cit.; type: near Dulce, New Mexico, 1911, Standley 8129, US). Another species included in this group was *C. leptophyllum* (Nutt. ex Moq.) S. Wats., which was originally described as *C. album* var. *leptophyllum* Nutt. ex Moq. [DeCandolle, Prod. 13(2):71. 1849; type: Gordon 260, K, with the locality given as LaPlatte (on the Platte River?)]. Aellen and Just (Amer. Midl. Naturalist 30:47–76, 1943) considered *C. inamoenum* to be the same as *C. leptophyllum*. Wahl (Bartonia 27: 1–46, 1952–53) commented that the type of the former "does not agree with any material seen". Examination of the type specimen reveals that it is the top of a plant with what appear to be few primary leaves and with many seeds. The seeds (actually fruits, since the pericarp is attached) of the type closely resemble those of *C. leptophyllum* in being 1.0 mm or less in diameter and with black pericarps. A couple of what I interpret as primary leaves have two very weakly developed veins. *Chenopodium hians* typically has leaves oblong to linear in outline with a midrib and two well developed lateral veins whereas the leaves of *C. leptophyllum* bear only a strong midrib and no discernable lateral veins. While no definitive conclusion can be reached regarding the type of *C. inamoenum*, the seed characters are strong evidence for its being considered as nearer to *C. leptophyllum*.

*Chenopodium flabellifolium* was viewed by Standley (op. cit.) as closely related to the *C. neomexicanum* complex, since he placed it in his "group" Fremontiana with several other species having basally lobed leaves. These other taxa included *C. neomexicanum* Standley, *C. arizonicum* Standley, *C. palmeri* Standley, and *C. parryi* Standley, all of which he described in this same paper in 1916. In an earlier paper (Madroño 22:185–195, 1973), I considered the types of these names to be conspecific, and *C. lenticulare* Aellen, (Feddes Repert. Spec. Nov. Regni Veg. 26:31–64, 119–160, 1929) was likewise considered to belong to the same species. Whereas Standley considered *C. flabellifolium* to be related to *C. neomexicanum*, Aellen and Just (op. cit.) placed the former in synonymy under *C. opulifolium*, which is a sparingly introduced European species (Schrader in Koch and Ziz, Cat.

pl. Palat. 6, 1814, type not seen). Wahl (op. cit.) treated *C. flabellifolium* in the same manner as Aellen and Just, but he added "probably" parenthetically after the name. This I take as an indication of doubt concerning the proper placement of this species. Wahl, who had a remarkable understanding of *Chenopodium* in North America despite limited field work, did not publish further on the relationships of *C. inamoenum* and *C. flabellifolium*. He did, however, annotate a number of specimens in various herbaria and these annotations suggest that in later years he came to quite a different conclusion on relationships than was expressed in his papers. Wahl annotated the type of *C. flabellifolium* as *C. inamoenum*, and moreover he indicated that types of both are conspecific with the type of *C. arizonicum* (type: Arizona, Santa Rita Forest Reserve, D. Griffiths 5982, US). Thus, if one were to combine this concept of Wahl with my latest treatment of the *C. neomexicanum* complex in which I consider the types of *C. arizonicum*, *C. lenticulare*, *C. neomexicanum*, *C. palmeri*, and *C. parryi* to be conspecific, then one would have these five names plus *C. flabellifolium* and *C. inamoenum* refer to one species. This is not tenable, and I shall present my concepts of relationships among these species.

The type of *C. flabellifolium* is similar to that of *C. neomexicanum*. The lower and primary leaves are about as wide and as long and have mostly bipartite basal lobes. The leaf shape falls easily into the variation encountered in *C. neomexicanum*. The more mature seeds measure 1.1–1.2 mm in diameter and the pericarp is strongly attached. The type of *C. flabellifolium* differs from *C. opulifolium* (as I understand it) in several respects, the most notable being the more strongly keeled sepals of the latter. In my opinion, *C. flabellifolium* is closely related to *C. neomexicanum*, and indeed they may be conspecific. I have found only two collections in addition to the type collection that could be referred to *C. flabellifolium*, and both were made prior to the present century. The question of whether or not *C. flabellifolium* is conspecific with *C. neomexicanum* cannot be answered with certainty at present; however, there is no question that the types of *C. flabellifolium* and *C. inamoenum* are distinct. *Chenopodium inamoenum* is probably the same as *C. leptophyllum*, although the depauperate nature of its type specimen precludes a confident decision.

Supported by NSF Grants GB-29793X and BMS-21384.—DANIEL J. CRAWFORD, Department of Botany, University of Wyoming, Laramie 82071.

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# MADROÑO

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A NEW SPECIES OF DRYPETES (EUPHORBIACEAE)  
FROM PANAMA

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*Drypetes*, which with about 200 species is one of the larger genera of Euphorbiaceae (Airy Shaw, 1966), is best represented in the Old World tropics; only about 20 valid species have been recognized from neotropical America. The genus is rather isolated in the Euphorbiaceae (Webster, 1967); together with the satellite (and scarcely distinct) genera *Neowawrea* and *Putranjiva*, it is referable to the tribe Drypeteae, which has no very close neighbors in subfamily Phyllanthoideae (Webster, 1975). The species of *Drypetes* are rather poorly understood, partly because the erratic flowering, dioecious flower distribution, and nondescript foliage make recognition of imperfect specimens difficult.

The elusiveness of *Drypetes* is indicated by the fact that the species here described, a tree 15–25 m high, was overlooked by many botanists on Barro Colorado Island—one of the best-explored localities in the tropics—until 1971, when it was collected by Dr. Thomas Croat and Dr. Robin Foster. Recently I have examined two sheets of what appears to be the same species from southern Venezuela; these collections were annotated by Dr. Paul C. Standley with a manuscript name. Since both of the Venezuelan specimens are pistillate, and it is not absolutely certain that they are conspecific with the Panamanian plants, it seems best to describe the species from the Panama specimens and to commemorate Dr. Standley's association with the plant by dedicating the specific epithet to him.

*Drypetes standleyi* Webster, sp. nov. sect. *Drypetitis*, ad *D. variabilem* Uitt. accedens sed foliis chartaceis abrupte acuminatis, staminibus 8 vel 9 minoribus, pedicellis ♀ brevioribus; a *D. amazonica* Steyerem. differt antheris glabriusculis, foliis chartaceis integris.

Tree c. 15–25 m high; trunk c. 0.25–1.25 m diam., buttressed at base; twigs terete, minutely hispidulous when young (trichomes 0.1 mm long or less), glabrate and pale in age and prominently lenticellate. Leaves chartaceous; petioles glabrous or nearly so, flattened adaxially, mostly 5–10 mm long; stipules scarious, very inconspicuous (less than 1 mm long); blades nearly glabrous (slightly strigose on midrib beneath), elliptic to broadly lanceolate, rather abruptly short-acuminate at tip, asymmetrically cuneate at base, mostly 7–11 cm long, 2.5–6 cm broad, plumbaceous and somewhat lucent on both sides; midrib salient beneath, main lateral veins 7–9 on a side, distinctly raised beneath, brochidodromous, veinlets forming a prominulous reticulum; margins entire. Staminate

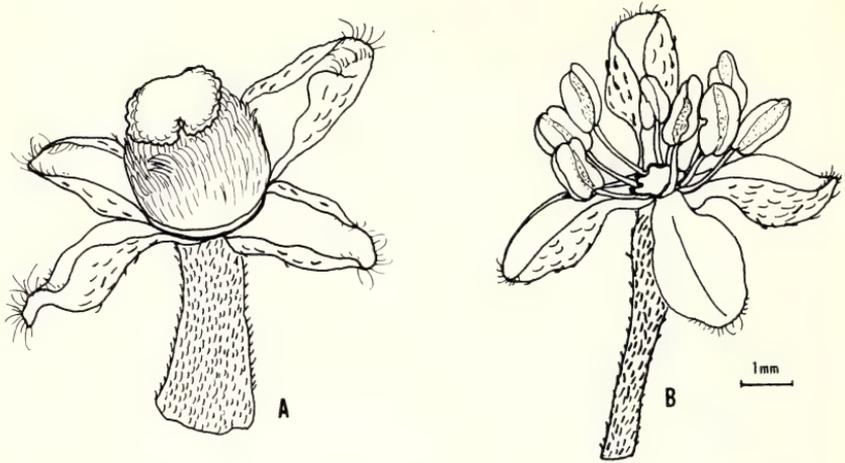


FIG. 1. Flowers of *Drypetes standleyi*. A, pistillate flower (Foster & Croat 2307). B, staminate flower (Croat 14849).

flowers in axillary clusters subtended by scarious bracteoles; pedicels 7–11 mm long, densely hispidulous; sepals 4, recurved, oblong-spathulate, marginally ciliate, appressed-hirsutulous on the back, glabrous or nearly so within, c. 2.5–3 mm long, 1.7–2.2 mm broad; disk somewhat fleshy, 1–1.5 mm across, glabrous; stamens 8 (rarely 9), filaments 1–2 mm long; anthers linear-oblong, glabrous (sometimes obscurely and very sparsely pubescent), (1.0–) 1.2–1.6 mm long; pistillode absent. Pistillate flowers axillary, 1–4 per cluster; pedicels stout (0.6–1 mm thick), straight, densely hispidulous, 2–6 mm long; sepals 4, deciduous, broadly obovate, minutely strigose on the back, glabrous within, marginally ciliate, 2.8–4.4 mm long, 2.5–3.2 mm broad; disk strigillose-ciliate, 2.0–2.3 mm across; ovary globose or ellipsoidal, c. 2 mm across, densely whitish-tomentose, 1-locular; stigma sessile or nearly so, reniform, glabrous, c. 1.7–2.5 mm across. Fruits somewhat compressed, strongly reticulate-wrinkled, appressed-hirsutulous, scarcely beaked, 2–2.2 cm long, 1.3–1.5 cm across; endocarp lignified, c. 1.5 mm thick with a pronounced obtuse ventral carina within; ovule attached apically by an elliptical scar, mature seeds not observed.

TYPE: Panama, Canal Zone, Barro Colorado Island, E of Armour Trail, 31 May 1971, *R. Foster & T. B. Croat* 2307 (pistillate; holotype, DAV; isotypes DUKE, MO, and to be distributed). Paratype (staminate flowers): Barro Colorado Island, Armour Trail, 31 May 1971, *T. B. Croat* 14849 (DAV, MO) (Fig. 1).

ADDITIONAL COLLECTIONS. PANAMA. Canal Zone: Barro Colorado I., 300 m E of Armour Trail, *Croat 14843* (DAV, MO); S of big trees on Armour Trail, *Croat 16516* (DAV, MO); S of Zetek 11, *Foster 1122* (DAV, DUKE). VENEZUELA. Apure: Las Piedras, alrededor de Puerto Paez, *J. Velez 2635* (VEN; fruits immature and determination somewhat uncertain). Bolivar: en los rebalsos de Guayape, Bajo Caura, *L. Williams 11986* (VEN).

*Drypetes standleyi* clearly belongs in sect. *Drypetes* (sect. *Hemicyclia* auct.) because of its small stipules, staminate flowers without pistillode, and unilocular ovary (Pax & Hoffmann, 1922; Webster, 1967). In the treatments of neotropical *Drypetes* by Monachino (1948) and Jablonsky (1967), the plants from Barro Colorado would key out to the South American species *D. amazonica* Steyrm. or *D. variabilis* Uitt., while in the revision by Pax and Hoffmann (1922) they would be close to the West Indian species *D. dussii* Kr. & Urb. or *D. glauca* Vahl. At first, it appeared that the Panamanian plants could be accommodated in *D. variabilis*, but they clearly differ in the thinner less rigid leaves and in a number of reproductive characters: smaller staminate sepals, stamens mostly 8 (occasionally 8 in *D. variabilis*, but usually 7), shorter fruiting pedicels, densely tomentose ovary, and wrinkled fruits. The differences between *D. standleyi* and its near congeners may be summarized in the following key:

Stamens 4, anthers only 0.5 mm long, glabrous; leaves crenate, cuspidate-acuminate; Guiana . . . . . *D. fanchawei* Sandw.

Stamens 4–12, anthers larger (or else pubescent).

Stamens mostly 4–7; leaves entire or nearly so.

Staminate flowers several per axil; sepals less than 1 mm broad; anthers less than 1 mm long, pubescent; fruiting pedicels 5–12 mm long; drupes 0.8–1.3 cm long, oblique at tip; leaves chartaceous; West Indies . . . . . *D. alba* Poit.

Staminate flowers 1–3 per axil; pistillate sepals more than 1 mm broad; anthers over 1 mm long, glabrous; fruiting pedicels 15–21 mm long; drupes 2–2.5 cm long, symmetrical; leaves coriaceous; northern South America . . . . *D. variabilis* Uitt.

Stamens mostly 8–12 (rarely 7).

Drupes 2.5–3 cm long; staminate sepals at least 3.5–4 mm long, glabrous except for marginal ciliae; anthers slightly pubescent; Martinique . . . . . *D. dussii* Kr. & Urb.

Drupes less than 2.5 cm long; staminate sepals 2.5–3.5 mm long, pubescent on the back.

Anthers glabrous (or very nearly so), 1.2–1.6 mm long; leaves chartaceous, entire; Panama and Venezuela . . . . .  
. . . . . *D. standleyi* Webster

Anthers distinctly pubescent, 2.0–2.4 mm long; leaves coriaceous, entire to crenate; Brazil . . . . . *D. amazonica* Steyrm.

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I wish to thank Dr. Tom Croat and Dr. Robin Foster for providing the material from Barro Colorado Island, the Missouri Botanical Garden (MO) and the Instituto Botánico in Caracas (VEN) for loan of specimens, and Ms. Mary Breckon for making the drawings.

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DARMERA, THE CORRECT NAME FOR  
PELTIPHYLLUM (SAXIFRAGACEAE), AND A NEW  
COMBINATION IN PELTOPHYLLUM (TRIURIDACEAE)

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Current work by the senior author on vegetative and floral anatomy of Burmanniaceae, Petrosaviaceae, and Triuridaceae, which are obscure, mainly tropical families of achlorophyllous, saprophytic monocotyledons, has led to two realizations: (1) the long discarded triuridaceous name *Peltophyllum* Gardner (1843) must be used in preference to *Hexuris* Miers (1850), and (2) of particular relevance to horticulturists and to western North American botanists, the well-known saxifragaceous genus *Peltiphyllum* (Engler) Engler (1891) requires a substitute name.

In 1841 John Miers (see also his 1845 paper) described *Triuris* with a single species, *T. hyalina*. Later, George Gardner (1843, 1845) published a new genus and species, *Peltophyllum luteum*. Gardner's original description follows (1843: 176; 1845):

PELTOPHYLLUM, *Gardner*.

*Flores* dioici. *Masc.* ignoti. *Fæm.* *Perigonium* 6-partitum, coloratum, patens, persistens; laciniis ovatis, longè acuminatis; acumine plano. *Ovaria* plurima, in tori apice sessilia, adpressa, libera. *Styli* ad apicem incrassati, obliquè truncati. *Fructus* ignotus.

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Herba *parvula Brasiliensis*. Folia a scapo distantia, longè petiolata, peltata, valdè reticulata. Radix tuberosa, fibrosa. Scapus subramosus, basi squamosus; pedunculis basi bracteatis, unifloris; floribus luteis.

*Peltophyllum luteum*, Gardn. Herb. Bras. n. 3570.

*Peltophyllum luteum* was based on a single collection (*Gardner 3570*), which we have not seen, and which apparently has been lost (Giesen, 1938; Malme, 1896). The Fielding-Druce Herbarium at Oxford University, which has a "very full set" (Clokie, 1964: 169) of Gardner's specimens, informed us (pers. comm., 1976) that it does not have *Gardner 3570*.

*Peltophyllum* differed from *Triuris* in having 6 instead of 3 caudate tepal lobes and also in having remarkable peltate leaves associated with the flowering scapes. Miers (1850, 1852) pointed out that the peltate leaves do not belong to the triuridaceous plant, but probably are of seedlings of Menispermaceae. Rejecting *Peltophyllum*, Miers (1850, 1852) created the new name *Hexuris gardneri* for Gardner's fertile material, and since then, *Peltophyllum* Gardner seems not to have been accepted other than by Schumann (1894) (for later references see Giesen, 1938, the most recent monograph on the family).

The name *Hexuris* Miers (1850) is clearly illegitimate. Miers substituted this name for *Peltophyllum* Gardner (1843) because "peltophyllum" is scarcely applicable to the exclusively squamate Triuridaceae. However, according to the International Code of Botanical Nomenclature (Art. 62), a legitimate name cannot be rejected merely because it is inappropriate or disagreeable. Therefore, the name *Peltophyllum*, however descriptively inappropriate, must be retained since it is clearly possible from Gardner's description (1843, 1845) to select the fertile material as the type (which is here designated the lectotype of *Peltophyllum luteum* Gardner). It should be emphasized that apart from the accounts of the peltate leaves and attached tuberous roots, which apparently belong to Menispermaceae (Miers, 1850, 1852), Gardner (1843, 1845) adequately described the new triuridaceous plant, although fruits and male flowers were not discovered until much later by Malme (1896). Gardner in 1845 also accurately figured a female plant complete with its roots and scale leaves.

The consequence of the above is that the well-known name *Hexuris* Miers must be replaced with the more obscure *Peltophyllum* Gardner. Schumann (1894) and the staff workers of *Index Nominum Genericorum* had come to the same conclusion. Following Giesen's (1938) circumscription of *Hexuris* Miers, *Peltophyllum* then includes 2 species: *P. luteum* Gardner (1843) and *P. caudatum* (Poulsen) Schmid & Turner.

The consequence to western North American botanists of the imbroglio over Triuridaceae comes with the recognition that the saxifragaceous

name *Peltiphyllum* (Engler) Engler (1891)<sup>2</sup> is illegitimate because it is a mere orthographic variant (Art. 75) of the earlier, legitimate *Peltophyllum* Gardner (1843, Triuridaceae) and thus is a later homonym (Art. 64). Therefore, a different generic name must be used for the single species of *Peltiphyllum* (Engler) Engler, the familiar "umbrella plant" (or "Indian rhubarb") of California and southern Oregon, *P. peltatum* (Torrey in Benth) Engler, a name that has been used in all manuals of our region since the Englerian genus was established (see also Engler, 1930, and Wagner, 1907).

In 1899 the horticulturist Andreas Voss [1857–1924—see obituary in *Gartenwelt* 28:238–240 (1924)] published the name *Darmera*<sup>3</sup> with *Peltiphyllum* (Engler) Engler (1891) [the latter name corrected to *Peltophyllum* Engler in Post and Kuntze (1903)] in synonymy. The reason for Voss's (1899) erection of *Darmera* was his recognition of the prior publication of the form genus *Peltophyllum* Massalongo (1854, 1859a), which was applied to a fossil leaf and fruit attributed to Nymphaeaceae (see Summary). *Peltophyllum* Massalongo, however, is also an illegitimate later homonym of *Peltophyllum* Gardner, a fact that Voss (1899) overlooked.

*Darmera* Voss (1899), not *Peltiphyllum* (Engler) Engler (1891),<sup>4</sup> therefore is the correct name for the saxifrage. Voss clearly made the combination *Darmera peltata* (Torrey in Benth) Voss in 1899 in a highly obscure horticultural journal, *Gärtnerisches Zentral-Blatt* (full citation in *Just's botanischer Jahresbericht* 27 (Abt. 2):194 (1899), which ceased publication after only a single volume, issued in 1899.

<sup>2</sup> The genus *Peltiphyllum* is based on *Saxifraga* Linnaeus section *Peltiphyllum* Engler (1872), with the single species *Saxifraga peltata* Torrey in Benth.

<sup>3</sup> *Darmera* commemorates Karl Darmer of Berlin, the founder and first president of the *Allgemeinen Deutschen Gärtner-Verein*, and an indefatigable promoter of horticulture in Germany (Voss, 1899).

<sup>4</sup> Because it lacks a Latin description, *Peltiphyllaceae* Krach (1976: 23) is not validly published (Art. 36); however, were this name validly published, it would be illegitimate since *Peltiphyllum* (Engler) Engler is illegitimate (Art. 18). The proper designation for a familial segregation of *Darmera* Voss (syn.: *Peltiphyllum*) from Saxifragaceae would, of course, be one based on the generic name *Darmera*. Although this might be supported by the growing body of organographic, cytological, chemical, anatomical, and especially embryological evidence (Krach, 1976; also Bense and Palser, 1975a, b; Saxena, 1973; Sponberg, 1972), familial recognition (*sensu* Krach, 1976) at this time seems premature. Perhaps segregation at the tribal or subtribal level is more appropriate. On the other hand, the distinctness of *Darmera* from other Saxifragaceae (e.g., *Darmera* differs from all other saxifrages in its embryo development and unitegmic testa) precludes submerging the genus in *Saxifraga*, a return to the original Englerian (1872) concept (see footnote 2). As noted by Takhtajan (1959, 1973), *Darmera* is certainly worthy of further detailed investigation.

Consequently, *Darmera* Voss (1899) has been overlooked by subsequent botanists (including *Index Kewensis*), the name appearing only in a 1903 publication by Voss, but not in his later books; in Post and Kuntze (1903), to which Voss had contributed; in Pilger (1906-08); Engler (1930); Lemée (1930); and in *Index Nominum Genericorum*. Curiously, the last 4 sources all relegate *Darmera* Voss to the synonymy of *Peltiphyllum* (Engler) Engler (1891) despite the fact that the latter is doubly bastardly in view of the prior legitimate *Peltiphyllum* Gardner (1843) and the prior illegitimate *Peltiphyllum* Massalongo (1854). None of the preceding sources, incidentally, correctly cite the original and valid publication of *Darmera* and *Darmera peltata*, namely, Voss (1899).

The lamentable conclusion is that two admirably appropriate descriptive names, *Peltiphyllum* (Engler) Engler and *Hexuris* Miers, are illegitimate. It is ironic that the legitimate but descriptively inappropriate *Peltiphyllum* Gardner must be used for plants bearing only minute scale leaves. It is also regrettable that *Peltiphyllum peltatum* (Torrey) Engler, a familiar and striking Californian/Oregonian plant that is often cultivated, must yield its generic name to insignificant South American saprophytes and assume the obscure name *Darmera* Voss. The only alternative to these required changes is to conserve *Peltiphyllum* (Engler) Engler against *Peltiphyllum* Gardner.

#### SUMMARY

##### (1) Triuridaceae:

PELTOPHYLLUM Gardner, Proc. Linn. Soc. 1:176 (1843), Trans. Linn. Soc. 19:157, pl. 15 (1845), non Massalongo (1854), non Engler (1891). Type: *Peltiphyllum luteum* Gardner.

*Hexuris* Miers, Proc. Linn. Soc. 2:72 (1850), Trans. Linn. Soc. 21:44 (1852), nom. superfl., illeg.

(a) PELTOPHYLLUM LUTEUM Gardner, op. cit. (1843, 1845).

*Hexuris gardneri* Miers, op. cit. (1850, 1852), nom. superfl. illeg.

*Triuris lutea* (Gardner) Bentham & J. D. Hooker, Gen. Pl. 3:1002 (1883).

(b) **PELTOPHYLLUM CAUDATUM** (Poulsen) Schmid & Turner, comb. nov.

*Sciaphila caudata* Poulsen, Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 36-38:165 (1886).

*Hexuris caudata* (Poulsen) Giesen, Pflanzenreich Heft 104:75 (1938).

##### (2) Saxifragaceae:

DARMERA A. Voss, Gärt. Zentral-Bl. 1:645 (1899).

*Saxifraga* L. sect. *Peltiphyllum* Engler, Monograph. Gatt. *Saxifraga*, 108 (1872). Type: *Saxifraga peltata* Torrey in Bentham. *Peltiphyllum* (Engler) Engler in Engler & Prantl, Nat. Pfl. 3 (2a): 61 (1891), Nachtrag 3:141 (1906), Nachtrag 4:109 (1914), nom. illeg., later homonym of *Peltophyllum* Gardner (1843).

DARmera PELTATA (Torrey in Bentham) Voss, op. cit. 646 (1899).

*Saxifraga peltata* Torrey in Bentham, Pl. Hartweg., 311 (1849).

*Peltiphyllum peltatum* (Torrey in Bentham) Engler, op. cit. (1891).

(3) ?Nymphaeaceae, fossil leaf and fruit:

PELTOPHYLLUM Massalongo, Monograf. Dombeyaceae Foss., 22 (1854), Spec. Photo. Anim. Quor. Pl. Foss., 75, pl. 28 (1859a), nom. illeg., non Gardner (1843), non Engler (1891—"Peltiphyllum"). Type: *Peltophyllum nelumbioides* Massalongo.

PELTOPHYLLUM NELUMBIOIDES Massalongo, op. cit. (1854, 1859a).

A check of the *Compendium Index of Paleobotany* (see Schmid and Schmid, 1973) and of the paleobotanical literature revealed acceptance of Massalongo's illegitimate genus only by Schimper (1874: 603), Meschinelli and Squinabol (1893: 326), and, of course, Massalongo himself (1854, 1858, 1859a, b). Other than the listing of the genus by Andrews (1970) in his index of generic names, there has been no recent discussion or acceptance of *Peltophyllum* Massalongo. The taxonomic affinities of Massalongo's fossil leaves from the Eocene of north-eastern Italy are not known. Massalongo's assignment of the fossils to Nymphaeaceae ("Cabombee" or "Cabombeae"—Massalongo, 1858, 1859a, b, but initially to Dombeyaceae in Massalongo, 1854) was based on strictly superficial resemblances (Schmid and Schmid, 1973, 1974), as was typical of paleobotanical work of this era. After examining the original photograph in Massalongo (1859a), Hickey had "serious doubts that the type is really nymphaeaceous" (pers. comm., 1976). In view of the above, we are not perpetuating *Peltophyllum* Massalongo with a substitute generic name.

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## FROST SENSITIVITY AND RESPROUTING BEHAVIOR OF ANALOGOUS SHRUBS OF CALIFORNIA AND CHILE

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Detailed comparisons of the structure and function of sclerophyll vegetations centered in the matched climatic regions of central Chile and coastal California have shown a large degree of similarity in spite of divergent evolutionary histories of the floras of these 2 areas (Mooney *et al.*, 1970; Mooney *et al.*, 1977; Parsons, 1976). Principal differences are related to features responsive to land-use treatment which has differed substantially between regions, particularly in the past century (Mooney *et al.*, 1972; Aschmann and Bahre, 1977).

Additional functional differences between these vegetations, particularly in phenological patterns of the woody plants, have been ascribed in part to the small climatic dissimilarities that exist between regions (Mooney *et al.*, 1977). The broad aspects of the climate of the 2 regions are, however, quite similar. Monthly rainfall, drought duration, and mean temperatures can be matched station for station in coastal California and Chile (di Castri, 1973). Furthermore, the direction and magnitude of climatic changes that have occurred from the Pleistocene to the present have been quite comparable (Miller *et al.*, 1977).

The principal climatic difference between regions is that Chile has a more equable thermal environment, evidently because of the more pronounced maritime influence. Frosts are uncommon in coastal Chile but frequent at equal latitude California stations (Miller *et al.*, 1977). This could explain the more prolonged flowering and fruiting period of shrubs in Chile than in California at sites that are otherwise closely matched (Mooney *et al.*, 1977).

If indeed differences in climatic equability between regions have had an important evolutionary impact on the vegetation, this might be evident in their differing frost sensitivities. A spell of unusually cold weather in California led to a test of this possibility.

During December 1972 there was a record freeze in California of a duration that had not occurred for the previous 40 yrs. In the San Francisco Bay region, at Palo Alto, temperatures dipped to  $-5$  C on 2 separate days (U.S. Weather Bureau, 1972). Widespread damage occurred to exotic plantings in this area.

In 1968 a garden was established at the Carnegie Institution of Washington, at Stanford University, consisting of a large number of species of evergreen trees and shrubs characteristic of the Californian chaparral and of the Chilean matorral. Additionally, a number of subligneous species, generally drought deciduous, from both regions were planted. Plants were grown from seed, mostly collected from the same latitude in California and Chile ( $33^{\circ}$ ), thus from comparative generalized mediterranean-type climates (di Castri, 1973). The Carnegie garden is located at a higher latitude ( $37^{\circ}$ N) than the origin of the study populations; however, many species extend naturally to these higher latitudes. At the time of the 1972 freeze these plants had grown to full-sized shrubs.

Considerable damage was noted on many plants subsequent to the freeze. Observations were made on the extent of their recovery the following summer. For most species 10 individuals were observed.

#### RESULTS

Only 2 of the 9 California evergreen species were damaged by the freeze; both were *Rhus* species (Table 1). Both species are restricted to latitudes lower than the other Californian evergreens. *Rhus laurina*, normally found only at the lowest elevations within the chaparral or within the coastal sage drought-deciduous community, had the greatest mortality. Both species, however, had individuals that base-sprouted. Resprouting from stems of *Rhus ovata* was also noted.

Three Californian drought-deciduous species, *Artemisia californica*, *Encelia californica*, and *Ptelea aptera*, had individuals that were frost killed, as well as those that recovered by base sprouting. The other 5 Californian drought-deciduous species were undamaged.

Thus, less than one-third of the Californian species were frost damaged. Of these, all had individuals that recovered by base-sprouting.

TABLE 1. CONDITION OF PLANTS SIX MONTHS SUBSEQUENT TO FREEZE.

CALIFORNIA ORIGIN	% No damage	% Dead	% Resprouting
Evergreen species			
<i>Rhus laurina</i>	0	60	40
<i>Rhus ovata</i>	0	20	80
<i>Adenostoma fasciculatum</i>	100	0	0
<i>Cercocarpus betuloides</i>	100	0	0
<i>Heteromeles arbutifolia</i>	100	0	0
<i>Prunus ilicifolia</i>	100	0	0
<i>Quercus agrifolia</i>	100	0	0
<i>Rhamnus ilicifolia</i>	100	0	0
<i>Umbellularia californica</i>	100	0	0
Drought Deciduous species			
<i>Artemisia californica</i>	0	60	40
<i>Encelia californica</i>	0	40	60
<i>Ptelea aptera</i>	0	40	60
<i>Adolphia californica</i>	100	0	0
<i>Fraxinus trifoliata</i>	100	0	0
<i>Salvia apiana</i>	100	0	0
<i>Salvia leucophylla</i>	100	0	0
<i>Salvia mellifera</i>	100	0	0
CHILEAN ORIGIN			
Evergreen species			
<i>Azara celastrina</i>	0	0	100
<i>Baccharis paniculata</i>	0	0	100
<i>Beilschmiedia miersii</i>	0	0	100
<i>Colliguaya odorifera</i>	0	0	100
<i>Cryptocarya alba</i>	0	20	80
<i>Escallonia pulverulenta</i>	0	0	100
<i>Lithraea caustica</i>	0	66	33
<i>Schinus latifolius</i>	0	40	60
<i>Escallonia illinita</i>	100	0	0
<i>Quillaja saponaria</i>	100	0	0
<i>Maytenus boaria</i>	100	0	0
Drought Deciduous species			
<i>Flourensia thurifera</i>	0	60	40
<i>Lepechinia salviae</i>	0	75	25
<i>Lobelia chilensis</i>	0	20	80
<i>Lobelia polyphylla</i>	0	60	40
<i>Podanthus mitiqui</i>	0	0	100
<i>Trevoa trinervis</i>	0	33	66

In contrast, over 80% of the Chilean species were frost damaged, including all the drought-deciduous elements. As with the Californian species, all the damaged species had individuals that recovered by resprouting. There was a somewhat higher mortality of drought-deciduous than of evergreen plants, particularly among the Chilean species.

## DISCUSSION AND SUMMARY

There was a considerable difference in tolerance of Chilean and Californian species to a substantial freeze. As a group the Chilean species were considerably more sensitive, as was predicted. It can be inferred from these results, which are supported by modern climatic data, that the Chilean species have not been subjected to as cold temperatures as have those from California, in their native habitat. Thus, although the general climatic pattern of summer drought and cool, wet winter is comparable in the 2 regions, the climates differ in a biologically important parameter, i.e., frequency of cold temperatures.

This evidently has resulted in the selection of vegetations that, although similar appearing (Mooney *et al.*, 1970; Parsons, 1976) and similarly adapted physiologically (Mooney and Dunn, 1970), differ in certain significant physiological features.

All Californian and Chilean frost-damaged species recovered by base or "stump" sprouting. Stump sprouting is often cited as an evolutionary response to a fire climate. However, as Axelrod (1973) has noted, most species that are associated with California chaparral today have been in existence for over 12 to 18 million yrs.—long *before* the origin of a regional summer drought; hence a pronounced fire climate.

It is thus quite likely that resprouting behavior has evolved as a more general adaptive response to such environmental stresses as cold and drought, both of which increased in intensity coincident with evolution of the sclerophyll vegetation (Axelrod, 1973). This survival feature would thus be a "pre-adaptation" to fire, which would be reinforced as the mediterranean climate developed fully.

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## TWO NEW LOCAL UMBELLIFERAE (APIACEAE) FROM CALIFORNIA

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Current interest in the possible extirpation of increasing numbers of restricted populations of native plants in California has focussed attention on narrow endemics of all sorts, since they are especially vulnerable. The names of two such examples have been entered on one or more of the lists of rare or endangered species without having been properly legitimized. The purpose of this contribution is to describe and illustrate them, since it seems unwise to delay their debut any longer.

***Angelica callii*** Mathias & Constance, sp. nov. *Plantae caulescentes crassae* 1–2 m altae, *foliis glabris minute scaberulisve, inflorescentia scaberula hirsutulave; folia ovata ternato–1–2–pinnata, divisionibus principalibus interdum reflexis rhacidibus geniculatis, foliolis lanceolatis ovato-lanceolatisve* 3–13 cm longis, 1.5–4 cm latis, *acutis vel obtusis, acute serratis; petioli* 0.5–3 dm longi *basi anguste vaginantes; folia cauline sursum reducta plerumque pinnata, foliis summis dilatatis sine lamina; pedunculi paulo graciles* 1–2 dm longi; *involucrum nullum; involucellum plerumque nullum; radii* 25–50 subaequales *patenti-adscendentes basi conspicue connati* 2.5–7(–10) cm longi; *pedicelli plures inaequales patenti-adscendentes basi conspicue connati* 5–15 mm longi; *flores albi vel subrosei, petalis ovalibus obovatisve basi extra paulo hirsutulis, stylopodio conico quam stylis gracilibus brevior, ovariis hirsutulis; carpophorum bipartitum; fructus ovalis obovatusve* 3.5–5 mm longus, 2.5–4 mm latus, *hirsutulus glabratusve, costis dorsalibus demissis rotundatis coarctatis suberosis quam intervallis multo latioribus, costis lateralibus quam eis dorsalibus multo latioribus suberosis, quam corpore fructus plerumque angustioribus; vittae ad valleculas solitariae magnae ad pericarpium adherentes; chromosomatum numerus*  $n = 11$ . Fig. 1.

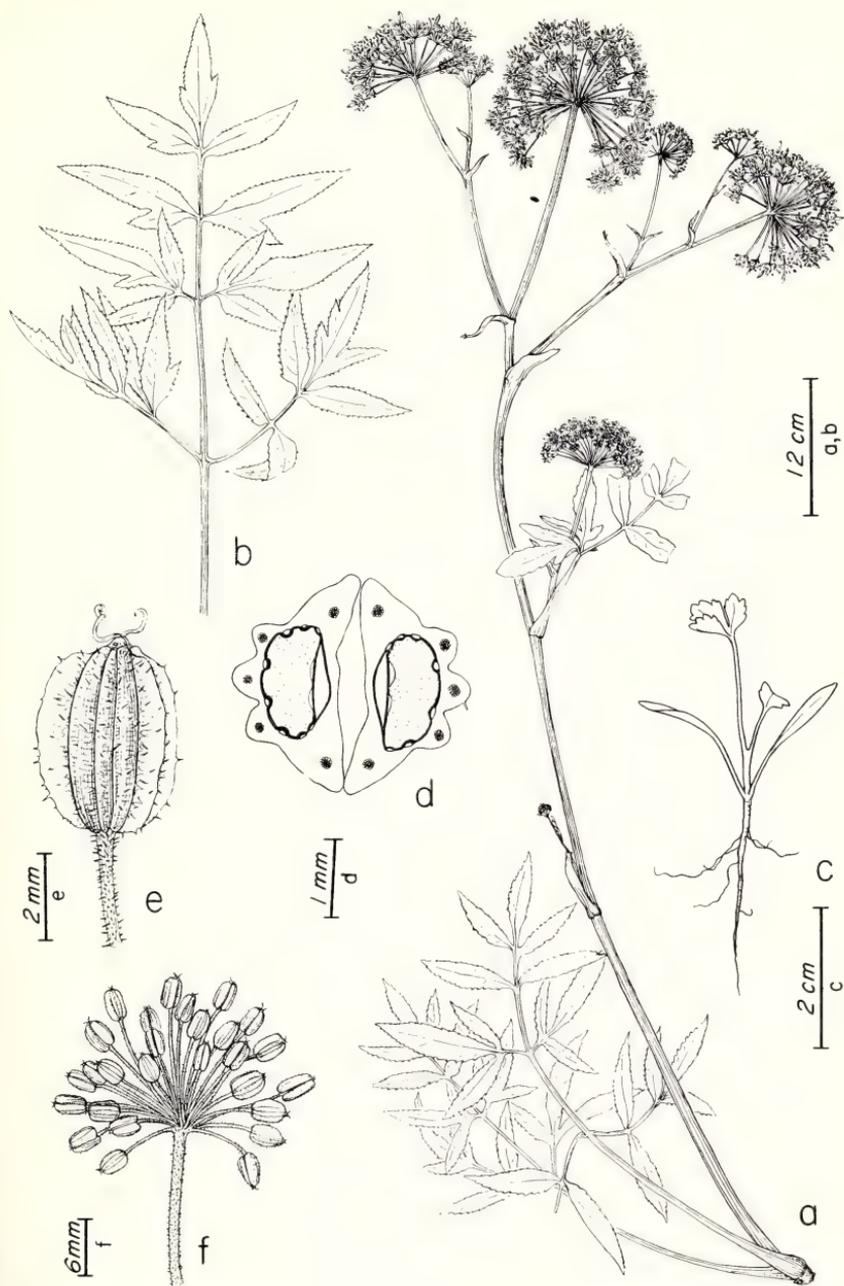


FIG. 1. *Angelica callii*. a, habit. b, basal leaf. c, seedling. d, transection of fruit. e, dorsal view of entire fruit. f, fruiting umbellet. All from Call & Call 2459, 2544, and 2550.

Plants stout, 1–2 m tall, the foliage glabrous to minutely scaberulous, strongly scented, the inflorescence scaberulous to hirsutulous; leaves ovate, 1–4 dm long, 1–3 dm broad, ternate-pinnately divided, the main divisions sometimes reflexed and the rachis geniculate, the leaflets lanceolate to ovate-lanceolate, 3–13 cm long, 1.5–4 cm broad, acute to obtuse, the larger petiolulate and with one or 2 narrow lobes or leaflets at base, the others sessile, sharply serrate; petioles stout, 0.5–3 dm long, narrowly sheathing at base; cauline leaves reduced upward, mostly pinnate, with moderately dilated sheaths, the uppermost sheaths bladeless; peduncles rather slender, 1–2 dm long; involucre wanting; rays 25–50, 2.5–7 (–10) cm long, spreading-ascending, subequal, conspicuously webbed; involucre of a few inconspicuous filiform bractlets, or lacking; pedicels 5–15 mm long, spreading-ascending, unequal, conspicuously webbed; flowers white or pinkish, the petals oval to obovate, a little hirsutulous at base dorsally; styles slender, much longer than the conical stylopodium; ovaries hirsutulous; fruit oval to obovate, 3.5–5 mm long, 2.5–4 mm broad, hirsutulous to glabrate, the dorsal ribs low, rounded, crowded, much broader than the intervals, the lateral ribs broader than the dorsal, narrower than to about equalling the body, all corky-thickened; vittae large and solitary under the intervals, apparently with smaller ones under the ribs, making them continuous about the seed and adhering to it when and if it becomes loose in the pericarp; chromosome number  $n = 11$ .

TYPE: California, Tulare Co., on stream banks 2 mi E of Lookout Guard Station near Sequoia National Park, 4600 ft altitude, 18 Oct 1965, *Tracey & Viola Call 2459* (Holotype: UC).

DISTRIBUTION: Stream banks between altitudes of 3800 and 6500 ft, W slope of Sierra Nevada in Tulare County and adjacent Kern County, California.

SPECIMENS EXAMINED: Tulare Co.: banks of Bear Creek near Coy Flat E of Springville, 5000 ft, 6 Nov 1965, *Call & Call 2461*; banks 0.5 mi E of California Hot Springs, 3300 ft, 15 Sep 1966, *Call & Call 2549*; steep E-facing rocky stream bed above Redwood Meadow ca 15 mi NE of California Hot Springs, 6500 ft, 15 Oct 1966, *Call & Call 2550* (garden-grown progeny and chromosome voucher, *Constance 693*); shaded banks of Bear Creek above Coy Flat near Camp Nelson, 3800 ft, 15 Oct 1966, *Call & Call 2551*. Kern Co.: small stream on N-facing slope 1 mi N of Greenhorn Summit, 5800 ft, 7 Sep 1966, *Call & Call 2544*.

This appears to be closest to *Angelica wheeleri* S. Wats. of Utah, but is distinguishable by (1) subequal fruiting rays, (2) much less inflated and hence narrow and inconspicuous upper cauline leaf sheaths, and (3) lower and broader dorsal fruit ribs. In pubescence, leaf serration, webbing of rays and pedicels, and in the shape and pubescence of the ovary and fruit, the two are strikingly similar.

This interesting new *Angelica* was discovered a decade ago by Dr. and Mrs. Call of California Polytechnic State University, San Luis Obispo,

who are discerning students and discriminating collectors of Umbelliferae. It has not, so far as we are aware, been secured by anyone else. The chromosome count was made by Dr. and Mrs. Tsan-Iang Chuang.

***Lilaeopsis masonii*** Mathias & Constance, sp. nov. Plantae perennes horizontaliter rhizomatosae caespitosae glabrae; folia teretia linearifiliformia 1.5–7 cm longa diametro usque 1 mm, septiis paucis obscurisque; pedunculi 7–15 mm longi debiles quam folia breviores; umbellae 3–8-flores; pedicelli adscendentes vel patentisque vel reflexi 2–6 mm longi; fructus ovoideus 1.5–1.8 mm longus, 1.25–1.5 mm latus, costis dorsalibus acutis obscuris, eis lateralibus prominentibus latis suberoso-incrassatis; chromosomatum numerus  $n = 22$ . Fig. 2.

Plants perennial rhizotamous, forming a low turf, glabrous; leaves quill-shaped, terete, linear-filiform, 1.5–7 cm long, less than 1 mm in diameter, the septae few and obscure; peduncles 7–15 mm long, weak, shorter than leaves; umbels 3–8-flowered; pedicels ascending to spreading or reflexed, 2–6 mm long; fruit ovoid, 1.5–1.8 mm long, 1.25–1.5 mm broad, corky-thickened; chromosome number  $n = 22$ .

TYPE: California, Sacramento Co., moist sandy soil with *Scirpus* and *Equisetum*, Twitchell Island, margin of Sacramento River 6.5 mi S of RioVista, at sea level, 14 Jul 1955, *L. Constance & H. L. Mason 3611* (Holotype: UC).

DISTRIBUTION: Low-lying shores of San Francisco Bay at the deltaic mouths of its tributaries. Mason has recently reported verbally that the plant occurs on some of the islets elsewhere in the delta, but we have seen no material.

SPECIMENS EXAMINED: Napa Co.: am Ufers des Napaflusses südlich von Napa, 24 Jul 1913, *W. N. Saksdorf 630* (K, UC). Solano Co.: wet soil at edge of slough with *Triglochin* and *Juncus*, Suisun Marsh ca 1 mi S of Suisun, 19 May 1957, *J. M. Tucker 3332* (CAS, DS, UC). Sacramento Co.: moist sand and mud with *Limosella*, *Hydrocotyle*, *Helenium*, *Arundinaria*, *Scirpus* and *Salix*, Sherman Island, margin of San Joaquin River 0.5 mi E of N end of Antioch Bridge, 14 Jul 1955, *Constance & Mason 3610* (UC, including garden-grown progeny and chromosome voucher); N end of Antioch Bridge, Apr 1954, *Mason s. n.* (UC). Contra Costa Co.: lower San Joaquin River, Antioch, Oct 1942, *Mason 12,556* (UC); along lower river just above Antioch, 12 Jun 1955, *P. H. Raven 8292* (CAS).

In his "Flora of the Marshes of California," Mason (1957) stated: "On the basis of vegetative characters there appear to be two forms of this species: (1) the coastal form, extending southward to Marin County, California, from British Columbia, which has somewhat broad, often flattened, and conspicuously septate phyllodes; and (2) the San Francisco Bay and river-mouth form, which has very fine, terete, and only obscurely septate phyllodes. Additional collections and further study may show that these merit taxonomic recognition" (p. 631). Also Hill, in his classic monograph of the genus *Lilaeopsis* (1927), in citing the Saksdorf specimen listed above as his only California representative,

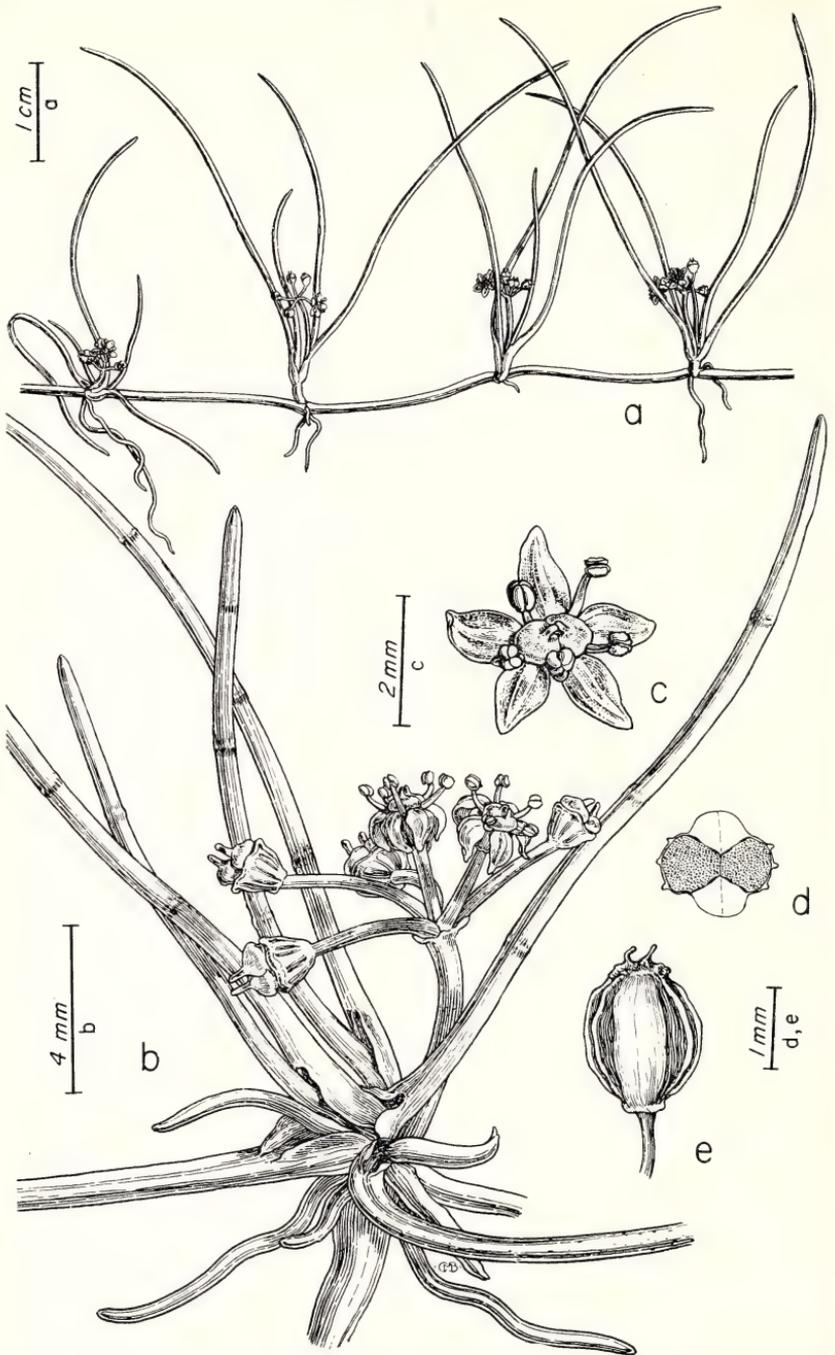


FIG. 2. *Lilaeopsis masonii*. a, habit. b, individual node showing foliage and inflorescence. c, flower. d, transection of fruit. e, lateral view of entire fruit. All from Constance & Mason 3610.

remarked its narrower and more slender leaves, but referred it to *L. occidentalis* Coult. & Rose because of the agreement in fruit structure between the California plant and those from further north.

The most critical distinguishing feature between the coastal and delta plants is that the leaves of the latter are not only narrower, more slender, and usually shorter, but that they are truly terete, have proportionately fewer septae, particularly toward the apex, and that these septae are so obscure that they are likely to remain unobserved. The fruit characters, upon which Hill relied so heavily to distinguish species, are essentially identical. Even chromosome number is of no taxonomic assistance since *L. masonii* like *L. occidentalis*, has a complement of  $n = 22$ ; both are presumably tetraploid. The taxon referred to as *Lilaeopsis* sp. in Constance, Chuang & Bell (1976, No. 481, p. 619) is *L. masonii*.

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### VEGETATION ANALYSIS OF A NORTHERN CALIFORNIA COASTAL PRAIRIE: SEA RANCH, SONOMA COUNTY, CALIFORNIA

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The northern coastal prairies of California are distributed along parts of the coastal zone from the California-Oregon border south to Monterey Bay. Previous authors have outlined the natural history and the distribution of species of the coastal grassland ecosystem (Beetle, 1947; Burcham, 1957; Munz, 1973; Crampton, 1974; Ornduff, 1974) and a number of floristic surveys have been completed (Davy, 1902; Peñalosa, 1963; Barbour, 1970, 1972; Howell, 1970; Hardham and True, 1972). Ecological analysis of the coastal grassland, however, has been limited (Huffaker and Kennett, 1959; Batzli and Pitelka, 1970; Barbour et al., 1973; Elliott and Wehausen, 1974; Davidson, 1975); Heady et al. (1977) also reached this conclusion.

In 1974, we began an analysis of the coastal perennial grassland community at Sea Ranch, Sonoma County, California. The two major goals of this program are first to document the structure of a coastal grassland that has not been grazed by livestock for approximately 10 years, and secondly to develop hypotheses about dominance and diversity relationships suitable for experimental tests.

For many years the coastal grasslands have been strongly influenced by persistent livestock grazing. With increased coastal development for residential purposes and with the proliferation of park reserves large sections of the coastal grassland are no longer grazed and are undergoing changes in species composition and standing crop. We set out to document the changes as one such area recovers from grazing. Over the long term we hope to understand the regulation of dominance, species diversity, and patchiness of vegetation distribution by studying population parameters of selected species using methods described elsewhere (Foin and Jain, 1976).

This paper presents the results of our first survey of the Sea Ranch grasslands in 1974. An annotated species list for the Sea Ranch coastal terraces is being published elsewhere (Hektner and Foin, 1977).

#### THE STUDY SITE

Sea Ranch ( $38^{\circ} 40' N$ ,  $123^{\circ} 24' W$ ) is a low density subdivision approximately 180 km north of San Francisco (Fig. 1). It is situated along 16 km of the northern Sonoma County coastline and extends up to 2 km inland. The 729 ha of terrace grassland under study are bounded by California State Highway 1 on the east, Gualala Point Sonoma County Park on the north, the Sea Ranch southern boundary line, and the Pacific Ocean. Approximately 95% of the coastal terrace area has been reserved as permanent open space by the Sea Ranch Homeowner's Association and allowed to develop with minimum disturbance. Hence, these open areas permit long term studies of the dynamics of the coastal prairie.

The area that is now Sea Ranch was included in an 8,100 ha Spanish land grant, known as Rancho German, given to Ernst Rufus in 1846. Lumbering soon became an important industry and a mill was established at the mouth of the Gualala River. The grant was eventually broken up and one of the parcels sold was Black Point (now part of the Sea Ranch), from which lumber and cattle were shipped to San Francisco (Morgan and Morgan, 1974). Horses, cattle and sheep grazed the Sea Ranch area (then known as Del Mar Ranch) continuously until the mid-1960's. Parts of the terrace were occasionally plowed for planting peas, potatoes, and even artichokes. Unspecified species of clover were also sown by the former owner to provide additional forage for sheep (Ohlson, pers. comm.). Development began in 1963 in the southern portion, and pastures were abandoned as it proceeded northward. The last sheep were removed from the northern section in 1968, but cattle grazed the north end from 1967 to 1969.

Like most of northern California, Sea Ranch receives most of its precipitation during late fall, winter, and spring. Records kept by local residents on the terrace (elevation 22 m) and published in the *Independent Coast Observer* (a local newspaper) show a 5-year average seasonal

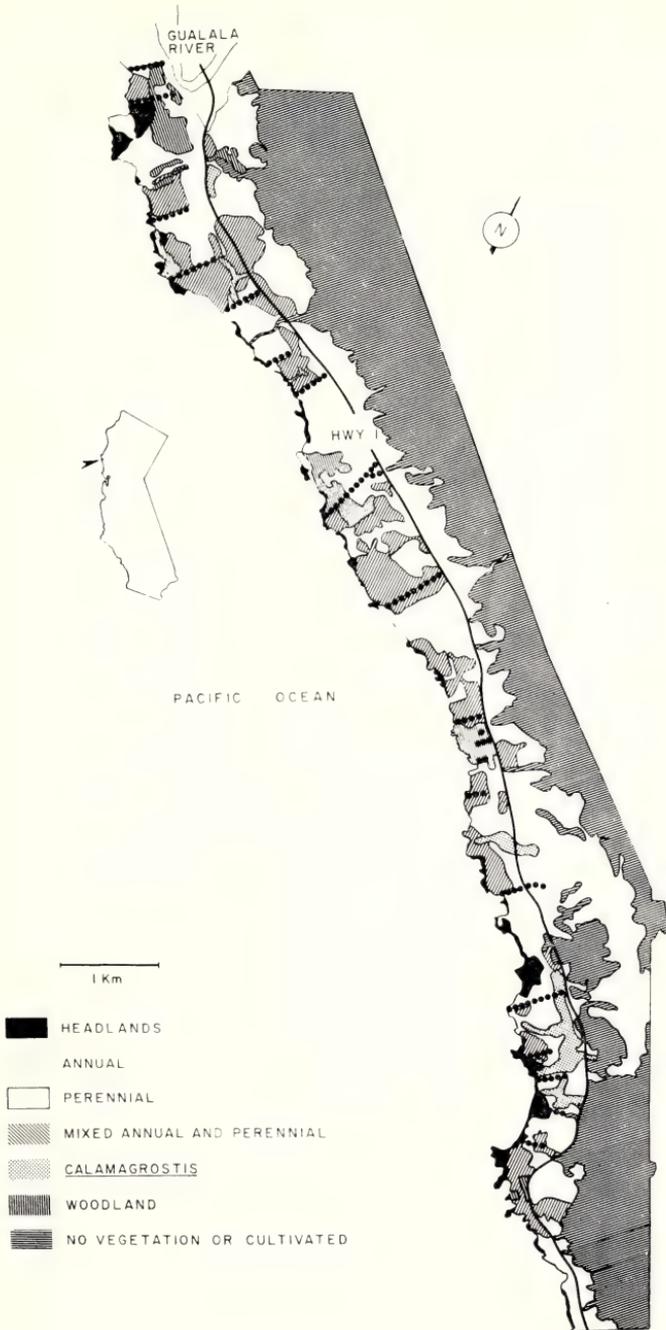


FIG. 1. Distribution of major vegetation types at Sea Ranch, California. Rows of dots represent hedgerows of *Cupressus macrocarpa*.

rainfall of 842 mm (range, 458–1308 mm), with 92% falling from October through March. For the same period (July 1970–June 1975), at the top of German Ridge (elevation 274 m) 6.4 km to the north, seasonal rainfall averaged 1609 mm (range, 932–2475 mm).

Fog associated with periods of slack winds during summer contributes an unknown amount of moisture. Wind direction varies seasonally, coming mainly from the north and northwest during summer, and from the south and southeast during winter. Checks of wind velocities during planning studies for the development of Sea Ranch (Lawrence Halprin and Associates, unpubl.) during 1954 through 1961 showed that in general winds of less than 5 kph seldom occurred more than 10% of the time in any month. Winds in the 6–24 kph class persisted for 50–65% of every month and 25–30% of any month had winds in excess of 26 kph.

There are no continuous temperature records for Sea Ranch, but mean monthly temperature records are available for the past 43 years for Fort Ross, 31 km south. Annual mean temperature is above 11C, with monthly means ranging from 6.5C in the winter to 15C in the summer (Davidson, 1975).

Due to the proximity of Fort Ross to Sea Ranch, the long-term climatic records for Fort Ross were used to construct a Thornthwaite climatic diagram (Fig. 2) as an approximation of the Sea Ranch climate. Climatic data representing 86 years of recorded precipitation and 11 years of temperature (U.S. Environmental Data Service, 1964) were used to determine potential evapotranspiration and thus calculate the water balance throughout the year. We used an unpublished computer program written by Randall and Major of the U.C. Davis Botany Department and calculations follow Black (1966) and Thornthwaite et al. (1957). These calculations assume 100 mm of water available from soil storage and that the rate of water removal by plants from the soil is proportional to the amount remaining in the soil.

As in most areas having Mediterranean climates, growth is slow during winter, peaks in spring and fall and declines sharply during summer.

Most of the terrace area on the coastal side of Highway 1 is nearly level with slopes of less than 10%. The coastal terrace consists of two wave-cut benches, both formed during the Quaternary, but subsistence and erosion have greatly obliterated their boundaries (Moore, pers. comm.).

Soils of the terrace areas are predominantly of two types: Baywood loamy sand and Rohnerville loam (U.S.D.A., 1972). The Baywood series, generally directly adjacent to the ocean, consists of very well drained loamy sand formed in wind-modified sandy coastal plain sediments and soft sandstone. The Rohnerville soils, formed in material weathered from soft sandstone, are moderately well drained, with a subsoil mainly of sandy clay. At one point where the terrace is very narrow a small area of Kneeland loam extends down to the ocean bluff at 15–30% slopes. Be-

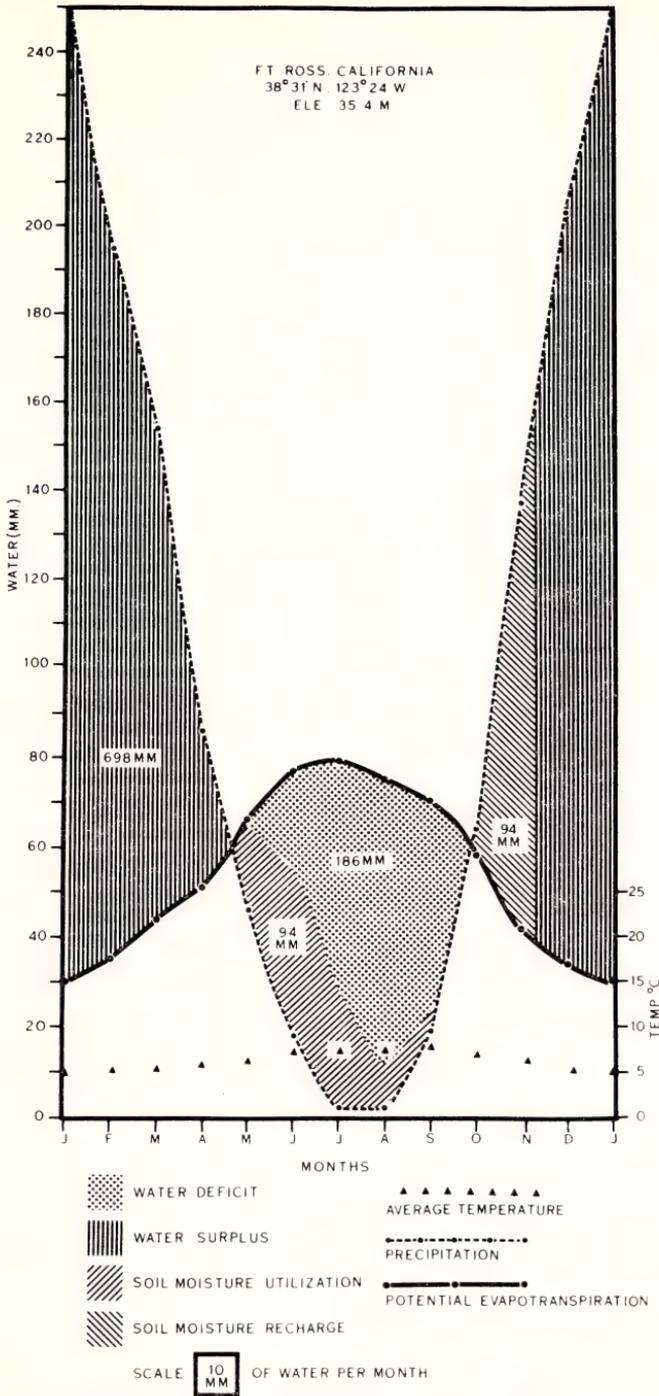


FIG. 2. Thornthwaite climatic diagram for Fort Ross, California.

cause of their thick dark color, granular structure, and generally high base saturation, these soils are considered typical prairie soils similar to those of the Midwest (Ornduff, 1974; Burcham, 1957; Barshad, 1946). In addition there are two small areas of dune sand, both stabilized by beachgrass (*Ammophila arenaria*).

#### METHODS AND MATERIALS

The first step in the vegetation analysis was the production of a map to establish the location of major vegetation types and to estimate the contribution of each type to vegetative cover (Fig. 1). This map was constructed from infrared aerial photographs taken by the National Aeronautics and Space Administration for the U.S. Army Corps of Engineers using an RC-86" focal length camera at an altitude of 6,096 m in 1972, and at 914 m in 1974. Slide projections were superimposed on a base map and differences in infrared color were used to establish tentative vegetation boundaries. Boundaries were later verified by ground survey.

Vegetation units selected for sampling included headlands, shrub (lupine)-dominated, mixed grassland, perennial grassland, and *Calamagrostis*-dominated. The criteria used to distinguish each unit were as follows: headlands—areas along the ocean bluffs with very low vegetative height, usually 20 cm or less, with abundant forbs; lupine areas—where lupine cover (*Lupinus arboreus*) extended through more than 2–3 contiguous adult individuals (the patch of bushes defined the area); grasslands—mixed, when neither annual nor perennial grass relative cover exceeded 50%, and perennial, those having  $\geq 50\%$  relative cover of perennial grass species; *Calamagrostis* areas—where those in which the relative cover of *Calamagrostis nukaensis* was  $\geq 50\%$ . These five types were selected because they were quantitatively important (as determined from the aerial map) or were an essential element in the successional sequence, or both. In particular, annual grasslands were not sampled because they were quantitatively unimportant and because they appear to be restricted to sites where disturbance from construction or horse grazing continues to be heavy.

Sampling of the vegetation was conducted during August and September, 1974, at 5 sites ranging from 4,500–16,000 m<sup>2</sup>. At each site, sample quadrats were placed randomly within a 10 m distance along parallel transects themselves placed randomly within a 10 m band, giving one sample per 100 m<sup>2</sup>. For each quadrat percentage bare ground and cover of each species in the quadrat were recorded. Each species was coded for analysis using mnemonics in Reed et al. (1963) and tabulated using cross tabulation and Chi<sup>2</sup> homogeneity tests from the SPSS/FASTABS program (Nie et al., 1975). Taxonomy and nomenclature follow Munz (1973) except for *Deschampsia holciformis*, which follows Crampton (1974). Voucher specimens have been deposited in the Botany Department Herbarium of the University of California, Davis.

Quadrat size varied, depending on the mean diameter of the species. *Lupinus arboreus* and *Calamagrostis nutkaensis* were sampled in quadrats of 50.25 m<sup>2</sup> area; bunchgrass, 12.26 m<sup>2</sup>; and all others, 0.25 m<sup>2</sup>. Circular quadrats were used with the differing sized quadrats placed concentrically for sampling of all species.

Cover estimates were made using a Domin Index (modified by Major, after Evans and Dahl, 1955). In this study, the scale was defined as follows: 1 = 1 or 2 individuals, cover less than 0.01%; 2 = few individuals, cover less than 0.1%; 3 = several individuals, cover less than 1%; 4 = numerous individuals, cover less than 4%; 5 = cover 5–10% of the total area; 6 = cover 11–20% of the total area; 7 = cover 21–33% of the total area; 8 = cover 34–50% of the total area; 9 = cover 51–75% of the total area; 10 = cover 76–90% of the total area; and 11 = cover 91–100% of the total area.

Note that values 1–3 are measures of density; those from 4–11 are true cover estimates. Total cover for a species was estimated as the percentage of the quadrat occupied by a vertical projection onto the ground surface of all individuals of that species. The Domin Index was also used to estimate bare ground. For tabulation purposes, Domin indices were converted to the midpoint value of their corresponding percentage range; for example, a Domin value of 11 = 91–100% is equivalent to 95.5%.

## RESULTS

As might be expected, analysis of the vegetation map (Fig. 1) reveals that major map units (headlands, perennial grasslands (including *Calamagrostis* areas), mixed grasslands, annual grasslands, and woodland) are not uniformly distributed along the coastline-inland gradient. To show this, 61 transect lines perpendicular to the coast were randomly placed on the map and 30 chosen randomly for sampling of vegetation type at each of 6 stations 0, 30, 122, 244, 488, and 975 m from the bluff edge. Chi<sup>2</sup> tests for uniform distribution of each type along the inland gradient revealed that 3 types (perennial grasses, headlands, and woodlands) are significantly localized ( $p < 0.025$ ) with the modal frequency from coastline inland in the order headlands, perennial, and woodland. Annual grasslands were too infrequently sampled to test, and mixed grasslands were not significantly localized ( $p > 0.10$ ), although the modal frequency is closer to the coast (122 m) than that for the perennial type (244–488 m). More recent surveys suggest that succession toward greater dominance by perennial grasses is progressing. This analysis suggests that large scale vegetation unit patchiness is related to environmental gradients from the coastline inland.

We digitized the map and used the computer to estimate the area occupied by each vegetative unit. For the entire area of Sea Ranch, headlands cover approximately 3%, perennial grasslands 33%, mixed grasslands 11%, annual grasslands 2%, *Calamagrostis* 2%, woodland

47%, and 2% has no vegetation or is cultivated. For the coastal terrace only, headlands occupy 10%, perennial grasslands 38%, mixed grasslands 33%, annual grasslands 8%, *Calamagrostis* 5%, woodland 1%, and 5% has no vegetation or is cultivated.

The dominants of the 5 vegetation types sampled are given in Table 1. Dominance in this table is defined on the basis of frequency ( $\geq 5\%$  occurrence in all samples taken in a particular vegetation type) and relative cover ( $\geq 5\%$ ; relative cover is defined as the summation of cover values of a species, normalized as a percentage of all cover values for all species). Despite this rather generous interpretation of dominance, no vegetation unit has more than 4 or less than 3 dominants even though the least rich type has 24 species. In each unit the small number of dominant species accounts for 62 to 92% of the total relative cover. Dominance is spread over a number of species, with only 3 (*Anthoxanthum odoratum*, *Holcus lanatus*, and *Rubus* spp.) dominant in more than one

TABLE 1. DOMINANT SPECIES OF FIVE VEGETATION TYPES AT SEA RANCH. Dominants have a frequency  $\geq 5$  samples and relative cover  $\geq 5\%$ . I = introduced species, N = native, A = annual, P = perennial, G = grass, F = forb, S = shrub or vine.

Vegetation type	Taxon	Life history pattern	Frequency (%)	Relative cover (%)
HEADLANDS	<i>Aira praecox</i>	IAG	100	34.87
	<i>Hypochoeris radicata</i>	NPF	100	26.47
	<i>Lupinus variicolor</i>	NPS	90	18.39
	<i>Lasthenia chrysostoma</i>	NAF	50	12.34
	Total			92.07
LUPINUS	<i>Lupinus arboreus</i>	NPS	96	28.27
	<i>Anthoxanthum odoratum</i>	IPG	63	16.90
	<i>Holcus lanatus</i>	IPG	86	16.33
	Total			61.50
MIXED	<i>Plantago lanceolata</i>	NPF	68	23.71
	<i>Cynosurus echinatus</i>	IAG	76	15.27
	<i>Anthoxanthum odoratum</i>	IPG	50	13.24
	<i>Danthonia pilosa</i>	IPG	69	11.64
	Total			63.86
PERENNIAL	<i>Deschampsia holciformis</i>	NPG	65	28.21
	<i>Anthoxanthum odoratum</i>	IPG	63	26.88
	<i>Holcus lanatus</i>	IPG	61	13.17
	<i>Rubus</i> spp.	NPS	36	5.11
	Total			73.37
CALAMAGROSTIS	<i>Calamagrostis nutkaensis</i>	NPG	100	55.15
	<i>Rubus</i> spp.	NPS	100	11.03
	<i>Veratrum fimbriata</i>	NPF	72	10.41
	Total			76.59

vegetation type. Among the dominants, perennials are predominant over annuals ( $t = 4.01$ ,  $p < 0.005$ ), with dominance among grasses, forbs, and shrubs differing from unit to unit ( $F = 5.11$ ,  $p < 0.025$ ). Annual forbs and grasses, perennial forbs, and prostrate shrubs (primarily *Lupinus variicolor*) are more important near the ocean than inland, where perennial grasses dominate to the near exclusion of everything else.

There is no significant difference in representation between native and introduced dominants ( $t = 0.476$ ,  $p > 0.50$ ).

Tables 2-6 present a quantitative list of all species in each of the vegetation types. For each taxon, we have tabulated the origin (introduced or native), the frequency of occurrence in samples, the percentage of relative cover, the mean absolute cover, and the standard error of mean absolute cover. A factor for converting relative cover to absolute cover is given in the legend for each table. Absolute cover is defined as the percentage of total sampled area actually covered by a species, and mean absolute cover is the sum of all cover values for that species divided by the number of plots in which it occurs.

By definition, the dominant species discussed above have high frequency and relative cover values, so it is expected that they have high mean cover values as well. However, there are many more species in each vegetation type of intermediate or low importance value. In Tables 2-6, these fall into 3 main groups: 1) species with high frequency and low cover values, i.e., species that are well dispersed; 2) species that are infrequent but which have high mean cover values; and 3) species that are both infrequent and low in cover value. The last category includes rare and unsuccessful species of little relative importance in the grassland, while the second is more complex because it includes infrequent but large species, and highly overdispersed species in the sense of Hairston (1959). *Myrica californica* is an example of the first, while *Cardionema ramosissimum*, *Juncus effusus* var. *brunneus*, and *Lasthenia chrysostoma* are examples of the second.

The patchiness observed between vegetation units (Fig. 1) may also be seen in the distribution of species among these units. Only 3 species (*Deschampsia holciformis*, *Hypochoeris radicata*, and *Horkelia californica*) were found in all 5 vegetation types, compared to 13 species in 4 of the 5 types, 20 in three, 30 in two, 26 in only one.

Within a type there is also considerable heterogeneity. The estimated standard errors, when converted into coefficients of variation, are lowest for dominants within each type. There are no evident trends, however, when nondominant species are considered. Some species are highly variable in mean cover (*Anagallis arvensis* is the best example); others are not (*Cynosurus echinatus* and *Danthonia pilosa*, Table 4). For those species occurring in more than one type, the coefficients of variation may differ widely (e.g., *Deschampsia holciformis*, Table 2, = 3.627; Table

5, = 0.169). Presumably the size of the coefficient is a function of colonization and species growth form as well as species interactions, but there is no clear trend.

TABLE 2. COVER VALUES OF SPECIES OF THE SEA RANCH HEADLANDS VEGETATION TYPE. I/N = introduced (I) or native (N); F = frequency of occurrence (percent of total samples); RC = percent relative cover; MC = mean actual percent cover; SE = standard error of mean actual percent cover; t = species present, relative cover < 0.01%. When a species only occurs in one plot, mean actual percent cover and standard error are not applicable and therefore indicated by a dash (—). Ten plots were sampled at one site. For conversion to absolute cover of each species multiply relative cover value by 0.79.

Taxon	I/N	F	RC	MC	SE
ANNUAL GRASSES					
<i>Aira praecox</i>	I	100	34.87	27.40	4.76
<i>Bromus mollis</i>	I	10	0.25	—	—
<i>Festuca dertonensis</i>	I	70	0.20	0.23	0.11
<i>Bromus diandrus</i>	I	10	t	—	—
ANNUAL FORBS					
<i>Lasthenia chrysostoma</i>	N	50	12.34	19.40	5.22
<i>Plantago hookeriana</i> var. <i>californica</i>	N	40	0.20	0.39	0.11
<i>Orthocarpus pusillus</i>	N	30	0.06	0.34	0.17
<i>Clarkia davyi</i>	N	10	0.06	—	—
<i>Daucus pusillus</i>	N	10	0.01	—	—
<i>Anagallis arvensis</i>	I	10	t	—	—
<i>Silene gallica</i>	I	10	t	—	—
BIENNIAL GRASSES					
<i>Bromus carinatus</i>	N	20	0.01	0.05	0.00
BIENNIAL FORBS					
<i>Gnaphalium purpureum</i>	N	10	0.95	—	—
PERENNIAL GRASSES					
<i>Deschampsia holciformis</i>	N	90	0.77	0.68	0.78
<i>Hordeum californicum</i>	N	90	0.65	0.57	0.19
PERENNIAL FORBS					
<i>Hypochoeris radicata</i>	I	100	26.47	20.80	3.13
<i>Plantago lanceolata</i>	I	30	1.02	2.68	2.41
<i>Convolvulus occidentalis</i> var. <i>saxicola</i>	N	30	0.57	1.50	0.50
<i>Cirsium quercetorum</i>	N	10	0.25	—	—
<i>Eschscholzia californica</i>	N	10	0.25	—	—
<i>Horkelia californica</i>	N	10	0.06	—	—
<i>Oxalis corniculata</i>	I	20	0.07	0.32	0.19
WOODY VINES, SHRUBS, AND SMALL TREES					
<i>Lupinus variicolor</i>	N	90	18.39	16.06	4.56
LONGEVITY UNKNOWN					
<i>Trifolium</i> sp.	—	10	t	—	—
BARE GROUND					
	—	—	2.44	—	—

TABLE 3. COVER VALUE OF SPECIES OF THE SEA RANCH LUPINE VEGETATION TYPE. I/N = introduced (I) or native (N); F = frequency of occurrence (percent of total samples); RC = percent relative cover; MC = mean actual percent cover; SE = standard error of mean actual percent cover; t = species present, relative cover < 0.01%. When a species only occurs in one plot, mean actual percent cover and standard error are not applicable and therefore indicated by a dash (—). 71 plots were sampled at one site. For conversion to absolute cover of each species multiply relative cover value by 1.10.

Taxon	I/N	F	RC	MC	SE
ANNUAL GRASSES					
<i>Bromus diandrus</i>	I	14.1	1.35	10.57	9.44
<i>Bromus mollis</i>	I	14.1	0.62	4.86	4.14
<i>Aira caryophylla</i>	I	15.4	0.35	2.50	1.47
<i>Gastridium ventricosum</i>	I	1.4	0.20	—	—
<i>Festuca dertonensis</i>	I	15.4	0.13	0.93	0.71
<i>Lagurus ovatus</i>	I	4.2	0.03	0.08	0.06
<i>Cynosurus echinatus</i>	I	8.5	0.03	0.17	0.11
<i>Hordeum leporinum</i>	I	2.8	0.01	0.03	0.21
<i>Briza minor</i>	I	1.4	t	—	—
<i>Lolium multiflorum</i>	I	1.4	t	—	—
ANNUAL SEDGES AND RUSHES					
<i>Juncus bufonius</i>	N	2.8	0.12	4.75	2.75
ANNUAL FORBS					
<i>Lotus angustissimus</i>	I	7.0	3.02	47.30	17.37
<i>Carduus pycnocephalus</i>	I	1.4	0.10	—	—
<i>Madia capitata</i>	N	7.0	0.15	2.31	3.06
<i>Geranium dissectum</i>	I	2.8	t	0.10	0.00
<i>Silene gallica</i>	I	2.8	t	0.01	0.00
<i>Lotus micranthus</i>	N	1.4	t	—	—
ANNUAL OR BIENNIAL FORBS					
<i>Cirsium brevistylum</i>	N	1.4	0.10	—	—
<i>Cirsium vulgare</i>	I	4.2	0.20	5.20	5.15
PERENNIAL GRASSES					
<i>Anthoxanthum odoratum</i>	I	63.4	16.90	29.45	4.92
<i>Holcus lanatus</i>	I	85.9	16.33	21.00	3.38
<i>Deschampsia holciformis</i>	N	18.3	0.33	2.01	0.88
<i>Lolium perenne</i>	I	7.0	0.03	0.40	0.40
<i>Danthonia pilosa</i>	I	2.8	t	0.03	0.21
<i>Elymus glaucus</i>	N	1.4	t	—	—
PERENNIAL SEDGES AND RUSHES					
<i>Juncus effusus</i> var. <i>brunneus</i>	N	7.0	2.21	47.21	14.85
<i>Cyperus eragrostis</i>	N	1.4	0.62	—	—
<i>Juncus effusus</i> var. <i>pacificus</i>	N	3.9	0.42	5.33	1.29
<i>Carex obnupta</i>	N	1.4	0.20	—	—
<i>Carex</i> spp.	—	2.8	0.03	1.00	1.00
PERENNIAL FORBS					
<i>Plantago lanceolata</i>	I	15.5	0.94	6.68	2.20
<i>Rumex acetosella</i>	I	14.1	0.82	6.40	2.48
<i>Horkelia californica</i>	N	1.4	0.80	—	—
<i>Hypochoeris radicata</i>	I	19.7	0.61	3.40	1.30
<i>Oenanthe sarmentosa</i>	N	2.8	0.54	12.25	5.75
<i>Cardionema ramosissimum</i>	N	2.8	0.20	7.78	7.73
<i>Stachys rigida</i>	N	1.4	0.10	—	—

TABLE 3 (CONT.)

Taxon	I/N	F	RC	MC	SE
<i>Abronia latifolia</i>	N	1.4	0.10	—	—
<i>Lotus corniculatus</i>	I	2.8	0.03	2.00	0.00
<i>Rumex</i> sp.	—	1.4	t	—	—
<i>Lythrum hyssopifolia</i>	N	2.8	t	32.71	22.60
<i>Mimulus guttatus</i>	N	1.4	t	—	—
<i>Veronica scutellata</i>	N	1.4	t	—	—
WOODY VINES, SHRUBS, AND SMALL TREES					
<i>Lupinus arboreus</i>	N	95.8	28.37	32.72	3.87
<i>Rubus ursinus</i> — <i>R. vitifolius</i>	N	9.9	2.13	23.86	7.67
<i>Salix</i> spp.	N	2.8	0.22	8.75	6.75
FERNS					
<i>Pteridium aquilinum</i> var. <i>pubescens</i>	N	2.8	0.83	32.50	30.50
LONGEVITY UNKNOWN					
<i>Galium</i> spp.	—	2.8	0.20	7.75	7.75
<i>Trifolium</i> sp.	—	1.4	0.26	—	—
<i>Lotus</i> spp.	—	1.4	t	—	—
BARE GROUND		—	21.48	—	—

Species cover also varies depending on the time of year. Sampling was conducted in August and September when annuals had already dropped seed. Had an earlier sample been taken, comparison would probably show an increase in cover values for the annual species. A number of perennial species such as *Brodiaea laxa*, *Calochortus tolmiei* and *Ranunculus californicus* had been observed in the study sites during the spring but by August were not evident. The extent of cover increase of these species given an earlier sampling date is unknown, but we believe that their cover importance relative to all other species would remain minimal. Even at peak activity, these species are not dominants in the vegetation and therefore might be expected to change relative covers by no more than 5–10% at most.

Finally, the tables do not adequately reflect the small scale patchiness in each vegetation type. Within the perennial type, for example, some areas are almost exclusively *Deschampsia*, while in others *Holcus* is dominant, and in others, *Anthoxanthum* and *Danthonia pilosa*. Furthermore, there appears to be variation in patch size, from several hundred m<sup>2</sup> to less than one, with and without clear boundaries. By combining samples we have constructed an overall view of species composition in the grassland.

TABLE 4. COVER VALUES OF SPECIES OF THE SEA RANCH MIXED GRASSLAND VEGETATION TYPE. I/N = introduced (I) or native (N); F = frequency of occurrence (percent of total samples); RC = percent relative cover; MC = mean actual percent cover; SE = standard error of mean actual percent cover; t = species present, relative cover < 0.01%. When a species only occurs in one plot mean actual cover and standard error are not applicable and therefore indicated by a dash (—). 144 plots were sampled from four sites. For conversion to absolute cover of each species multiply relative cover value by 0.78.

Taxon	I/N	F	RC	MC	SE
ANNUAL GRASSES					
<i>Cynosurus echinatus</i>	I	75.7	15.27	15.74	1.96
<i>Aira caryophyllea</i>	I	67.4	3.45	3.99	0.73
<i>Aira praecox</i>	I	4.2	0.55	10.25	3.91
<i>Bromus mollis</i>	I	62.5	1.48	1.85	0.63
<i>Festuca dertonensis</i>	I	37.5	0.29	0.60	0.20
<i>Briza minor</i>	I	52.1	0.27	0.40	0.14
<i>Lagurus ovatus</i>	I	1.4	0.26	14.50	12.50
<i>Bromus diandrus</i>	I	12.5	0.24	1.39	0.81
<i>Avena barbata</i>	I	4.2	0.16	2.92	2.54
<i>Hordeum leporinum</i>	I	0.7	0.02	—	—
ANNUAL SEDGES AND RUSHES					
<i>Juncus bufonius</i>	N	1.4	0.02	1.25	0.75
ANNUAL FORBS					
<i>Lasthenia chrysostoma</i>	N	1.4	0.24	13.50	13.50
<i>Lotus angustissimus</i>	I	0.7	0.24	—	—
<i>Sherardia arvensis</i>	I	20.1	0.15	0.60	0.27
<i>Hemizonia multicaulis</i>	N	2.1	0.14	5.17	8.95
<i>Silene gallica</i>	I	26.4	0.12	0.35	0.20
<i>Clarkia davyi</i>	N	1.4	0.07	3.75	5.30
<i>Anagallis arvensis</i>	I	31.3	0.05	0.13	0.34
<i>Geranium dissectum</i>	I	2.8	0.02	0.50	0.50
<i>Pogogyne serpylloides</i>	N	0.7	0.02	—	—
<i>Trifolium tridentatum</i>	N	0.7	0.02	—	—
<i>Plantago hookeriana</i> var. <i>californica</i>	N	2.1	t	0.02	0.02
<i>Madia capitata</i>	N	1.4	t	0.01	0.00
<i>Navarretia squarrosa</i>	N	0.7	t	—	—
<i>Trifolium dubium</i>	I	0.7	t	—	—
<i>Vicia benghalensis</i>	I	0.7	t	—	—
BIENNIAL GRASSES					
<i>Bromus carinatus</i>	N	13.2	0.23	1.37	0.63
ANNUAL OR BIENNIAL FORBS					
<i>Linum bienne</i>	I	47.2	0.48	0.79	0.34
PERENNIAL GRASSES					
<i>Anthoxanthum odoratum</i>	N	50.7	13.24	20.37	2.70
<i>Danthonia pilosa</i>	I	69.4	11.64	13.08	1.99
<i>Holcus lanatus</i>	I	20.1	0.95	3.73	1.53
<i>Stipa pulchra</i>	N	22.9	0.40	1.38	0.42
<i>Elymus glaucus</i>	N	31.3	0.25	0.65	0.19
<i>Deschampsia holciformis</i>	N	7.6	0.13	1.37	0.66
<i>Hordeum californicum</i>	N	4.2	0.08	1.42	1.22
<i>Lolium perenne</i>	I	19.4	0.04	0.16	0.08
<i>Danthonia californica</i>	N	0.7	t	—	—

TABLE 4 (CONT.)

Taxon	I/N	F	RC	MC	SE
PERENNIAL SEDGES AND RUSHES					
<i>Juncus effusus</i> var. <i>brunneus</i>	N	2.1	0.31	11.50	8.05
<i>Juncus effusus</i> var. <i>pacificus</i>	N	0.7	0.07	—	—
<i>Carex</i> spp.	N	0.7	t	—	—
<i>Eleochoeris palustris</i>	N	0.7	t	—	—
PERENNIAL FORBS					
<i>Plantago lanceolata</i>	I	68.5	23.71	21.48	1.57
<i>Iris douglasiana</i>	N	9.7	3.74	20.04	5.61
<i>Hypochoeris radicata</i>	I	34.7	1.24	2.79	0.65
<i>Horkelia californica</i>	N	7.6	1.01	11.31	2.65
<i>Corethrogyne californica</i> var. <i>obovata</i>	N	2.8	0.66	—	—
<i>Achillea borealis</i> ssp. <i>arenicola</i>	N	5.6	0.58	8.19	4.99
<i>Convolvulus occidentalis</i> var. <i>saxicola</i>	N	7.6	0.52	5.33	1.77
<i>Cardionema ramosissimum</i>	N	1.4	0.39	22.00	2.00
<i>Rumex acetosella</i>	I	17.4	0.31	1.42	0.55
<i>Stachys rigida</i>	N	1.4	0.14	8.00	7.50
<i>Aster chiloensis</i>	N	1.4	0.08	4.75	3.89
<i>Plantago hirtella</i> var. <i>galeottiana</i>	N	0.7	0.07	—	—
<i>Fragaria chiloensis</i>	N	1.4	0.02	1.03	0.98
<i>Oxalis corniculata</i>	I	1.4	0.02	1.00	1.00
<i>Sisyrinchium bellum</i>	N	1.4	t	0.05	0.00
<i>Lythrum hyssopifolia</i>	N	2.1	t	0.02	0.02
<i>Brodiaea coronaria</i>	N	1.4	t	0.03	0.02
<i>Epilobium watsonii</i> var. <i>franciscanum</i>	N	0.7	t	—	—
<i>Veronica scutellata</i>	N	0.7	t	—	—
WOODY VINES, SHRUBS, AND SMALL TREES					
<i>Rubus ursinus</i> — <i>R. vitifolius</i>	N	27.8	4.67	13.13	1.56
<i>Salix lasiolepis</i>	N	0.7	0.85	—	—
<i>Lupinus arboreus</i>	N	2.1	0.04	1.50	0.50
FERNS					
<i>Pteridium aquilinum</i> var. <i>pubescens</i>	N	10.4	1.56	11.70	2.47
LONGEVITY UNKNOWN—FORBS					
<i>Trifolium</i> spp.	—	1.4	t	0.03	0.02
<i>Lotus</i> spp.	—	2.1	t	0.01	0.00
<i>Galium</i> spp.	—	0.7	t	—	—
BARE GROUND			10.13		

TABLE 5. COVER VALUES OF SPECIES OF THE SEA RANCH PERENNIAL GRASSLAND VEGETATION TYPE. I/N = introduced (I) or native (N); F = frequency of occurrence (percent of total samples); RC = percent relative cover; MC = mean actual percent cover; SE = standard error of mean actual percent cover; t = species present, relative cover < 0.01%. When a species occurs in only one plot mean actual percent cover and standard error are not applicable and therefore indicated by a dash (—). 181 plots were sampled from 3 sites. For conversion to absolute cover of each species multiply relative cover value by 0.96.

Taxon	I/N	F	RC	MC	SE
ANNUAL GRASSES					
<i>Aira caryophylla</i>	I	33.7	1.24	3.55	1.03
<i>Bromus mollis</i>	I	28.2	0.83	3.60	1.34
<i>Aira praecox</i>	I	7.2	0.39	5.27	2.36
<i>Lagurus ovatus</i>	I	6.6	0.31	4.50	3.46
<i>Festuca dertonensis</i>	I	22.1	0.29	1.30	0.55
<i>Briza minor</i>	I	23.2	0.12	5.19	0.52
<i>Cynosurus echinatus</i>	I	12.2	0.06	0.50	0.17
<i>Avena barbata</i>	I	1.7	0.01	0.84	0.09
<i>Bromus diandrus</i>	I	3.3	t	0.01	0.00
ANNUAL SEDGES AND RUSHES					
<i>Juncus bufonius</i>	N	0.5	t	—	—
ANNUAL FORBS					
<i>Sherardia arvensis</i>	I	4.4	0.02	0.30	0.11
<i>Trifolium dubium</i>	I	1.7	0.01	0.80	0.58
<i>Silene gallica</i>	I	7.2	t	0.10	0.03
<i>Plantago hookeriana</i> var. <i>californica</i>	N	1.7	t	0.20	0.17
<i>Anagallis arvensis</i>	I	5.0	t	0.06	0.06
<i>Pogogyne serpylloides</i>	N	0.5	t	—	—
<i>Hemizonia multicaulis</i>	N	1.1	t	—	—
<i>Lotus angustissimus</i>	I	1.1	t	0.01	0.00
<i>Galium aparine</i>	I	1.1	t	0.03	0.02
<i>Geranium dissectum</i>	I	3.3	t	0.10	0.08
<i>Orthocarpus castillejoideus</i>	N	1.1	t	0.03	0.02
<i>Daucus pusillus</i>	N	1.1	t	0.01	0.00
<i>Clarkia davayi</i>	N	0.5	t	—	—
<i>Lotus micranthus</i>	N	1.1	t	0.01	0.00
<i>Madia capitata</i>	N	1.4	t	0.01	0.00
<i>Trifolium</i> spp.	—	0.5	t	—	—
<i>Vicia benghalensis</i>	I	0.5	t	—	—
BIENNIAL GRASSES					
<i>Bromus carinatus</i>	N	1.7	t	0.17	0.17
BIENNIAL FORBS					
<i>Erechtites prenanthoides</i>	I	1.1	0.09	7.80	7.85
<i>Gnaphalium purpureum</i>	N	3.3	0.01	0.18	0.07
<i>Erechtites arguta</i>	I	0.5	t	—	—
ANNUAL OR BIENNIAL FORBS					
<i>Linum bienne</i>	I	10.5	0.01	0.33	0.12
PERENNIAL GRASSES					
<i>Deschampsia holciformis</i>	N	65.2	28.21	41.61	2.22
<i>Anthoxanthum odoratum</i>	I	63.0	26.91	32.48	2.48

TABLE 5 (CONT.)

Taxon	I/N	F	RC	MC	SE
PERENNIAL GRASSES (continued)					
<i>Holcus lanatus</i>	I	61.3	13.18	20.65	2.43
<i>Calamagrostis nutkaensis</i>	N	0.5	0.55	—	—
<i>Hordeum californicum</i>	N	7.7	0.09	4.00	2.00
<i>Danthonia pilosa</i>	I	12.2	0.07	0.58	0.35
<i>Elymus glaucus</i>	N	5.5	t	0.10	0.01
<i>Danthonia californica</i>	N	2.8	t	0.14	0.01
<i>Lolium perenne</i>	I	2.2	t	0.01	0.00
<i>Festuca arundinacea</i>	I	0.5	t	—	—
PERENNIAL SEDGES AND RUSHES					
<i>Juncus effusus</i> var. <i>brunneus</i>	N	6.6	1.59	15.34	9.16
<i>Carex</i> spp.	N	7.2	0.48	6.39	2.34
<i>Carex obnupta</i>	N	2.2	0.29	12.63	5.69
<i>Juncus effusus</i> var. <i>pacificus</i>	N	6.1	0.10	1.51	0.66
PERENNIAL FORBS					
<i>Plantago lanceolata</i>	I	50.2	4.92	10.51	1.05
<i>Hypochoeris radicata</i>	I	37.0	1.89	5.86	0.94
<i>Iris douglasiana</i>	N	20.4	1.59	7.47	1.28
<i>Rumex acetosella</i>	I	14.4	0.28	1.85	0.72
<i>Fragaria chiloensis</i>	N	4.4	0.24	5.13	2.43
<i>Aster chilensis</i>	N	0.5	0.09	—	—
<i>Cirsium quercetorum</i>	N	0.5	0.09	—	—
<i>Eryngium armatum</i>	N	3.9	0.08	1.86	0.98
<i>Acaena californica</i>	N	0.5	0.04	—	—
<i>Oxalis corniculata</i>	I	2.8	0.01	0.42	0.39
<i>Sisyrinchium bellum</i>	N	1.7	0.01	0.35	0.15
<i>Convolvulus occidentalis</i> var. <i>saxicola</i>	N	1.1	t	0.28	0.02
<i>Horkelia californica</i>	N	1.1	t	0.28	0.02
<i>Lotus corniculatus</i>	I	1.1	t	0.01	0.00
<i>Cardionema ramosissimum</i>	N	0.5	t	—	—
<i>Scrophularia californica</i>	N	0.5	t	—	—
WOODY VINES, SHRUBS, AND SMALL TREES					
<i>Rubus ursinus</i> — <i>R. vitifolius</i>	N	35.9	5.11	13.68	1.85
<i>Lupinus arboreus</i>	N	15.5	2.15	13.36	2.55
<i>Myrica californica</i>	N	0.5	0.55	—	—
<i>Lupinus variicolor</i>	N	1.1	0.02	2.00	0.00
FERNS					
<i>Pteridium aquilinum</i> var. <i>pubescens</i>	N	19.9	2.48	11.98	2.24
UNKNOWN LONGEVITY—FORBS					
<i>Galium</i> spp.	—	0.5	0.09	—	—
<i>Lotus</i> spp.	—	1.1	t	0.01	0.00
BARE GROUND					
		—	5.93	—	—

TABLE 6. COVER VALUE OF SPECIES OF THE SEA RANCH CALAMAGROSTIS VEGETATION TYPE. I/N = introduced (I) or native (N); F = frequency of occurrence (percent of total samples); RC = percent relative cover; MC = mean actual percent cover; SE = standard error of mean actual percent cover; t = species present, relative cover < 0.01%. When a species only occurs in one plot mean actual percent cover and standard error are not applicable and therefore indicated by a dash (—). 25 plots were sampled at one site. For conversion to absolute cover of each species multiply relative cover value by 1.10.

Taxon	I/N	F	RC	MC	SE
ANNUAL FORBS					
<i>Sonchus asper</i>	I	8	t	0.03	3.33
BIENNIAL FORBS					
<i>Erechtites prenanthoides</i>	I	36	2.21	6.73	3.07
<i>Erechtites arguta</i>	I	8	0.02	0.28	0.23
ANNUAL OR BIENNIAL FORBS					
<i>Cirsium vulgare</i>	I	4	t	—	—
PERENNIAL GRASSES					
<i>Calamagrostis nutkaensis</i>	N	100	55.15	61.50	3.83
<i>Elymus glaucus</i>	N	24	3.49	15.94	15.91
<i>Holcus lanatus</i>	I	100	3.14	3.49	0.88
<i>Anthoxanthum odoratum</i>	I	28	0.08	0.32	0.29
<i>Deschampsia holciformis</i>	N	20	t	0.03	0.01
PERENNIAL SEDGES AND RUSHES					
<i>Carex obnupta</i>	N	60	5.77	10.54	3.06
<i>Juncus effusus</i> var. <i>brunneus</i>	N	52	0.48	1.01	0.58
<i>Carex</i> spp.	N	8	t	0.01	0.00
<i>Juncus effusus</i> var. <i>pacificus</i>	N	4	t	—	—
PERENNIAL FORBS					
<i>Veratrum fimbriata</i>	N	72	10.41	16.88	1.59
<i>Oenanthe sarmentosa</i>	N	60	2.18	3.97	0.78
<i>Iris douglasiana</i>	N	68	2.13	3.42	1.23
<i>Vicia gigantea</i>	N	64	0.74	1.27	0.47
<i>Galium trifidum</i> var. <i>subbiflorum</i>	N	48	0.63	1.44	0.83
<i>Stachys rigida</i>	N	48	0.51	1.18	0.61
<i>Veronica scutellata</i>	N	52	0.34	0.71	0.23
<i>Mimulus moschatus</i>	N	32	0.29	1.01	0.30
<i>Campanula californica</i>	N	64	0.23	0.39	0.17
<i>Sidalcea malvaeflora</i>	N	4	0.07	—	—
<i>Achillea borealis</i> ssp. <i>arenicola</i>	N	4	t	—	—
<i>Horkelia californica</i>	N	4	t	—	—
<i>Hypochoeris radicata</i>	I	4	t	—	—
<i>Smilacina stellata</i> var. <i>sessilifolia</i>	N	4	t	—	—
WOODY VINES, SHRUBS, AND SMALL TREES					
<i>Rubus ursinus</i> — <i>R. vitifolius</i>	N	100	11.03	12.16	1.79
<i>Myrica californica</i>	N	4	0.27	—	—

TABLE 6 (CONT.)

Taxon	I/N	F	RC	MC	SE
FERNS					
<i>Pteridium aquilinum</i> var. <i>pubescens</i>	N	8	0.28	3.78	3.73
LONGEVITY UNKNOWN					
<i>Trifolium</i> spp.	—	4	t	—	—
BARE GROUND		—	0.46	—	—

## DISCUSSION

Floristic comparisons between the Sea Ranch grasslands and other areas of coastal prairie show a consistent set of characteristic species. In a 1902 description of the north coast prairie, Davy stated that the prevailing grasses were *Danthonia californica*, *Festuca rubra*, *Calamagrostis aleutica* (now *C. nutkaensis*), and *Deschampsia caespitosa*. These native perennial grasses have now been joined by a number of introduced grasses that are an equally important component of today's grasslands: *Holcus lanatus*, *Anthoxanthum odoratum*, *Agrostis tenuis*, *Festuca arundinacea*, and *Danthonia pilosa* (Beetle, 1947; Peñalosa, 1963; Howell, 1970; Batzli and Pitelka, 1970; Crampton, 1974; Elliott and Wehausen, 1974; Heady et al., 1977).

Some of the non-grass species also considered to be indicators of the coastal prairie are *Iris douglasiana*, *Carex tumicola*, *Carex obnupta*, *Camassia quamash* var. *linearis*, *Spiranthes romanzoffiana*, *Viola adunca*, and *Juncus effusus*. Most of these are more or less restricted to the coastal area, but various floral descriptions include an even greater number of species that are also common to the annual grasslands inland. Some of the more prominent species include *Aira caryophyllea*, *Briza minor*, *Avena barbata*, *Avena fatua*, *Bromus mollis*, *Bromus diandrus*, *Lolium multiflorum*, *Brodiaea pulchella*, *Sisyrinchium bellum*, *Lasthenia chrysostoma*, *Eschscholzia californica*, and *Plantago lanceolata*.

Note that most of these species were found at Sea Ranch. However, the data emphasize patchiness over uniformity: patchiness in the distribution of vegetation units, patchiness of species and dominant distributions from area to area, and patchiness within any one area. Clearly, the Sea Ranch grasslands are not uniform entities and part of the patchiness must result from variation in the physical environment. For example, Barbour et al. (1973) have shown that soil salinity decreases inland. At Bodega Head they showed that the higher salinity near the bluffs and the physical effects of onshore winds affect the distribution of certain species (*Lupinus arboreus*, in particular). In drier areas *Festuca idahoensis* and *Danthonia californica* may be more important dominants than

*Deschampsia holciformis* or *Calamagrostis nutkaensis* (Huffaker and Kennett, 1959; Crampton, 1974). Other than the restriction of the headlands type to exposed bluffs and the *Calamagrostis* type to very wet-claypan areas, we have not observed obvious correlations between presumed soil gradients and grassland vegetation type. In particular, the distributions of major soil types (U.S.D.A., 1972) and vegetation types seem unrelated, although Baywood soils do tend to be immediately adjacent to the ocean bluffs and the Rohnerville soils further inland.

Soil moisture is probably a factor in the distribution of at least some species. Since the area is made up of a series of terraces, the inland soils are older and deeper, and this, together with the fact that the ridge behind the terrace receives twice the amount of rainfall, suggests that the terrace areas at the base of slopes receiving the greatest amount of runoff might be particularly favorable for perennial development. The southern portion of Sea Ranch, with its narrow terrace, apparently permits enough seepage and runoff to support the stands of *Calamagrostis* there. In this case, the *Calamagrostis* vegetation type indicates the abundance of water.

In addition to the effects of physical environment, we feel that disturbance (grazing and construction) has a large influence on species composition. This finds some support in the literature. Burcham (1957) suggests that perennials disappeared from California's Central Valley under grazing pressures. Similarly, Clements and Shelford (1939) stated that three-fourths of the land south of Mt. Shasta, and from the coast to the foothills of the Sierra Nevada in Northern California, was originally perennial climax grassland and that replacement by annuals was largely caused by overgrazing. Hormay and Fausett (1942) estimated that 90-100% of the forage available on heavily grazed rangeland consisted of annuals. With perennials remaining green throughout the dry summer season, they are subject to heavy use, which reduces plant vigor and leaves space for the increase of less palatable species characteristic of earlier seral stages (Burcham, 1957).

Huffaker and Kennett (1959) documented an example in Humboldt County where prior range practices had changed a once-perennial grassland dominated by *Danthonia californica* to one of mostly annuals. By withholding grazing until seed shattered and by rotating grazing, perennials again increased. More recently, Elliott and Wehausen (1974) showed that the coastal grassland at Pt. Reyes was highly responsive to grazing. With increased grazing pressure, there was an increase of exotic annual species and a decrease in the native, predominantly perennial vegetation. In particular, perennial species dominant at the Sea Ranch were prominent when protected from grazing at Pt. Reyes (*Deschampsia holciformis*, e.g.).

With grazing having ended less than 10 years earlier, we have shown that the grassland at the Sea Ranch is dominated by perennials, although

no one species has yet established anything approaching uniform dominance. This analysis enables us to make some predictions to be confirmed by future sampling of the vegetation: we expect the dominant perennial grasses to continue to spread and increase their cover values, and to this extent to clarify the picture of succession within the grassland from annuals to perennials. We expect the restricted areas of annual grasses to become more scarce and more restricted to areas of disturbance, and the mixed grasslands to become perennial grasslands within a few years.

#### ACKNOWLEDGMENTS

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## OBSERVATIONS ON ANTHOCARP ANATOMY IN THE SUBTRIBE MIRABILINAE (NYCTAGINACEAE)

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Flowers of Nyctaginaceae have a uniseriate perianth. The calyx is petaloid and of short duration throughout the upper portion and morphologically simple compared to the lower portion, which forms a persistent, fleshy to hard and leathery, glabrous or pubescent, often 5(-10) ribbed to winged accessory fruit, the anthocarp. Anthocarp is used here to designate "the accrescent perianth base comprising the accessory fruit enclosing the mature ovary, which is itself an achene or utricle" (Bogle, 1974). The terms anthocarp and diclesium (Lawrence, 1963) are used synonymously in reference to Nyctaginaceae fruit. We have chosen to use the former which is traditional in American botanical literature.

Within Nyctaginaceae anthocarp morphology has long been useful in distinguishing taxa (Standley, 1918; Heimerl, 1934). Recent delimitation of taxa at specific (Smith, 1975) and generic (Galloway, 1975) levels has also been partially based on anthocarp morphology. Anthocarp morphology and anatomy have been considered in ecological and taxonomic studies within subtribe Abroniinae (Wilson, 1972, 1974, 1975, 1976; Galloway, 1971, 1975) and in *Boerhavia*, (Bhargava, 1932; Maheshwari, 1929), but the scope of these investigations does not include comparative examination of anthocarp anatomy to determine the phylogenetic information these data may hold.

This paper reports results of preliminary investigations to determine the feasibility of utilizing anthocarp anatomy to elucidate phylogenetic and taxonomic relationships in subtribe Mirabilinae, tribe Mirabileae. The subtribe Mirabilinae was selected for preliminary investigation because we believe it is a natural group and because within this subtribe anthocarp structure is more diverse than in other subtribes. Morphological diversity of the anthocarp in subtribe Mirabilinae is expressed primarily by the formation of ridges or wings from a portion of the anthocarp wall. Anthocarps of subtribe Mirabilinae may be morphologically placed into 3 general types: 1) those with smooth walls or slightly rounded or angled ridges; 2) those with narrow wings acute in cross section; and 3) those with broad laminar wings (Fig. 1). The anatomical basis of this morphological diversity among species serves as the focal point of this study. We felt it was necessary in an anatomically based preliminary phylogenetic study of the subtribe Mirabilinae to include not only congeneric species which exhibit one or more anthocarp types, but species from different genera which exhibit the same general anthocarp type. The following species were selected: *Mirabilis oblongifolia* (Gray) Heimerl, *M. viscosa* Cav. and *Boerhavia coccinea* Mill.

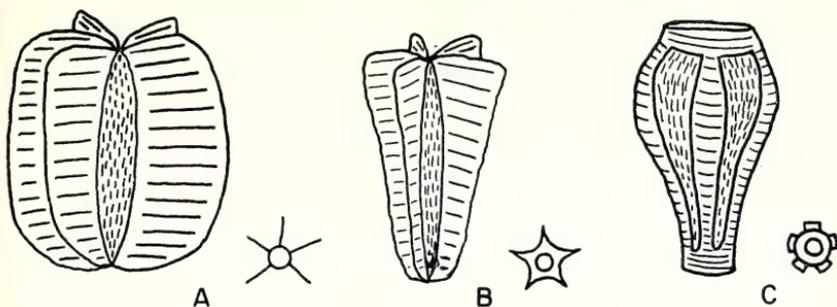


FIG. 1. Diagrammatic side views and cross sections of 3 general diclesium types. A, broad membranous wings. B, narrow wings. C, ridges.

exhibit rounded ridges; *B. intermedia* M. E. Jones and *B. spicata* Choisy have angled ridges; *B. alata* S. Wats. has narrow wings; *Selinocarpus lanceolatus* Gray and *Ammocodon chenopodioides* Standl. have broad laminar wings.

#### METHODS AND MATERIALS

Anthocarps in late stages of maturation were killed and fixed in the field using FAA (Sass, 1966), then transferred to tetrahydrofuran (THF) for dehydration (Leuty, 1964). Standard methods of paraffin infiltration, embedding, and sectioning at 12  $\mu\text{m}$  were employed (Sass, 1966). Sections were stained in toluidine blue (Feder and O'Brien, 1968), mounted in Permount, and drawn using a micro-projector. Several anthocarps from each plant or population were studied. Where advisable, confirmation of anatomical observations was made by examining anthocarps from geographically distant conspecific populations.

#### RESULTS

Anthocarp walls and accompanying wings or angles of each species are constructed from 5 common elements: epidermis, sclerenchyma, polyhedral parenchyma, vascular strands, and columnar parenchyma cells. Raphide bundles are common in all anthocarps but there is no trend in number or distribution. In *Selinocarpus* and *Ammocodon* no sclerenchyma is present in the walls between the wings, whereas in species of *Mirabilis* sclerenchyma is present in the wall between the angles in a band discontinuous from sclerenchyma within the angles. In species of *Boerkavia* sclerenchyma forms a continuous band, the sclerenchyma in the anthocarp wall contiguous with that of the wing or angle bases.

Graphic representation of transverse sections for each species is presented in Figs. 2-4. These illustrations are meant to replace complete and routine anatomical descriptions. Instead, a brief description of anthocarp morphology and citation for voucher specimens deposited at NMC

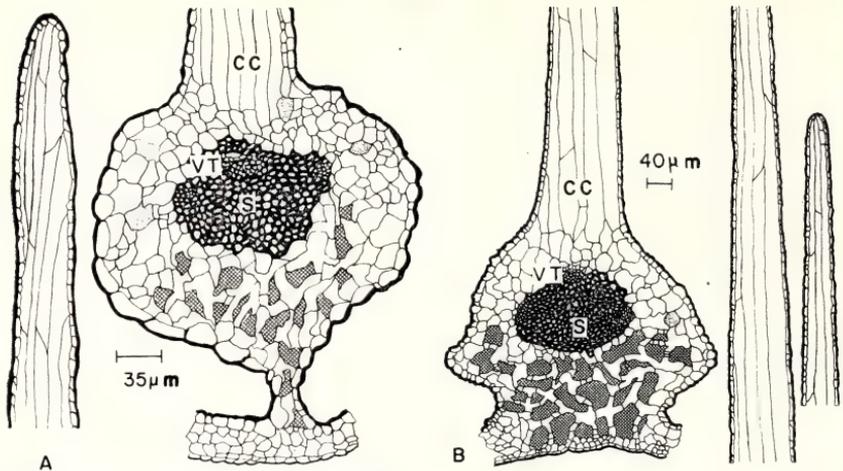


FIG. 2. Transverse sections of diclesium wings. A, *Ammocodon chenopodioides*. B, *Selinocarpus lanceolatus*. Cross hatched areas represent intercellular spaces within aerenchyma. CC = columnar cells, VT = vascular trace, S = sclerenchyma cylinder.

are followed by description of anatomical features which conspicuously differ between taxa.

*Ammocodon chenopodioides* (Fig. 2A): (USA, New Mexico, Doña Ana Co., Las Cruces, R. Spellenberg 2183). Anthocarp ca 5 mm long, wings ca 2 mm broad, glabrate, body sulcate between wings, sparsely puberulent. *Anatomy*: A single vascular strand is embedded in each sulcus region. Adaxial one-third of enlarged wing base filled with aerenchyma. Sclerenchyma cylinder in wing base with 3 vascular strands spaced equidistantly around abaxial edge of cylinder. Columnar parenchyma cells extend into each wing section filling wing lamina.

*Selinocarpus lanceolatus* (Fig. 2B): (USA, New Mexico, Doña Ana Co., NE tip of county, R. Spellenberg and T. K. Todsen 2640). Anthocarp ca 6–7 mm long, wings ca 2–3 mm broad, glabrate, body finely costate, truncate at both ends. *Anatomy*: A single vascular strand is embedded in each region between the wings. Adaxial half of enlarged hastate wing base filled with aerenchyma. Sclerenchyma cylinder in wing base with 3 equidistantly spaced vascular strands positioned around abaxial edge. Columnar parenchyma cells extend into each wing section filling wing lamina.

*Mirabilis oblongifolia* (Fig. 3A): (USA, New Mexico, Lincoln Co., 3 mi W of Alto, R. Spellenberg and D. Jackson 2657). Anthocarp obovoid, ca 3–5 mm long, minutely pilose, 5-angled, angles broad and usually tuberculate, sides coarsely or finely tuberculate. *Anatomy*: Sclerenchyma cylinder bordered laterally by sclerified parenchyma, and with a vascular strand at abaxial edge of cylinder. Columnar parenchyma cells extend to each ridge tip.

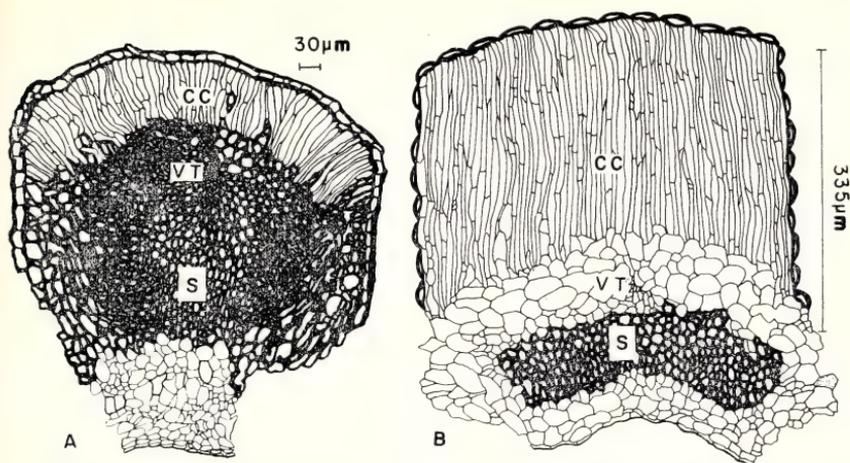


FIG. 3. Diclesium ridge anatomy. A, *Mirabilis oblongifolia*. Ridge anatomy with accompanying tubercule. B, *Mirabilis viscosa*. CC = columnar cells, VT = vascular trace, S = sclerenchyma cylinder.

*Mirabilis viscosa* (Fig. 3B): (Mexico, Guanajuato, just E of Silas, S of Cd. Guanajuato, R. Spellenberg 2969). Anthocarp obovoid, ca 5 mm long, angular, glabrous, densely covered with large coarse tubercules. *Anatomy*: Sclerenchyma band in basal region of ridge and contiguous with a vascular strand along abaxial edge of band. Columnar parenchyma cells extend into ridge and tubercule.

*Boerhavia coccinea* (Fig. 4A): (USA, New Mexico, Doña Ana Co., NMSU Campus, R. Spellenberg and J. Willson 3735). Anthocarp narrowly obovoid, ca 2.5–4 mm long, rounded at the apex, densely glandular-puberulent or glandular-pilose, 5-sulcate angles and sulci smooth. *Anatomy*: Sclerenchyma band thickened in ridge base, extending acutely into angle, and contiguous with a vascular strand at abaxial tip. Columnar parenchyma cells extend into angle.

*Boerhavia spicata* (Fig. 4B): (USA, Arizona, Maricopa Co., 5 mi SE of Morristown. R. and M. Spellenberg 2646). Anthocarp narrowly obovoid, ca 2.5 mm long, rounded at the apex, acute to acuminate at the base, stramineous, 5-angulate, angles from thick to thin, acute, sulci broad, open and rugulose. *Anatomy*: Sclerenchyma band broadened in angle base, projecting obtusely into angle. Four or 5 vascular strands present about the abaxial surface of the sclerenchyma cylinder. Columnar parenchyma cells extend into the angle.

*Boerhavia intermedia* (Fig. 4C): (USA, Arizona, Pima Co., 21.6 mi SE of Why, R. Spellenberg and J. Willson 3607). Anthocarp narrowly obpyramidal, ca 2–3 mm long, glabrous, truncate at apex, 5-angulate,

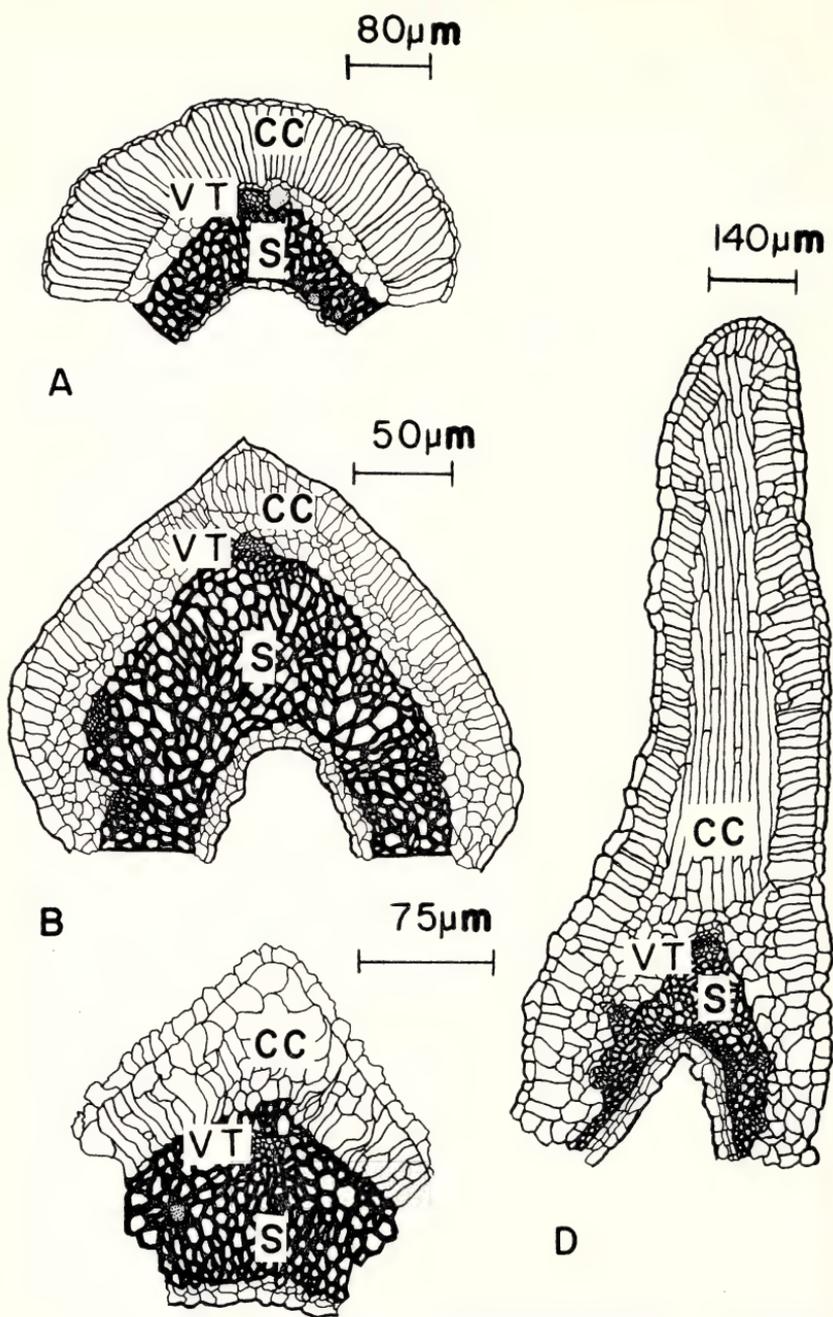


FIG. 4. Diclesium ridge anatomy. A, *Boerhavia coccinea*. B, *Boerhavia spicata*. C, *Boerhavia intermedia*. Diclesium wing anatomy. D, *Boerhavia alata*. CC = columnar cells. VT = vascular trace, S = sclerenchyma cylinder.

angles smooth, obtuse, sulci narrow, transverse-rugulose. *Anatomy*: Obtuse tip of sclerenchyma band barely projecting into angle where it is contiguous with a single vascular strand. Irregular columnar and isodiametric parenchyma cells fill angle.

*Boerhavia alata* (Fig. 4D): (Mexico, Sonora, Guaymas, SE section of city, *R. Spellenberg*, *D. Jackson* and *D. Martin 2696*). Anthocarp ca 4 mm long, sharply and broadly thin-winged, wings ca 1–1.5 mm wide, sulci narrow and transversely rugose. *Anatomy*: Sclerenchyma band thickened and forming a point in wing base, the point contiguous with 5 or 6 vascular strands about it abaxial periphery. Columnar parenchyma cells extend into the wing filling the interior wing lamina. Peripheral and laterally bordering the interior columnar cells is a second set of short columnar parenchyma cells.

#### DISCUSSION

The anatomical pattern within the wing or angle and corresponding anthocarp wall for each species suggests that wings or angles are modifications of the basic anthocarp wall structure. They are constructed from cells with similar position and morphology. The sclerenchymatous parenchyma of *Mirabilis oblongifolia*, the peculiar columnar parenchyma of *Boerhavia alata*, *Selinocarpus*, and *Ammocodon*, and the aerenchyma of *Selinocarpus* and *Ammocodon* are exceptions and are unique to wings or angles in those taxa.

Gray (1853) reported of *Pentacrophys wrightii* A. Gray (= *Acleisanthes*), subtribe Mirabilinae, that “. . . the superficial tissue of ribs abound in tubular cells, containing a spirally coiled thread, which is usually disengaged upon the application of moisture . . .” and that “. . . this structure was found in most Nyctaginaceae . . .” We did not observe this coiled thread in any species, but we did observe a discharge of mucilage or mucilage-like material when *Boerhavia* and *Mirabilis* anthocarps were placed in water. In *Selinocarpus* and *Ammocodon* the laminar portion of the wing exfoliates on contact with water, exposing the columnar cells, which separate like the bristles of a brush. *Phaeoptilum spinosum* Radlk. (subtribe Phaeoptilinae, tribe Mirabileae) possesses a broadly winged anthocarp somewhat similar to *Selinocarpus* and *Ammocodon* but these neither excrete mucilage nor exfoliate in water. The exact functional and ecological significance of the mucilage or mucilage-like material in *Boerhavia* and *Mirabilis* and the exposure of the columnar cells in *Selinocarpus* and *Ammocodon* is not known. However, mucilage excreted by wetted fruits or seeds may be involved with epizoochory and may be associated with germination (Kozłowski, 1972) or “carnivory” (Barber and Page, 1976). The rapid separation of the long tubular cells of the wings of the anthocarps of *Selinocarpus* and *Ammocodon* suggests (in addition to the importance of wings in seed dispersal) that these cells function in capillary retention of water near the seed. The absence of

both mucilage excretion and exfoliation in *P. spinosum* anthocarps suggests that wings in this species are associated primarily with wind dispersal.

Toluidine blue typically stains parenchyma walls pinkish-purple due to the binding of the stain with carboxylated polysaccharides and polyuronides. Walls containing polyphenolic compounds, such as lignified secondary walls, typically stain green, greenish-blue, or bright blue (O'Brien and McCully, 1969). The columnar cells in *B. coccinea*, *B. intermedia*, *B. spicata*, and *Mirabilis* and the exterior columnar cells of *B. alata* stain purple. The columnar cells of *Ammocodon*, *Selinocarpus* and the interior columnar cells of *B. alata*, however, stain blue. The parenchyma tissue adaxially adjacent to the columnar cells of *Ammocodon* and *Selinocarpus* and the short columnar cells of *B. alata* also stain bright blue rather than the purple of the polyhedral parenchyma within the wing or angle. These reactions indicate that in addition to similarity in morphology and position, interior columnar cells of *B. alata* and parenchymatous columnar cells of *Selinocarpus* and *Ammocodon* have similar wall composition. Also, the short columnar cells in *B. alata* and the columnar cells in *Mirabilis*, *B. coccinea*, *B. intermedia*, and *B. spicata* stain similarly and probably contain similar compounds in their walls or cytoplasm. Species that emit mucilage have purple-staining columnar cells and those that do not have blue-staining columnar cells. *Boerhavia alata* contains both types of columnar cells but those nearest the exterior surface and initially exposed to water are the purple-staining peripheral columnar cells; they enclose blue staining columnar cells. Since *B. alata*, *Selinocarpus*, and *Ammocodon* are in the same tribe (although the first seems fairly distantly related to the others), the presence of the similar blue staining columnar cells in *Boerhavia* may be a result of parallelism. Blue staining columnar cells in *Boerhavia* occur only in *B. alata*. It is not possible to ascertain whether wings of *Selinocarpus* and *Ammocodon* arose from the purple staining, mucilage-excreting columnar cells through development of a secondary set of elongate cells (as in *B. alata*) with subsequent loss of the mucilage-excreting cells, or in some other manner. Future studies of the ontogeny and ecology of Mirabilinae anthocarps may support one of these sequences and thus aid in elucidating phylogenetic relationships in these taxa.

The southwest African *Phaeoptilum spinosum*, the sole member of the subtribe Phaeoptilinae, has an anthocarp outwardly similar to *Selinocarpus* and *Ammocodon*. Limited material and difficulties in sectioning precluded a complete anatomical study of the mature anthocarp. However, it was noted that the laminar portion of the wing is filled with long, narrow, columnar cells that stain bright blue as in *Selinocarpus* and *Ammocodon*; these cells arise from polyhedral parenchyma cells, which also stain bright blue. A single, continuous band of sclerenchyma fibers is present in the anthocarp wall between the wings and forms a cylinder in the wing base, as in *Boerhavia*. Morphological and anatomical similari-

ties between the anthocarp of *P. spinosum* and the species with winged or ridged anthocarps of the Mirabilinae are probably also the result of parallel evolution. We concur with Nowicke (1970) who suggested that only a remote connection for *Phaeoptilum* and the Mirabilinae is possible when pollen type, endemism to southwest Africa, and the unisexual flowers of *P. spinosum* are considered.

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# TAXONOMY OF BEBBIA (COMPOSITAE: HELIANTHEAE)

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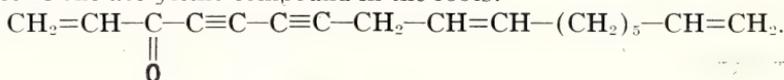
*Bebbia* is a genus of Mexico and the southwestern United States with its center of diversity in Baja California, where all 3 of its taxa occur. It is named for the botanist Michael S. Bebb, who worked on *Salix*. *Bebbia* is a small genus of little economic importance. Since it was proposed by Greene in 1885, it has been largely ignored, except for some controversy regarding its tribal position. A taxonomic treatment is provided here with keys and distribution maps.

## GENERIC RELATIONS

The generic position of what has come to be known as *Bebbia* has been questionable since it was first described as *Carphephorus* sect. *Kuhnoides* (Eupatorieae) by Asa Gray (1873). Greene renamed the taxon as a distinct genus, *Bebbia*, in the Heliantheae. It has certain superficial characteristics of the Eupatorieae, particularly a long plumose pappus and striate involucre bracts. However, these characters are also found, although less frequently, in the Heliantheae. Other characters of *Bebbia* clearly unite it with the Heliantheae: the persistent chaff subtending each floret, the Helianthoid achenes, the style branches, and the deep yellow corollas.

King and Robinson (1970) note that the Eupatorieae can be easily separated from the Helenieae-Heliantheae complex on the basis of microcharacters. They describe anther appendages of Helenieae-Heliantheae as keeled with the abaxial surface concave and with a thickened central region. They also state that members of this group often have glands (not visible with a dissecting microscope) on the abaxial surface of the anther appendages. They report clusters of such glands in *Bebbia juncea*. Although I do not know how these characters hold up throughout the Heliantheae, King and Robinson's description of the anther appendages in *Bebbia* is correct. I examined a number of specimens of each of the 3 taxa in *Bebbia* and usually found a cluster of glands (rarely 1 or 2) on the abaxial side along the thickened central region of the anther appendage. To the extent that these characters are valid in distinguishing the Eupatorieae from the Heliantheae, they support the placement of *Bebbia* in the Heliantheae.

Naturally occurring acetylenic compounds are of taxonomic significance within the Compositae (Bohlmann et al., 1973). Recent examination of *B. juncea* by Bohlmann (pers. comm.) has established the presence of one acetylenic compound in the roots:



This compound is the most common thus far detected in the Heliantheae, occurring in 11 species of *Helianthus*, 3 of *Tridax*, 4 of *Galinsoga* (Bohlmann et al., 1973), and in one species of *Schistocarpha* (Bohlmann et al., 1976). However, it was not found in any of the 35 species of Eupatorieae examined (Bohlmann et al., 1973). Thus, there is chemical as well as morphological support for the placement of *Bebbia* in the Heliantheae.

Various suggestions have been made as to the position of *Bebbia* within the Heliantheae. It has been considered to belong to the Verbesininae or Madiinae (Greene, 1885) or Galinsoginae (Hoffmann, 1894, who followed Bentham, 1873; Torres, 1968). Stuessy (1977) places it in his Neurolaeninae, which he considers related to the Galinsoginae, the former distinguished from the latter in having alternate leaves, phyllaries of unequal length (increasing inward), lanceolate paleae, and setose pappus. Phyllaries of unequal length, lanceolate paleae, and setose pappus (characteristic of *Bebbia*) are found in members of Stuessy's Galinsoginae as well as his Neurolaeninae. Furthermore, *Bebbia* does not have alternate leaves. (The presence of alternate leaves is not diagnostic for the Neurolaeninae anyway since of the 2 core genera, *Neurolaena* has alternate and *Schistocarpha* has opposite leaves.) Thus, I believe *Bebbia* fits well within the Galinsoginae even as constituted by Stuessy. *Bebbia* appears close to *Tridax* (Galinsoginae) and not particularly close to *Schistocarpha* or *Neurolaena*, which differ from *Bebbia* in floral characters, i.e., in their truncate style branches, non-plumose pappus, glabrous achenes without distinct faces, and more chartaceous involucre. *Bebbia* is also related to *Dyscritothamnus*, *Clappia*, *Pseudoclappia*, and *Varilla*, which are treated as a distinct subtribe of the Heliantheae, the Varillinae, by Turner and Powell (1977) but are included in the Neurolaeninae by Stuessy (1977). If these genera, along with *Schistocarpha* and *Neurolaena*, constitute a natural group within the Heliantheae as Stuessy suggests, then *Bebbia* would appear to be transitional between the 2 subtribes, and it might prove taxonomically more expedient to recognize but a single large subtribe, the Galinsoginae, to include both Stuessy's Neurolaeninae and Turner and Powell's Varillinae.

The genera to which *Bebbia* probably is most closely related are *Dyscritothamnus* (Neurolaeninae) and *Tridax* (Galinsoginae), both of which may have radiate or eradiate heads. *Bebbia* and *Dyscritothamnus* are similar in habit and in many aspects of floral morphology (Table 1). Turner and Powell (1977) consider *Dyscritothamnus*, *Varilla*, *Pseudoclappia*, and *Clappia* to form a tightly knit group, alike in their succulent habit, distribution, and ecology, and having similar overall leaf and floral morphology. However, *Dyscritothamnus* seems to be more similar to *Bebbia* than the other genera in having a more pronounced plumose pappus, slender and more recurved style branches not appendaged at the

TABLE 1. COMPARISON OF *Dyscritothamnus* AND *Tridax* WITH *Bebbia*.

<i>Bebbia</i>	<i>Dyscritothamnus</i>	<i>Tridax</i>
Perennial shrubs	Perennial shrubs	Annual or weak-stemmed, perennial herbs
Pappus setose, uniseriate, plumose with lateral processes 0.1–0.3 mm long	Pappus setose, uniseriate, plumose with lateral processes 0.6–1.0 mm long	Pappus uniseriate, usually plumose, scales or bristles
Inner phyllaries wholly chartaceous, straw-colored with orange striae	Inner phyllaries wholly chartaceous, stramineous with orange striae	Inner phyllaries partially herbaceous, light green, often with purple margins, or wholly purple
Chaff with orange striae	Chaff with orange striae	Chaff usually with yellow-green striae
Outer phyllaries herbaceous	Outer phyllaries subscariosus	Outer phyllaries herbaceous
Lobes of disk corolla pubescent, tube densely glandular	Lobes and tube of disk corolla glabrous	Lobes of disk corolla usually pubescent, tube pubescent or glabrous
Leaves opposite throughout or opposite below and alternate above	Leaves alternate	Leaves opposite, or rarely alternate above and opposite below

top, more distinctly 3-angled, obpyramidal achenes, and similar chaff and phyllaries (Table 1). *Bebbia* also appears to be close to *Tridax* (Galinsoginae) and to approach *Tridax* in many of the characters that distinguish it from *Dyscritothamnus* (Table 1). Also, *Tridax* often has glandular-tipped trichomes on the peduncles and outer phyllaries, as are found in *Bebbia atriplicifolia*. These are not present in *Dyscritothamnus* and related genera discussed above. The achenes and floral morphology are similar in *Bebbia* and *Tridax*, although there is considerable variability within *Tridax* itself. *Bebbia* can be readily distinguished from both *Tridax* and *Dyscritothamnus* by the several characters listed in Table 1.

A chromosome number of  $2n = 9$  II has been consistently reported for the 3 taxa in *Bebbia*: *B. atriplicifolia* (Turner et al., 1973), *B. juncea* var. *juncea* (Turner et al., 1973), and *B. juncea* var. *aspera* (Powell and Turner, 1963; Solbrig et al., 1972; Sonora, Guaymas, *M. Whalen* 195, TEX). Chromosome numbers also support an affinity of *Bebbia* with the Galinsoginae and Neurolaeninae, genera of which are primarily based on  $x = 8$  and 9 (Stuessy, 1977). Chromosome counts for *Dyscritothamnus* have not been reported. *Tridax* has base chromosome numbers of  $x = 9$  and 10 (Powell, 1965).

## TAXONOMIC TREATMENT

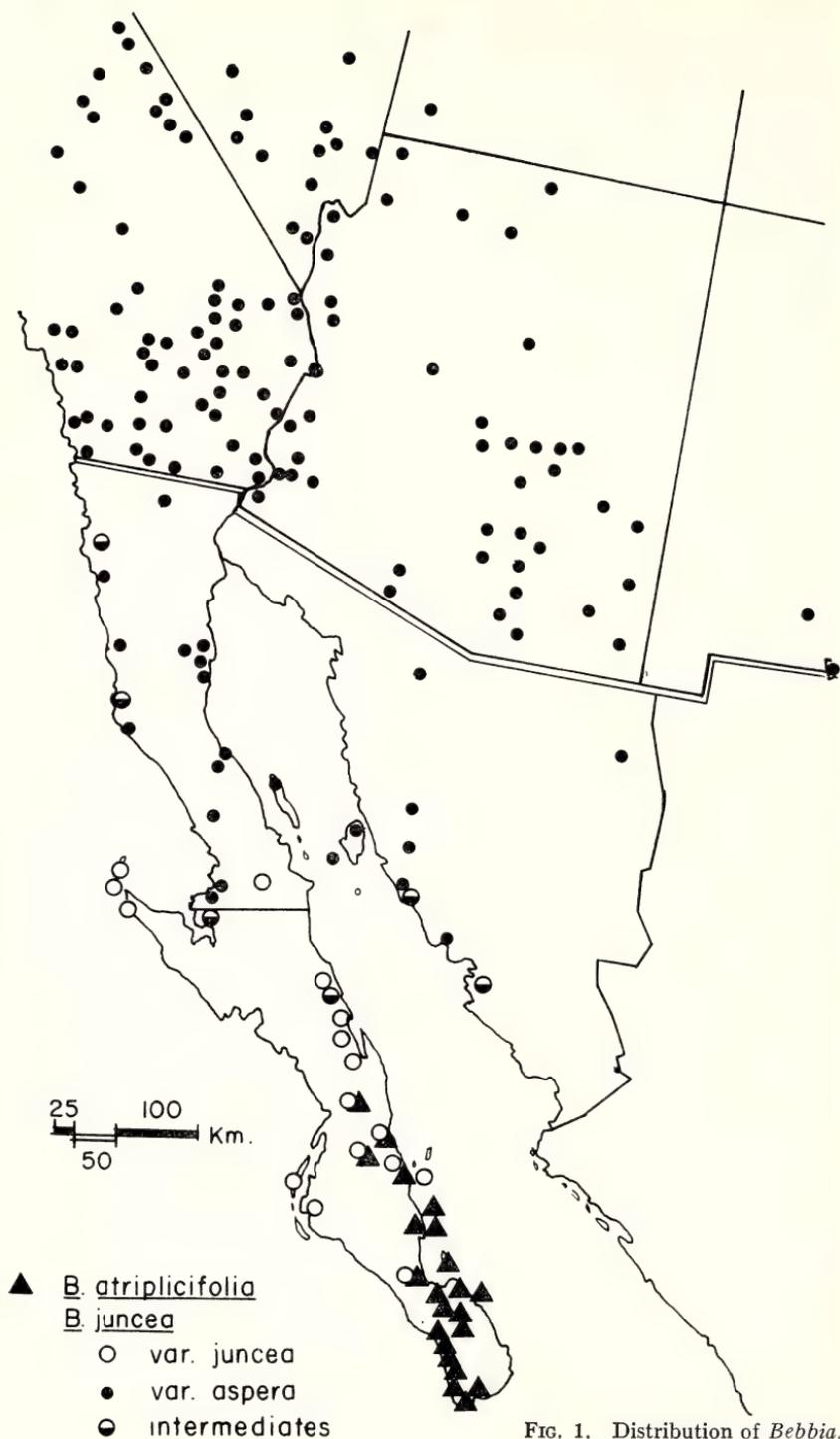
*Bebbia* was originally proposed by Greene (1885) to house 2 species: *B. atriplicifolia* and *B. juncea*, the latter containing 2 varieties. I. M. Johnston (1924) subsequently reduced *B. atriplicifolia* to a variety of *B. juncea*. For the reasons discussed below, I believe Greene's original treatment delimits better the natural taxa within *Bebbia*.

BEBBIA Greene, Bull. Calif. Acad. Sci. 4:179. 1885.—*Carphephorus*, sect. *Kuhnioides* Gray, Proc. Amer. Acad. Arts 8:632. 1873. LECTOTYPE (chosen here): *Bebbia juncea* (Benth.) Greene ≡ *Carphephorus junceus* Benth.

Perennial, strongly-scented, often leafless shrubs, low and spreading with upright annual branches or forming dense, rounded masses; the root thick, fusiform, woody, 1–5 cm in diameter (the basal portions with gray fissured bark); stems ribbed, glabrous or pubescent, leaves sparsely to moderately pubescent, sessile or petiolate, opposite throughout or opposite below and alternate above, blades linear to triangular and lobate, the margins entire to laciniately dentate; hairs of stems, leaves, and involucre simple, white, tuberculate-based, antrorsely-curved, 0.1–0.6 mm long (sometimes interspersed on the peduncle with glandular trichomes); heads discoid, 25–70 florets, campanulate, solitary or forming loose corymbose capitulescences; receptacle convex, chaffy; chaff 5.0–8.5 mm long, scarious, stramineous with red-orange striations and sometimes red-tipped, persistent, lanceolate, partly enclosing the achene; phyllaries 3–5 seriate, graduate, striate, unequal in length; outer series pubescent, herbaceous with chartaceous margins, inner series longer, becoming more glabrous and chartaceous; disk florets regular, the corolla 6.5–10.0 mm long, having a short glandular tube 1–2 mm long, a narrowly funnelform limb, and 5 broadly ovate, pubescent lobes; style branches ca 2 mm long, slender, exserted, recurved, with stigmatic lines on the inner surface running from base to tip; anthers linear-ob lanceolate, tapered to the base and with ovate-acute apical appendages ca 0.5 mm long; achenes 2.0–3.5 mm long, compressed, 3-angled, obliquely clavate with evident epigynous disk, black when mature, pubescent with ascending white hairs 0.2–0.6 mm long; pappus uniseriate, of 15–30 slender, white, subequal, plumose bristles as long as or longer than the corolla; base chromosome number,  $x = 9$ . (Figs. 1, 2).

Key to taxa of *Bebbia*

Leaves without distinct petioles, the blades narrow, linear to linear-ob lanceolate, entire or with one to a few lobes; peduncles and outer phyllaries without glandular hairs; perennial shrubs forming globose masses; heads solitary or few-clustered in loose corymbs borne on long branches. . . . . 1. *B. juncea*.



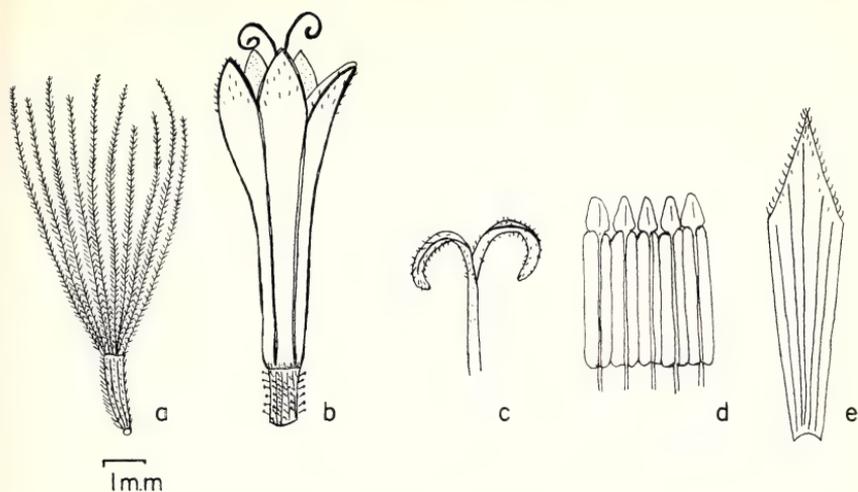


FIG. 2. Representative floral sketches of *Bebbia* (from *B. juncea* var. *aspera*, Clokey 8192, TEX). a, disc achene. b, disc corolla. c, style branches. d, stamens. e, chaff.

Involucral bracts imbricate and obtuse, rounded or mucronate, not acute; outer phyllaries ovate, 1–3 mm long, 1–4 mm wide, usually as wide as or wider than long; heads usually solitary, sometimes borne in a small corymb; central and northern Baja California. . . . . 1a. *B. juncea* var. *juncea*.

involucral bracts acute and not markedly imbricate; outer phyllaries narrow, lanceolate, longer than wide, 1–3 mm long, 0.7–1.5 mm wide; heads solitary or more often in open corymbs of a few heads; northern Baja California, Sinaloa, Sonora, and southwestern United States . . . . . 1b. *B. juncea* var. *aspera*.

Leaves with distinct petioles, blades hastate to lacinate-triangular with coarsely dentate margins; peduncles and outer phyllaries with glandular hairs; plants clambering, flat-topped, often scandent or semi-scandent on shrubs, trees, or rocks; capitulescence usually of many heads clustered in a compact corymb on short peduncles ca 1.5 cm in length; southern Baja California . . . . . 2. *B. atriplicifolia*

1. *BEBBIA JUNCEA* (Benth.) Greene, Bull. Calif. Acad. Sci. 4:180. 1885.—*Carphephorus junceus* Benth., Bot. Voy. Sulph. 21. 1884.—TYPE: Mexico, Baja California, Magdalena Bay, 1844, *Hinds s.n.* (Holotype: K, not seen; photograph of holotype, GH!).

*Bebbia filifolia* Jones, Contr. West. Bot. 18:80. 1933.—TYPE: Mexico, Baja California, Loreto, Cayuca Ranch, 23 Oct 1930, *Jones 27783* (Holotype: CAS!).

Perennial shrub with a dense crown of intricately branched, nearly leafless stems forming a rounded bush, 0.5–3.0 m high; upper stems lithe, woody, glabrous to hispidulous-pubescent, divergent at an angle of (10)30–45(55) degrees; leaves sessile, opposite below, alternate and often reduced to subulate bracts above, the blades narrow, linear to linear-oblongate, entire or with 1–5 deltoid to linear lobes, 0.5–6.0 cm long, 1–6 mm wide, moderately pubescent to canescent; peduncles 1.5–10.0 cm long, pubescent with simple, white trichomes; heads solitary or in small corymbs (2–5 heads) borne on the upper branches which are 5–8 cm long; outer phyllaries canescent; corollas yellow.

DISTRIBUTION (Fig. 1): Mostly in the Sonoran desert of northwestern Mexico and adjacent southwestern United States.

Blake (1945) took *B. filifolia* to be synonymous with *B. juncea*, i.e., he noted Jones' type specimen to be "*B. juncea* approaching var. *aspera*". The type of *B. filifolia*, however, appears to belong to *B. juncea* var. *juncea* since it has the more imbricate involucre and mucronate or rounded phyllaries characteristic of this taxon and was collected south of Comondu in the southern part of the range of var. *juncea*.

1a. *BEBBIA JUNCEA* (Benth.) Greene var. *JUNCEA*.

Bush 1–3 m high; stems smooth, glabrous to lightly pubescent; heads usually solitary, 1.0–1.7 cm long, 1.1–2.0 cm wide; phyllaries strongly imbricate in 3–5 series, obtuse, rounded or mucronate; outer bracts ovate, farinose, 1–3 mm long, 1–4 mm wide, usually as wide as or wider than long; inner bracts longer, narrower, 1–3 mm wide, 1.5–6.0 mm long, usually longer than wide (Figs. 3, 4a, 4b).

DISTRIBUTION (Fig. 1): Baja California from El Pilar (24°28'N) to Cedros Island (28°23'N), both on the peninsula and on islands offshore. Common on rocky or sandy soil between 5 and 1000 m, usually in washes and arroyos but also in the open desert. Flowering year round.

Plants of var. *juncea* collected south of Muleje, in the area of the type locality, have fewer (15–20) and broader phyllaries than those of plants to the north, which have 20–30 bracts per head. The leaves also tend to be larger in the southern forms. Heads of plants collected from basaltic cliffs of the Sierra Giganta above Pt. Escondido are particularly large, when pressed 2.5 cm wide and 1.3 cm long, with 50–60 florets per head.

1b. *BEBBIA JUNCEA* var. *ASPERSA* Greene, Proc. Calif. Acad. Sci. 4:180.

1885.—*Bebbia aspera* (Greene) A. Nels., Bot. Gaz. 37:273. 1904.—

TYPE: Greene cited "southeastern borders of California, and adjacent Arizona". Neotype (chosen here): United States, Arizona, Greenlee Co., mountains near Clifton, 3 Sep 1880, *E. L. Greene s.n.* (NY!).

Bush 0.5–1.5 m high; stems smooth and lightly pubescent or more pubescent and hispidulous; peduncles 1.5–6.0 cm long; heads 0.4–1.7 cm long, 0.4–2.0 cm wide, solitary or clustered in loose corymbs (2–5 heads) borne on long upper stems; involucre bracts in 2–4 series, weakly imbricate and acute; outer bracts narrow, lanceolate, canescent,



FIG. 3. Habit sketch of *Bebbia juncea* var. *juncea* (T. S. Brandegee s. n., UC).

1–3 mm long, 0.7–1.5 mm wide, usually longer than wide; inner bracts narrow, linear, longer, usually 3–7 mm long, 0.7–2.0 mm wide (Figs. 2, 4c).

**DISTRIBUTION** (Fig. 1): Northern Baja California, Sonora, and Sinaloa; southern California, Nevada, Arizona, southwestern Utah, New Mexico, and far western Texas where it is rare in the Franklin Mountains near El Paso. Common on rocky or sandy soil between 15 and 1450 m; in washes, canyons, and rocky stream beds in the desert, and on dry hillsides and gravel slopes. Flowering most of the year.

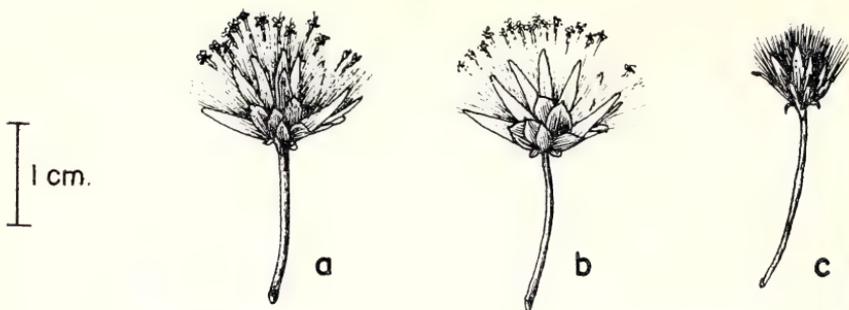


FIG. 4. Heads of *Bebbia juncea*. a, *B. juncea* var. *juncea* from the northern part of its range (A. L. Haines s. n., UT). b, *B. juncea* var. *juncea* from south-central Baja (Mason 1895, US). c, *B. juncea* var. *aspera* (Clokey 5948, UT).

Nelson (1904) elevated *Bebbia juncea* var. *aspera* to specific rank for the following reasons: "I believe that no one who will take the trouble to compare the description of *B. juncea* from Cedros Island, which furnished the type, with the full description of the inland forms will question their distinctness." Geographical intergrades between vars. *juncea* and *aspera* link the two taxa. Therefore, I agree with Greene that this taxon should be treated as a variety and not as a distinct species. Morphological intermediates are designated on the distribution map (Fig. 1).

Imbrication and shape of the involucre bracts, and *not* stem pubescence or size and number of heads, which Greene used to delimit the two varieties, are the most reliable characters in distinguishing these two taxa. Roughness of the stems is particularly variable. Plants of both varieties in Mexico have smooth, glabrous or almost glabrous stems, while in the United States plants may be smooth or rough-stemmed. There is a general trend for plants of var. *aspera* in the northern part of its range to be more hispid and to have smaller, more numerous heads, which are usually not solitary, but rather are borne in few-headed corymbs. Plants from Sonora and Sinaloa are closer to var. *aspera*, but occasionally approach var. *juncea*, especially in characters of the involucre.

2. *BEBBIA ATRIPLICIFOLIA* (Gray) Greene, Bull. Calif. Acad. Sci. 4:181. 1885.—*Carphephorus atriplicifolius* Gray, Proc. Amer. Acad. Arts 5:159. 1859.—*Bebbia juncea* var. *atriplicifolia* (Gray) I. M. Johnston, Proc. Calif. Acad. Sci., IV. 12:1197. 1924.—TYPE: Mexico, Baja Calif., Cape San Lucas, Aug 1859—Jan 1860, *L. J. Xanthus* 47 (Holotype: GH! Isotype: US!).

Plants with a stout woody base, forming dense, intricate, sprawling, flat-topped masses, 0.5–3.0 m wide, self-supporting or supported by other shrubs; stems brittle, pubescent, upper stems divergent at an angle of 40–85 degrees; leaves opposite, with distinct petioles, 3–17 mm long, blades hastate to triangular, 2.5 cm long, white tomentose, with coarsely dentate margins; capitulescence projecting above the plant, corymbose



FIG. 5. Habit sketch of *Bebbia atriplicifolia* (Carter 2261, UC).

with a clearcut branching system of usually 5–25 heads clustered on short peduncles; peduncles 0.3–4.0 cm long, on the average 1.5 cm in length, with stalked, glandular hairs and simple trichomes; heads 0.9–2.0 cm long, 1.0–2.5 cm wide with involucre bracts broadly acute, in 2–4 series, not markedly imbricate; the outer rows herbaceous, 1.3–5.0 (–7.0) mm long, moderately pubescent with both simple and glandular hairs; inner rows more chartaceous and glabrous with the innermost bracts 4–9 mm long; involucre bracts and chaff often red-tipped; corolla yellow-orange to orange-red (Fig. 5).

**DISTRIBUTION** (Fig. 1): Common in gravelly or sandy soils between 5 and 1450 m from the southern tip of Baja California at Cape San Lucas north to Comondu ( $26^{\circ}03'N$ ); in washes and on dunes and granitic bluffs near the ocean, also frequent in arroyos and on rocky hillsides. Flowering year round.

Plants of this species are larger-headed to the north. At the southern margins of its range the heads of *B. atriplicifolia* have from 25–30 florets with average head size 1.3 cm long by 1.2 cm wide. At the northern extreme of its distribution, large-headed forms occur with from 35–60 florets per head and a usual head size of 2.5 cm long and 1.2 cm wide.

I. M. Johnston reduced *B. atriplicifolia* to varietal rank because "Although the two forms [*B. atriplicifolia* and *B. juncea*] seemed distinct in the field, a study of the material in the Brandege Herbarium has seemed to substantiate Mr. Brandege's statements (Proc. Calif. Acad. Sci. II, 2:180. 1889, and Zoë 1:271. 1890) that the forms approach each other too closely" (Johnston, 1924). These plants would appear more distinct in the field because they differ in habit. Furthermore, based on my study of herbarium material, including that from the Brandege Herbarium, the two taxa appear to be good species readily distinguishable by their habit, characters of the leaves and inflorescence, and the presence or absence of glandular hairs on the peduncles. The range of *B. atriplicifolia* overlaps in central Baja California with that of the more northerly *B. juncea* var. *juncea*, and the two have been collected in close proximity at four different localities. No sign of morphological intergradation can be inferred from herbarium material from these sites.

Brandegee (1889) reports finding connecting forms between *B. juncea* and *B. atriplicifolia* at Comondu and San Gregorio in Baja California. He distinguishes between the two taxa solely on the basis of ovate versus acuminate involucre bracts and lanceolate versus triangular leaves. The shape of the bracts will not differentiate between *B. juncea* as a whole and *B. atriplicifolia*. However, the characters listed in the present key easily separate the two taxa.

#### ACKNOWLEDGMENTS

I am grateful to the curators and staffs of the following herbaria for loans of specimens. The number of specimens borrowed from each institution is given in parentheses: CAS (65), GH (110), MO (67), LL (32), ND (15), NY (120), TEX (26), UC (161), and US (124). I am indebted to B. L. Turner for guidance in the completion of this study, and along with Roger Sanders and M. D. Whalen, for critically reading the manuscript.

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#### NOTES AND NEWS

THE "GERMINATION FLAP" IN CERTAIN GRAMINEAE.—In a recent paper (Madroño 23: 68–72. 1975), T. L. Rost & A. D. Simper report on "the germination lid" and its occurrence on lemmas of grasses. The statement is made that this structure was first observed in *Setaria* in 1949 by Keys (*Trans. Kansas Acad. Sci.* 52:474–477). This is quite incorrect. Hitchcock & Chase as long ago as 1910 recognized this feature and commented on it in their monograph of *Panicum* (*Contr. U.S. Nat. Herb.* 15: XIV + 396 pp). On page 18 they state, "fertile lemma chartaceous-indurated, typically obtuse, the nerves obsolete, the margins inrolled over an inclosed palea of the same texture, a *lunate line of thinner texture at the back just above the base, the radicle protruding through this at germination;*" (italics mine). That this "germination lid" was recognized as being characteristic of *all* genera of Paniceae by Hitchcock & Chase is indicated by the statement under the Tribe Paniceae, on page 26 of Hitchcock's Manual (U.S. Dept. of Agric. Misc. Publ. 200. 1935): "fertile lemma and palea indurate or at least firmer than the glumes and sterile lemma, a lunate line of thinner texture at the back just above the base, the rootlet protruding through this at germination."

Rost & Simper mention also that there is some question regarding the systematic position of *Antheophora* and *Olyra*. Although this might have been true several years ago, it is certainly not so today. Fifteen years ago, I published a detailed study of *Antheophora* (Reeder, J. R. in *Trans. Amer. Microscop. Soc.* 79:211–218. 1960) which left little doubt that this genus is a member of the Tribe Paniceae,

most closely related to *Cenchrus*. With respect to *Olyra*, the evidence is overwhelming that this genus is bambusoid. In 1947, Virginia Page (Bull. Torrey Bot. Club 74:232-239) demonstrated convincingly that the leaf anatomy of this genus is of the bamboo type. My investigations of the embryo (Amer. Jour. Bot. 44: 756-768, 1957) indicate that the affinities of this genus are bambusoid. The embryo in the Paniceae is very different. Most students of the Gramineae agree that the embryo characters give perhaps the most powerful evidence regarding affinities of genera in this group. Another indication that *Olyra* is bambusoid comes from cytology. Chromosome counts of *O. latifolia* by Reeder et al. (Taxon 18:441,442, 1969) and by Pohl & Davidse (Brittonia 23:293-324, 1971) gave  $2n = 22$ ; *O. yucatanana* was found to have this same number by Tateoka (Bull. Torrey Bot. Club 89:77-82, 1962); and  $2n = 22$  was also reported in *O. lorelensis* by Gould & Soderstrom (Canadian Jour. Bot. 48:1633-1639, 1970). This chromosome information supports the contention that *Olyra* has bambusoid affinities. Basic numbers of  $x = 12$  or  $11$  are usual among bamboos and their kin, whereas  $x = 9$  or  $10$  is characteristic of the Paniceae.

Another character of considerable importance in grass taxonomy is the hilum. In all members of the Paniceae, this structure is punctate; in Bambuseae it is linear. Examination of "seeds" of *Olyra* shows a hilum which is distinctly linear, clear evidence that this genus was wrongly placed in the Paniceae by Hitchcock & Chase. According to R. W. Pohl (pers. comm.) another bambusoid grass, *Streptochaeta*, has a distinct "germination flap" on the fertile lemma.

To suggest that *Olyra* belongs in the Paniceae merely because it has a "germination lid," and to ignore the other overwhelming contrary evidence is certainly naïve. This sort of reasoning led agrostologists of the past to group *Eragrostis* with *Poa*. A more satisfactory explanation for the occurrence of a "germination lid" in panicoid genera and in *Olyra* would seem to be not that this indicates close phyletic relationship, but rather that it is a case of parallelism. If the caryopsis is tightly enclosed within an indurated lemma and palea, there must be a means for the rootlet of the embryo to emerge at germination if the seedling is to become established. One would expect natural selection to favor those plants which developed a weak spot ("germination flap") directly above the position of the rootlet. The enhanced germination would permit an increased number of offspring.—JOHN R. REEDER, Department of Botany, University of Arizona, Tucson 85721.

#### REVIEW

*Marine Algae of California*. By ISABELLA A. ABBOTT and GEORGE J. HOLLENBERG. 827, 701 figs. Stanford University Press, Stanford, California 94305. 1976. \$22.50.

The publication of this massive contribution has been awaited eagerly by marine phycologists in California and elsewhere. The authors are noted for their major contributions to the systematics and morphology of Pacific marine algae. In some respects the book's format is similar to that of Smith's *Marine Algae of the Monterey Peninsula* published in 1944 which it now supplants. MAC, however, contains a number of very important features not present in Smith.

The extensive introduction has information on classification, form and physiology of marine algae, a brief geographical treatment of the California coast with simplified maps indicating major coastal landmarks and suggestions about techniques for collecting and preparing specimens. Following the introduction is one of the book's highlights—a 25 page account by G. F. Papenfuss entitled *Landmarks in Pacific North American Marine Phycology*, which emphasizes the early expeditions and botanists who provided our first knowledge of the remarkable flora on this coast. It includes photographs of several of the more noted phycologists associated with the flora, memorable anecdotal information about many, as well as mention of algal taxa named in their honor.

The main text of the book is divided into four sections treating the genus *Vaucheria* (Chrysophyta), and the phyla Chlorophyta, Phaeophyta and Rhodophyta. Keys and descriptions for the orders, families, genera and species are included. Illustrations of each species are on the page adjacent to its description. The main text is followed by a master dichotomous key to the genera of the three major phyla, a glossary, literature cited, and a taxonomic index.

In the preface the authors explain their rationale for the book's format and content. It is intended to serve as a manual for identification by students with minimal training in lower plant biology. Conservation of space was essential to keep the number of pages and price to a minimum. Consequently, descriptions are "concise", generally having somewhat less information than those in Smith. The authors chose 1972 as the cutoff date for changes and additions in the manuscript. As a result of this, new taxa, additions to the flora and nomenclature changes published since 1972 are not included.

Perfection is an elusive quality, seldom achieved, and although the book is a remarkable achievement it is not perfect. I would like to point out a few of its imperfections and positive features.

In the introduction (p. 7) several questionable statements are made. First, the authors state:

"The geographic area whose algal population is most like that of California is Japan. The marine flora of Northern Honshu and Hokkaido would seem very similar to a Californian . . . It is estimated that about 30-40 percent of the species occurring in California may also be found in Japan. This is a larger percentage than a comparison of California with the North Atlantic would realize, though temperature barriers in the Pacific are no less formidable as obstacles than the land barriers separating California from the Atlantic."

The figure of 30-40 percent species shared in common is a gross overestimate. Hommersand (1972, Proc. Intern. Seaweed Symp. 7:66-71) very generously estimates that perhaps 110 species are common to both California and Japan. This is only 16% of the 669 species listed in MAC. A more realistic figure based on hardcore evidence might reveal less than 10% are common between the two areas. Their statement that temperature barriers are no less formidable obstacles than land barriers cannot be taken seriously. Many temperate and cold water marine algae can withstand wide ranges in temperature (5-20°C) for several days or weeks and still remain viable. This seems a sufficient time for drift algae to be transported short distances and allows for progressive establishment along a coast line. Moreover, they apparently do not consider the possibility that migration of certain species may have occurred at times when water temperature patterns differed from those of the present, nor do they consider the possible involvement of continental drift in species distribution.

In the last paragraph on page 7 the authors state:

"Although California and Japan share many genera, there are usually larger numbers of species in given genera on one side of the Pacific than on the other, implying genetic if not ecological diversity. One genus, *Laurencia*, has 12 eastern Pacific species and 23 western Pacific species."

This is an unreasonable comparison because *Laurencia* is principally of tropical and subtropical distribution. In these particular ocean temperature zones there is a vastly greater coast line in the western Pacific than in the eastern Pacific. The greater number of habitats in the western Pacific should permit a greater species diversity. By contrast the coast line in temperate and colder water zones is closer to being

equal. Surprisingly, the authors do not consider upwelling as one of several possible factors influencing species diversity, yet that is one of the factors considered by zoogeographers in explaining the greater diversity of the Pacific North American biota relative to the Atlantic North American biota.

The integration of illustrations with species descriptions, the generally high quality of reproduction of the figures, the illustration of every species and most subspecific taxa included as well as the use of figures to show important diagnostic characters are all very useful features which make this flora vastly superior to others I have used. However, there are also a number of problems in regard to the figures. The single most cumbersome and time-consuming aspect is that the figure numbers are not directly next to the figure (although each figure in a composite plate is identified in the caption by a number and its position on the page, e.g., lower right, upper center). Moreover, figure numbers are not cited with the species descriptions. For rapid accurate reference it is essential that figure numbers be placed immediately next to the figure and, what is especially important, that they be cited in the description for each species. The captions generally fail to identify the types of reproductive structures illustrated. For the inexperienced student, to whom this flora is especially directed, these deficiencies could be very troublesome and frustrating.

In Fig. 23 (*Lithothamnion californicum*) the caption identifies the figure as a section through a tetrasporangial conceptacle, yet the figure shows binucleate bisporangia. Tetrasporangia but not bisporangia have been reported for this species. For Fig. 156 (*Punctaria hesperia*) the caption indicates that only the "unangia" are illustrated but "plurangia" are also present in the figure. Fig. 310 and Fig. 311 were transposed (Abbott, personal communication). Fig. 310 is of *Peyssonnelia rubra* var. *orientalis* instead of *P. profunda* as indicated in the caption. Surprisingly, the description of *P. rubra* var. *orientalis* does not refer to the zonately divided sporangia of this taxon, a unique character among the California species of *Peyssonnelia*. This would have been useful as a keying character and should have been mentioned in the generic description as an exception to the cruciately divided sporangia.

I should note here that misspellings are very infrequent but one is *Peyssonelliaceae* and *Peyssonellia* (sic). The accepted spelling is *Peyssoneliaceae* and *Peyssonellia*.

Some descriptions tend to be incomplete or inaccurate with respect to information on reproduction. For example, that of *Farlowia* includes a description of tetrasporangia, the implication being that tetrasporophytes and gametophytes are isomorphic. This report of tetrasporangia is based on Abbott's description of tetrasporangia in *Leptocladia conferta* which she transferred to the genus *Farlowia* in 1968 (J. Phycol. 4:180-98). However, tetrasporophytes are not recorded for any other species of *Farlowia*. It may be possible to return *F. conferta* to *Leptocladia* on this basis, although the female reproductive structures of *F. conferta* are more similar to those of *Farlowia* than of *Leptocladia*. It appears that California species of the crustose genus *Cruoriopsis* may be the tetrasporophyte for at least two species, *F. compressa* and *F. mollis* (DeCew and West, unpublished observations). In contrast, the description for *Gymnogongrus* states correctly that a tetrasporangial phase is unknown in certain species.

The red algal genus *Besa* was placed in the Phylloporaceae, although it is traditionally placed in the Gigartinaceae. The authors do not explain the basis for this transfer.

The northern limit of the geographic range for *Pachydictyon coriaceum* is given as Cape Arago. This is, however, based on confusion in identification and synonymy discussed by Dawson (1950, Wassman J. Biol. 8:267). The taxon involved is *Dictyota bringhamiae*. Furthermore, the description of *P. coriaceum* in MAC indicates that the thalli are 400-500  $\mu$ m thick, yet the scale shows a maximum thickness of 300  $\mu$ m in the specimen illustrated.

The authors state on page 119 that:

"Scagel (1960) and Chihara (1960) indicated the "*Collinsiella*" may be a stage in the life history of a species of *Enteromorpha* and/or *Monostroma*."

It is correct that Scagel considered *Collinsiella* as a stage in the life history of *Enteromorpha*, but Chihara's work in no way suggests this. The three species investigated by Chihara have multicellular gametophytic stages which are cushion-shaped or open sacs whereas the sporophytic stage is a unicellular "zygocyst" resembling *Gomontia*. Nowhere does Chihara state that *Collinsiella* is a stage of *Monostroma*, although it is known that *Gomontia*-like stages occur in the life histories of some species of *Monostroma*.

In general the keys seem quite workable and are less troublesome than many of those in Smith. However, it should be noted that the second part of the third dichotomy of the green algae key (p. 748) is incorrect and confusing. The genera of the Prasinophyceae, Chaetophoraceae, Ulvaceae, Ulotrichaceae and Monostromataceae to which this choice leads are certainly not coenocytes.

The use of quotation marks with "Chlorochytrium" (dichotomy 30 of the master key of green algae) implies that the authors do not accept the genus as being taxonomically valid, probably because *C. inclusum* was shown to be the sporophytic stage of a species of *Spongomorpha* by Chihara (1969, *Phycologia* 8:127-33) and other workers. However, this does not invalidate the genus because the life histories of the type species, *C. lemnae* (an endophyte of *Lemna* in freshwater), and other species, including *C. porphyrae* have not been investigated yet.

The first dichotomy of the *Acrochaetium* key (p. 309) does not enable one to identify *A. rhizoideum* because the erect filaments are considerably longer than the endophytic system. In addition, the illustration of *A. rhizoideum* (Fig. 260) does not show the diagnostic feature of the species, namely the numerous pyrenoids in each cell. Other California species lack a pyrenoid or have a single pyrenoid per cell.

Although there are minor deficiencies such as those mentioned above, the *Marine Algae of California* is exemplary in its overall quality and will serve phycologists well for many years. The authors and publisher should feel pleased with their efforts.—JOHN A. WEST, Department of Botany, University of California, Berkeley 94720.

#### REVIEW

*The Tactless Philosopher. Johann Reinhold Forster (1729-1798)*. By MICHAEL E. HOARE. x + 419, 13 illus. Hawthorne Press, Melbourne, Australia, 1976. \$15.95. Austr.

The author citation "Forst." (or more accurately Forst. & Forst. f.) is unfamiliar to most California botanists. However, *Dichondra* is one of their 75 new genera published in *Characteres genera plantarum* (1776), which included the first description of New Zealand plants, Queen Charlotte Sound being the probable source of *Dichondra repens*. The want of a "full-length biography" was noted by Michael Hoare in his sketches of the Forsters, father and son, in *Dictionary of Scientific Biography* (1972). Now this thoughtful, accurate, and attractive account of the foibles and fortunes of a fumbling Forster of two centuries ago is highly recommended.

E. D. Merrill was Forster's "most trenchant critic" of botanical matters. His condemnation of Forster's use of Solander's generic names is, in Hoare's opinion, unjustified and could not have rested on access to the Banks and Solander specimens

and manuscripts after Cook's Second Voyage (1772-1775). "No such hint or statement appears in even the most private correspondence" (p. 139), Hoare adding, "to argue, as Merrill does, that either Forster depended upon Solander's knowledge and experience for their botany is absurd. Forster admired the Swede's abilities and intellect but scarcely felt beholden to him."

Armchair navigators with Capt. Cook will find Hoare's biography of Forster high adventure. The story tells of New Caledonian "Cookpines," actually *Araucarias*, mistaken at first by Forster for basalt columns; of Tahiti where the natives named him *Fatara*; and much more. There are notes on the Americans, *Mannasseh Cutler* and *Samuel Vaughan*, watching for locally published travel narratives that Forster might translate; on *Dr. Lettsom* and *Thomas Pennant* in England; and on *Kurt Sprengel* who was at Forster's deathbed on December 9th, 1798, in Halle. Today the graceful Forster's Tern; a popular dining-hall palm, *Howea forsterana*; the lowly perennial New Zealand genus *Forstera*; and, of all things, a short street in the Fijian town of Suva are visible memories.—JOSEPH EWAN, Department of Biology, Tulane University, New Orleans, La. 70118.

#### REVIEW

*A Gazetteer of the Chihuahuan Desert Region.* By JAMES HENRICKSON and RICHARD M. STRAW. xxii + 272 pp., incl. 18 maps. Published by the authors. 1976. Available from Dr. J. S. Henrickson, P.O. Box 8495, University Station, Austin, Tex. 78712. \$12.00 incl. postage; in Texas add applicable sales tax. [Note: A complimentary copy of "Maps of the Chihuahuan Desert Region" (49 pp., offset, 43 by 28 cm.) compiled by José Garcia will be sent with each gazetteer.]

This gazetteer is coordinated with and is intended to be a supplement to M. C. Johnston's work toward a flora of the Chihuahuan Desert Region (CDR). As delimited for floristic treatment, CDR is the plateau between Sierra Madre Oriental and Sierra Madre Occidental extending from ca 34° N in SE Arizona and S New Mexico to ca 22° N in N Guanajuato and S San Luis Potosi.

The nearly 23,000 entries include place-names for natural (sierras, passes, canyons, lakes, streams) and man-made (cities, villages, ranches, railroad stops, reservoirs) localities. Each entry includes information as to type of locality (pass, village, lake, etc.), state, latitude, longitude, elevation (in meters), source, and serial number. Some peripheral, non-desert place-names are included. Sources of names include numerous maps and published records. The computer programs used in producing the gazetteer allow extraction of partial or alternate listings such as listings by elevation or latitude or listings for subregions within CDR.

The gazetteer includes maps showing county or municipio boundaries for all states in or bordering CDR. The topographic maps (from U.S.G.S. for United States and A.M.S. for Mexico) compiled by Garcia are well reproduced and provide a very useful and welcome supplement.

This compilation of information about CDR will be invaluable to naturalists concerned with the area.—JOHN L. STROTHER, Botany—Herbarium, University of California, Berkeley 94720.

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# MADROÑO

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TAXONOMY OF CHRYSACTINIA, HARNACKIA, AND  
LESCAILLEA (COMPOSITAE: TAGETEAE)

JOHN L. STROTHER

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Taxa reviewed here are remarkably diverse morphologically, still they form a close, and probably long-distinct, alliance. They are distinguished from other members of Tageteae by the following combination of characteristics:

- 1) Involucres turbinate to hemispheric, usually ecalyculate;
- 2) Phyllaries free to base, narrowly ovate to linear,  $\pm$  carinate, persistent in fruit;
- 3) Heads radiate (except *Lescaillea*);
- 4) Pappus of 20–40 bristles, free to the base; and
- 5) Style branches (disc florets) well-developed and stigmatic almost to the truncate-rounded apex.

These plants have received little attention outside floras or floristic lists. As part of monographic studies in Tageteae, I offer the following key, descriptions, observations, and comments, including accounts of nomenclature, typification, distribution, phenology, and reproductive biology. For poorly known taxa, all specimens seen are cited. For loans or other courtesies, I thank members of the staffs of the following herbaria: A, ASU, C, CAS, DS, E, F, GB, GOET, K, LD, LL, MICH, MO, NMC, NY, P, PENN, PH, POM, RSA, S, SD, SMU, TEX, UC, UPS, US, WIS.

*Chrysactinia* has five species, referred here to three sections. The section with the greatest concentration of primitive character expressions (sect. *Phylloloba*) includes *C. pinnata* and *C. truncata*, which are restricted to Sierra Madre Oriental of Mexico (Fig. 1). Two relatively advanced taxa form sect. *Chrysactinia*: *C. acerosa*, restricted to gypseous soils on western slopes of Sierra Madre Oriental (Fig. 1), and *C. mexicana*, widespread in the Mexican highlands and beyond from Oaxaca to New Mexico and Texas (Fig. 2). *Chrysactinia lehtoae*, which is known from only one locality (northern Sinaloa in Sierra Madre Occidental, Fig. 1), is the sole member of sect. *Tagetifolia*.

*Harnackia* and *Lescaillea* are monotypes endemic to Cuba on serpentine soils (Prov. Oriente and Prov. Pinar del Rio, respectively). *Lescaillea* seems certainly to have been derived from *Harnackia* (or an immediate ancestor) by reduction of leaves and loss of ray florets. *Harnackia* is very similar to *Chrysactinia truncata* with which it must have shared a recent ancestor. These three taxa together with *C. pinnata* are very closely related.

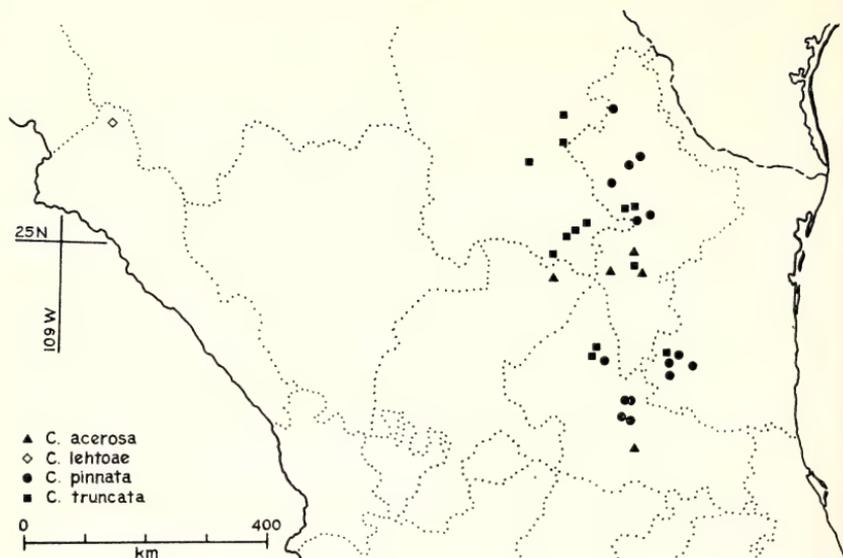


FIG. 1. Distribution of *Chrysactinia* spp.

The Cuban plants probably should be transferred to *Chrysactinia* sect. *Phylloloba*, but they are so little known that I am reluctant to make transfers at this time. An alternative treatment of these four species as a separate genus (*Lescaillea*) seemed appropriate until the recent discovery of *C. lehtoae*, which bridges the considerable morphological gap between sect. *Chrysactinia* and the 'Phylloloba'/Cuban alliance. For the present, a conservative, *status quo* treatment seems preferable.

The relatively restricted and mesic, montane or submontane distributions of *C. lehtoae*, *C. pinnata*, *C. truncata*, *Harnackia*, and *Lescaillea* are interesting in view of the presumably primitive position of these taxa within Tageteae. These may be relictual survivors of taxa delineated early in the history of Tageteae. The nearest allies of these plants are presently referred to *Porophyllum* Guett., which has discoid heads and, for several other characters, differs substantially from taxa treated here. *Nicolletia* A. Gray and *Leucactinia* Rydb. may also belong with this group.

#### Key to *Chrysactinia*, *Harnackia*, and *Lescaillea*

- a. Heads radiate; leaves linear to pinnately divided, not reduced to scales. . . . . b.
- aa. Heads discoid; leaves reduced to short, appressed, opposite scales. . . . . *Lescaillea*.
- b. Erect shrubs or subshrubs; leaves pinnately divided into 3–20 lobes or undivided and linear to acerose (*Chrysactinia*). . . . . c.
- bb. Scandent, suffrutescent plants; leaves pinnately divided into (1–3) linear-cuneate lobes. . . . . *Harnackia*.

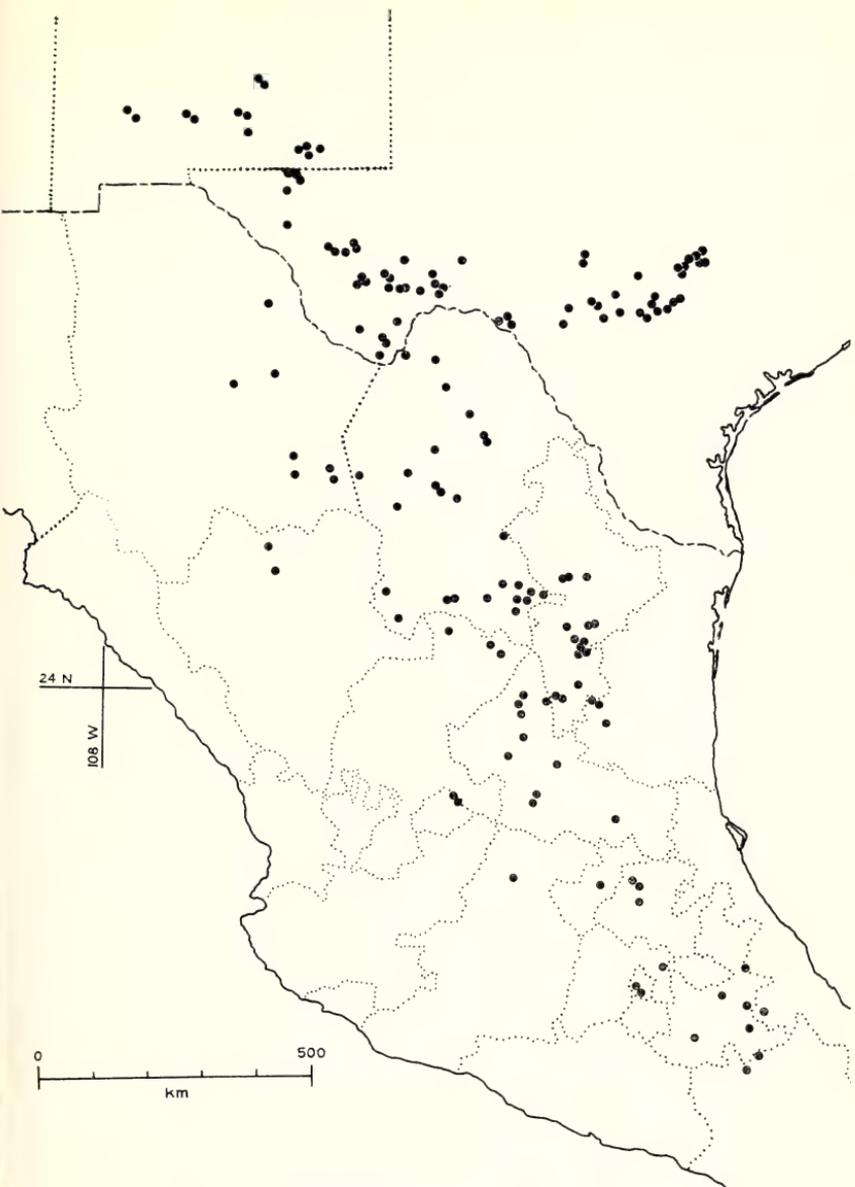


FIG. 2. Distribution of *Chrysactinia mexicana*.

- c. Leaves simple, linear to acerose (*C.* sect. *Chrysactinia*). . . . d.
- cc. Leaves pinnately divided. . . . . e.
- d. Leaves mostly alternate, linear, mostly 1–2 mm wide; phyllaries mostly 13, linear. . . . . *C. mexicana*.
- dd. Leaves mostly opposite, acerose, mostly 0.2–0.4 mm wide; phyllaries mostly 8, ovate. . . . . *C. acerosa*.

- e. Leaf lobes broadly cuneate to obliquely deltoid, 1–4 times longer than wide, bearing a few orange to brownish, pellucid glands (*C.* sect. *Phylloloba*). . . . . f.
- ee. Leaf lobes lance-linear, 8–12 times longer than wide, bearing numerous submarginal, greenish, pellucid glands (*C.* sect. *Tagetifolia*).  
 . . . . . *C. lehtoae*.
- f. Leaf lobes 8–12(–20), obliquely deltoid, acute; phyllaries mostly 8.  
 . . . . . *C. pinnata*.
- ff. Leaf lobes 3–7(–13), cuneate, truncate-apiculate; phyllaries mostly 13.  
 . . . . . *C. truncata*.

CHRYSACTINIA A. Gray, Mem. Amer. Acad. Arts, ser. 2. 4:93. 1849.  
 [Plantae Fendlerianae] TYPE: *Chrysactinia mexicana* A. Gray.

Evergreen, glabrous to puberulent shrubs or suffrutices, mostly 1–8 dm high at anthesis. Leaves opposite or alternate, simple and acerose to  $\pm$  linear or pinnately divided into lobes or leaflets, variously dotted with few to numerous, marginal or submarginal pellucid glands containing strongly scented oils. Heads solitary, terminal, peduncled to sessile. Peduncles slender, glabrous to puberulent, usually bracteolate. Involucres turbinate to hemispheric, 3–8 mm high. Calyculum none. Phyllaries mostly 8 or 13, free to the base, linear to ovate, usually carinate, persistent and remaining erect or becoming reflexed at maturity, usually each bract bearing 1–5 pellucid oil glands. Receptacle slightly convex to hemispheric, alveolate, glabrous or erose-hispid around the sockets, rarely bearing a few slender, deciduous paleae (*C. mexicana*). Ray florets mostly 8 or 13, pistillate, fertile; corollas yellow to orange, laminae mostly narrowly elliptic to linear-ovate. Disc florets 12–50(–70), perfect, fertile; corollas yellow, slender, cylindro-funnelform, glabrous to variously glandular-puberulent, tube much shorter than the throat, lobes 5, deltoid to lanceolate, erect to spreading or reflexed; anthers slender, minutely sagittate, collars 3–5 times as long as wide, apical appendages ovate to lanceolate; style branches often distally papillate-hispidulous, stigmatic almost to the truncate to rounded apex. Achenes slenderly to stoutly cylindric to fusiform, blackish, striate, subglabrous to hispidulous with short, whitish, antrorse hairs. Pappus of 20–40 tawny, free, uniseriate, subequal bristles, mostly longer than the achene.

CHRYSACTINIA A. Gray sect. PHYLLOLOBA S. F. Blake, Proc. Amer. Acad. Arts 51:525. 1916. TYPE: *Chrysactinia pinnata* S. Wats.

CHRYSACTINIA PINNATA S. Wats., Proc. Amer. Acad. Arts 25:154. 1890.  
 TYPE: Nuevo Leon, "On limestone ledges of mountains near Monterey" (Saddle Mountain, near 25°40'N, 100°20'W, cf. Davis, 1936), 28 May 1889, *Pringle 2524* (Holotype: US!; isotypes: BM! DS! E! F! GH! K! MO! NY(2)! PH! UC!).

Shrubs or suffrutices with erect, little branched, slender, terete stems from a rhizomatous(?) base, 6–8 dm high; internodes 25–45 mm long. Leaves mostly opposite, lance-elliptic in outline, 25–45 mm long, coarsely pinnatifid into 8–12(–20) obliquely deltoid, acutely pointed, somewhat coriaceous lobes, most lobes with a dark, pellucid gland in a sinus in the basiscopic margin. Peduncles 30–65 mm long, bearing 3–5 subulate bractlets; heads held well above foliage. Involucres turbinate, 6–8 mm high. Phyllaries mostly 8, narrowly ovate to lanceolate, basally carinate, marginally and distally scarious, each bract usually bearing a subapical pellucid gland and 1–2 pellucid glands near the basal margins. Ray florets mostly 8; corollas with golden yellow tube ca. 3 mm long, lamina narrowly ovate, whitish above, golden orange below, 4–7 mm long, 1.4–1.7 mm wide, narrowed and minutely 3-toothed at apex, glabrous. Disc florets 20–30; corollas orangish yellow, 4–6 mm long, tube 1.1–1.8 mm long, throat 2.2–3.5 mm long, marked with dark nerves below sinuses, lobes 0.6–0.7 mm long, lanceolate to lance-ovate, erect to spreading or reflexed, minutely papillate, throat (distally) and lobes (abaxially) glandular-puberulent; anthers ca. 2.6 mm long including collar (0.4 mm long) and ovate, blunt apical appendage (0.3–0.4 mm long); style branches ca. 1.8 mm long, papillate-hispidulous distally, stigmatic almost to truncate-papillate apex. Achenes 3–4 mm long, narrowly cylindrical to fusiform, blackish, finely striate, sparsely and evenly hispidulous with short, antrorse hairs on the striae. Pappus of ca. 40 fine, tawny, minutely barbellulate, subequal bristles 4–5 mm long.

Distribution (Fig. 1): *Lechugilla/Hechtia* scrub to submontane matorral and pinyon woodlands, mostly on relatively mesic, north-facing limestone slopes, sometimes bordering streams, in Sierra Madre Oriental of Nuevo Leon, Tamaulipas, and San Luis Potosi (ca. 28°–22°30'N); 600–1700 m; flowering May–Jun(–Nov).

CHRYSACTINIA TRUNCATA S. Wats., Proc. Amer. Acad. Arts 25:154. 1890.

TYPE: Nuevo Leon, "Summit ledges of the Sierra de la Silla" (Saddle Mountain, near 25°40'N, 100°20'W, *vide* Davis, 1936), 5 Jun (labels) or 16 Jul (see Davis, 1936) 1889, *Pringle 2601* (Holotype: US!; isotypes: BM! GH! K! MICH! MO! NY(2)! PH! UC!).

Shrubs or suffrutices, compact, much branched, 3(+?) dm high; old stems with thick, corky bark, young stems terete, striate, glabrous; internodes 10–20(–30) mm long. Leaves opposite or alternate, ovate to elliptic in outline, 20–45 mm long, pinnately divided into 3–7(–13) cuneate, entire or coarsely dentate, apically truncate-apiculate lobes, most lobes and some of the distal teeth bearing apical, subulate processes each subtended by a dark pellucid gland. Peduncles 15–30(–65) mm long bearing 3–5 subulate, glandless bractlets; heads usually held well above the foliage. Involucres broadly turbinate, 4–6 mm high. Phyllaries mostly

13, narrowly ovate to lanceolate, carinate, marginally and distally scarios and erose-ciliolate, each bract usually bearing a conspicuous, oval pellucid gland subapically and sometimes 1–2 pellucid glands near basal margins. Ray florets mostly 13; corollas mostly golden yellow, tube 1.5–2.6 mm long, lamina linear, 7–8(–12) mm long, 2(–3) mm wide, apically shallowly 3-lobed, glabrous. Disc florets 35–50; corollas dull yellow, 3.6–6.2 mm long, glabrous, tube 0.6–1.7 mm long, throat 2.4–3.8 mm long, lobes 0.6–1.0 mm long, lanceolate, papillate; anthers 2.3–3.5 mm long including basal collar (0.3–0.4 mm long) and lanceolate to ovate apical appendage (0.3–0.6 mm long); style branches 1.0–1.3 mm long, stigmatic almost to the conspicuously papillate-hispidulous apex. Achenes 2.8–3.9 mm long, weakly prismatic to fusiform, blackish, striate, sparsely hirtellous with subappressed, antrorse hairs ca. 0.1 mm long on the striae. Pappus of 25–30 coarse, tawny, barbellulate, subequal bristles 4–6 mm long.

Distribution (Fig. 1): Chaparral or oak/pinyon woodlands, mostly on relatively mesic north-facing slopes in limestone sierras along eastern border of Chihuahuan Desert, Sierra Madre Oriental of Coahuila, Nuevo Leon, Tamaulipas, and San Luis Potosi (ca. 28°–23°30'N); 1250–2550 m; flowering late May–mid Aug (–Oct).

One collection treated here as *C. truncata* (near 23°23'N, 99°51'W, Johnston *et al.*, 11179, LL) is morphologically anomalous. Leaf form and texture suggest that it may be a product of hybridization between typical *C. truncata* and *C. pinnata*. The latter is known from a nearby locality (near 23°21'N, 99°40'W, Johnston *et al.*, 11162c, LL). Pollen stainability for the aberrant collection is 47%. In four other collections of *C. truncata*, pollen stainabilities range from 79–98%. A fifth collection (near 23°35'30"N, 100°53'20"W, Johnston *et al.*, 11081, LL), has 38% stainability and is morphologically typical *C. truncata*. Pollen stainabilities for five collections of *C. pinnata* range from 84–95%.

**Chrysactinia** A. Gray sect. **Tagetifolia**, sect. nov. TYPE: *Chrysactinia lehtoae* Keil.

A ceteris sectiones *Chrysactinia*e lobis foliorum lanceolato-linearibus et glandulis pellucidis viridulis submarginalibus numerosis punctatis differt.

CHRYSACTINIA LEHTOAE Keil, Madroño 23:374. 1976. TYPE: Sinaloa, 18 mi NE of Coix, near 26°50'N, 108°11'W, 1300 m, 25–26 Nov 1975, Nash, Landye, and Lehto L19551 (Holotype: ASU!).

Shrublets to 3 dm high; young stems terete, dark reddish brown; internodes 12(6–14) mm long. Leaves opposite, lance-elliptic in outline, 25–40 mm long, pinnately divided into mostly 7–9 lance-linear lobes 12–20 mm long, 0.5–1.8 mm wide, bearing numerous, ovate, greenish

pellucid glands along margins at 1–3 mm intervals. Peduncles ca. 2 cm long, bracteolate; heads held scarcely above subtending foliage. Involucres broadly turbinate, ca. 5 mm high. Phyllaries 13, narrowly lanceolate to linear, somewhat carinate, very narrowly scarious-margined, apical margins minutely erose-ciliolate, each bract bearing a prominent pellucid gland subapically and 2–4 inconspicuous, lateral glands near the base. Ray florets 12–13; corollas bright yellow, tube ca. 3.5 mm long, lamina elongate-oblong, ca. 8 mm long, 2.8 mm wide, distally thickened and minutely 3-toothed, tube (distally) and lamina (proximally) sparsely glandular-puberulent; style branches ca. 1.8 mm long, apices papillate, rounded. Disc florets ca. 40; corollas greenish yellow, ca. 5.5 mm long, tube ca. 1.8 mm long, throat ca. 3.2 mm long, lobes ca. 0.6 mm long, deltoid, erect, thickened, minutely papillate, throat and lobes glandular-puberulent; anthers ca. 2.7 mm long including collar (0.4 mm long) and ovate apical appendage (0.4 mm long); styles branches ca. 1.8 mm long, stigmatic almost to papillate, rounded apex. Achenes (immature) ca. 3 mm long, slender, blackish, striate with white, antrorse hairs 0.05–0.09 mm long on the striae. Pappus of 25–30 coarse, tawny, barbellulate bristles 4–5 mm long.

Distribution (Fig. 1): Known only from the type collection.

#### CHRYSACTINIA A. Gray sect. CHRYSACTINIA.

CHRYSACTINIA ACEROSA S. F. Blake, Proc. Amer. Acad. Arts 51:524. 1916. TYPE: San Luis Potosi, Sierra de Guascama, Minas de San Rafael (near 23°13'N, 100°15'W, *fide* Sousa S., 1969), Jun 1911, *Purpus* 5136 (Lectotype [here designated]: US!; isotypes: BM! E! F! GH! MO! NY! UC!).

Compact shrublets 1(–2) dm high; young stems slender, terete, glabrous to minutely puberulent. Leaves mostly opposite, antrorse, acerose (rarely with 1–2 lateral lobes), 4–12 mm long, 0.2–0.5 mm wide, somewhat succulent, pungent-tipped, glabrous to minutely hispidulous, dotted with numerous pellucid glands. Peduncles short (2–15 mm), sparsely glandular-puberulent, usually bearing 1–5 subulate bractlets. Involucres broadly turbinate to campanulate, 3–4 mm high. Phyllaries 8, ovate, carinate, scarious-margined, erose-ciliolate distally, each bract usually bearing a single, ovate pellucid gland subapically, bracts spreading but not reflexed at maturity. Ray florets 7–9; corollas bright yellow, tube ca. 1.2 mm long, lamina linear, 7–8 mm long, 1.5–2.5 mm wide, often with 1–3 orange pellucid glands near the minutely 3-lobed apex, glabrous; style branches unequal. Disc florets 12–15; corollas yellow, ca. 5.5 mm long, glabrous, tube 1.2–1.4 mm long, throat 3.4–3.7 mm long, lobes 0.6–0.8 mm long, lance-triangular, erect, 0–3 bearing orange pellucid glands; anthers ca. 3 mm long including collar (0.5 mm long) and lance-

ovate appendage (0.6 mm long); style branches ca. 1.3 mm long, shaggy-papillate distally, stigmatic almost to the rounded-conical apex. Achenes ca. 2 mm long, stoutly cylindrical, blackish, striate, sparsely hispidulous with short (0.1 mm), antrorse hairs on the striae. Pappus of 20–30 coarse, tawny, scabrelous bristles 4–5 mm long.

Distribution (Fig. 1): Poorly known; gypseous outcrops in desert scrub or pinyon woodlands in mountains of eastern Chihuahuan Desert and southeast in San Luis Potosi (ca. 24°50′–22°20′N).

Specimens seen in addition to types: Nuevo Leon, W of San Roberto Junction, near 24°36′ N, 100°38′ W, 2100 m, 19 Jun 1972 (anthesis), *Chiang et al 8019*, LL. Nuevo Leon, W of Galeana, near 24°41′ N, 100°10′ W, 20 Jun 1972 (anthesis), *Chiang et al. 8038*, LL. Nuevo Leon, 17 mi E of San Roberto Junction then 2 mi S on dirt road, 24 Oct 1970 (anthesis), *Turner and Crutchfield 6321*, TEX. Zaca-tecas, Concepcion del Oro, 2600–2700 m, 18–19 Jun 1934 (anthesis), *Pennell 17431*, NY, US.

CHRYSACTINIA MEXICANA A. Gray, Mem. Amer. Acad. Arts, ser. 2. 4:93.

1849. TYPE: In protologue, Gray cited, "Dry valley west of Saltillo, April; and on high grounds near Buena Vista, May, *Dr. Gregg*. Also at 'Ojo del Agua,' near the city of Mexico? *Dr. Halstead* (in Herb. Torr.)." I have seen specimens labeled as follows: "west of Saltillo" at GH, MO, and NY; "near Buena Vista" at GH, MO, and NY; and "Ojo del Agua" at GH, K, and NY. At GH, the Gregg collections are apparently combined and are associated with a single label, which lists both localities. A small portion of the Halstead material is also mounted on that sheet. Although all these specimens are readily determined as conspecific and likelihood of confusion seems small, I here designate (in spite of questionable locality) *Halstead s.n.* (no date) at GH as lectotype in order to provide a peg on which to hang the name.

*Pectis taxifolia* E. L. Greene, Leafl. Bot. Observ. Crit. 1:148. 1905.

TYPE: New Mexico, Sierra Co., Black Range, Kingston, 5 Oct 1904, *O. B. Metcalfe 1440* (Holotype: US!; isotypes: BM! CAS! E! F! GH! MO! NMC! NY! UC!).

Strict, twiggy shrubs 2–3(–4) dm high; young stems slender, terete, glabrous to puberulous. Leaves mostly alternate, crowded to well-spaced, linear to narrowly oblanceolate or clavate, flattened or subterete and somewhat succulent, 5–10(–23) mm long, mostly 1–2 mm wide, usually apiculate, glabrous to sparsely hispidulous, margins minutely ciliate, conspicuously dotted with greenish pellucid glands near abaxial margins. Peduncles 30–50(15–75) mm long, minutely hispidulous to glabrous, usually bearing 1–7 lance-subulate bractlets; heads usually held well above the foliage. Involucres turbinate to hemispheric, 3.5–5.0 mm high. Phyllaries 13(8–14), linear to lance-linear, often acuminate, carinate, narrowly scarious-margined, ciliate distally, each bract usually bearing a single orange pellucid gland subapically. Receptacle rarely bearing a

few linear-subulate, deciduous paleae (e.g., *Kruckeberg 4746*, UC). Ray florets mostly 13(-8); corollas golden yellow (sometimes drying greenish), tube 1.6-2.5 mm long, lamina oblong to linear, 6.2-11.9 mm long, 1.8-3.6 mm wide, tube (distally) and lamina (proximally) sparsely glandular-puberulent. Disc florets 25-40(15-70); corollas yellow, 4.6-6.9 mm long, tube 1.1-2.6 mm long, throat 2.3-3.7 mm long, lobes 0.7-1.0 mm long, triangular-deltoid, acute or rounded, spreading, papillate, rarely sparsely glandular-puberulent; tube (distally) and throat (proximally) decidedly glandular-puberulent; anthers 1.8-3.3 mm long including collar (0.4-0.7 mm long) and lanceolate to ovate appendage (0.4-0.7 mm long); style branches 1.3-2.3 mm long, stigmatic almost to the papillate-rounded apex. Achenes 3-4 mm long, slender, black, striate, hispidulous with short (0.1-0.2 mm), antrorse hairs on the striae. Pappus of 30-40 coarse, tawny, barbellulate bristles 3.0-5.5 mm long.

Distribution (Fig. 2): Widespread and often common in many vegetation types, mostly on limestone, from southern New Mexico south and east through sierras of central Mexican Highlands to northern Oaxaca (ca. 33°30'-18°N), east on Edwards Plateau to Travis Co., Texas: 200-3100 m; flowering late Mar-early Nov.

Pollen stainabilities for 23 collections of *C. mexicana* from localities throughout its range are low (0-8%) and micrograins are present in all preparations. I found irregular meiosis in all (five) collections studied. Two of these were reported as  $2n = \text{ca. } 45$ ; III's, II's, and I's were noted at first metaphase and laggards were present at first anaphase in both (Strother, 1976). Michael Powell recorded " $n = 20 \pm 2$ ?" on a specimen at TEX (*King 4487*). The only other chromosomal observation for *Chrysactinia* known to me is " $n = 15$ " for *C. pinnata* (Powell and Turner, 1963). I assume that  $x = 15$  for *Chrysactinia* and that *C. mexicana* is triploid.

In spite of irregular meiotic behavior and low pollen fertility, plants of *C. mexicana* seem consistently to set abundant good fruit (*vide* appearance in herbarium specimens—I have not tested germination). Collectively, these observations suggest that reproduction in this taxon is largely or wholly apomictic. Tests of this hypothesis are planned.

HARNACKIA Urban, Feddes Repert. Spec. Nov. Regni Veg. 21:72-73. 1925. TYPE: *Harnackia bisecta* Urban.

A monotypic genus.

HARNACKIA BISETTA Urban, Feddes Repert. Spec. Nov. Regni Veg. 21:73. 1925. TYPE: Cuba, Prov. Oriente, Sierra de Nipe, *Ekman 15154* (Holotype: B(?), destroyed?). Paratypes: Urban cited *Ekman 2312, 9119, 9747, 15154*; I located only *9747* (NY!, Cuba, Prov. Oriente, Sierra de Nipe, in charrascales-tibisiales ad Brazos Dolores, ca. 800 m, "12.7.1919").

*Lescaillea nipensis* Carabia, Mem. Soc. Cub. Hist. Nat., "Felipe Poey" 17:16-17. 1943. TYPE: Cuba, Prov. Oriente, Pinal de Mayari, Sierra del Nipe, Loma del Winch, 18 Apr 1940, *Carabia 3628* (Holotype: NY!).

Scandent suffrutices or vines; old stems with thick, corky bark; young stems slender (ca. 1 mm diam.), striate-angular, glabrous; internodes 30-60 mm long. Leaves opposite, petioles 2-4 mm long, blades divided into 3 narrow, cuneate lobes 3-6 mm long, each lobe  $\pm$  truncate and usually bearing a lance-subulate process subtended by a conspicuous, swollen pellucid gland. Heads solitary at ends of branches, peduncles mostly 15-30 mm long, 0-1 bracteolate. Involucres turbinate, 3.5-4.5 mm high. Calyculum of 0-2 lanceolate bractlets. Phyllaries 7-8, free to the base, narrowly lanceolate to lance-ovate, weakly carinate, scarious-margined, each bract usually bearing a conspicuous pellucid gland subapically. Receptacle slightly convex, alveolate, naked. Ray florets 3-5, pistillate, fertile; corollas yellow(?), tube slender, ca. 2 mm long, lamina narrowly elliptic, ca. 4.5 mm long, 1.5 mm wide, entire; style branches 1.3 mm long, stigmatic almost to the rounded, papillate-hispidulous apex. Disc florets ca. 10, perfect, fertile; corollas yellow(?), narrowly funnel-form, ca. 5 mm long, glabrous, tube ca. 0.9 mm long, throat ca. 3.5 mm long, lobes 5, ca. 0.6 mm long, lance-ovate, erect, minutely papillate, glandless; anthers ca. 2.7 mm long including collar (0.3 mm long) and lance-ovate appendage (0.3 mm long); style branches ca. 1.8 mm long, stigmatic almost to the minutely papillate-hispidulous, conical-rounded apex. Achenes 2-3 mm long, slender, cylindrical to weakly angled, blackish, striate, minutely hairy distally. Pappus of ca. 35 fine, uniseriate, subequal, barbellulate bristles 3.5-4.5 mm long, weakly united at base.

Specimens seen in addition to types: All from Cuba, Prov. Oriente, Sierra de Nipe, ca. 500-800 m, near 20°30' N, 75°45' W. Pinal Colorado, Cayo Rey, serpentine barrens, 7 Jan 1956, *Alain, 4927*, NY. La Cueva, serpentine barrens, 27 Jul 1940, *Alain 19276*, NY. Same locality, 6 Apr 1941, *Alain 19875*, NY. Rio Naranjo, about the falls, 3 Feb 1910, *Shafer 3862*, NY.

Carabia (op. cit.) cited the following as being at GH: "Oriente, Sierra de Nipe, serpentine hills 15 km. from Woodfred, R. A. Howard no. 6092." In spring 1975, Dr. Howard reported (pers. comm.) "... we have been unable to find ..." *Howard 6092* at GH.

LESAILLEA Griseb., Catalog. Pl. Cubens. 156-157. 1866.—*Porophyllum* sect. *Lescaillea* (Griseb.) Gomez de la Maza, Anales Soc. Esp. Hist. Nat. 19:277. 1890, "Porophyllum". TYPE: *Lescaillea equisetiformis* Griseb.

A monotypic genus.

LESCAILLEA EQUISETIFORMIS Griseb., Catalog. Pl. Cubens. 157. 1866—*Porophyllum equisetiforme* (Griseb.) Gomez de la Maza & Molinet, Anales Soc. Esp. Hist. Nat. 19:277. 1890, 'Porophyllon'. TYPE: "Cuba occ.", 1863, *C. Wright 2868* (Holotype: GOET!; isotypes: BM! G! GH! K! MO! NY! P! S! [Notes with specimen at GH indicate that *Wright 2868* is a pooling of at least four gatherings from "San Marcos" and "Bahia Honda"]).

Scandent suffrutices or vines; old stems with thick, corky bark; young stems slender (1–2 mm diam.), striate-ribbed, glabrous; internodes 30–50 mm long. Leaves opposite, reduced to appressed, lance-ovate scales ca. 1.5 mm long, each bearing a conspicuous pellucid gland. Heads solitary at ends of branches, peduncles rather long, slender. Involucres turbinate, 3.5–4.8 mm high. Calyculum of 0–3 lanceolate bractlets. Phyllaries 7–8, free to the base, linear to narrowly lance-elliptic, basally thickened, navicular, persistent and reflexed at maturity, each bract bearing a pellucid gland subapically. Receptacle flat to slightly convex, alveolate, glabrous. Ray florets none. Disc florets (8–)12–20; corollas greenish yellow, tipped with purple, funnellform, ca. 4.5 mm long, glabrous, tube ca. 0.9 mm long, throat ca. 3 mm long, lobes 5, lance-ovate, erect, 0.6 mm long minutely papillate, each bearing a pellucid gland subapically; anthers ca. 2.2 mm long including collar (0.4 mm long) and ovate appendage (0.3 mm long); style branches ca. 1.8 mm long, stigmatic almost to the rounded, papillate-hirsutulous apex. Achenes ca. 4 mm long, slender, weakly angled, dark brown, striate, sparsely hairy distally, otherwise subglabrous. Pappus of ca. 35 reddish brown, free, uniseriate, subequal, barbellulate bristles 3–4 mm long.

Specimens seen in addition to types: All from Cuba, Prov. Pinar del Rio, near 22°45'N, 83°30'W. Cajalbana La Palma, serpentine barren, 3 Dec 1949, *Alain 1340*, NY. Loma de Cajabana, in cuabales, 10 Mar 1920, *Eckman 10470*, S. Same locality, 2 Jan 1921, *Eckman 12718*, NY, S. Pan de Cajalbana, grimpante, sur les buissons, 6 Apr 1915, *Leon and Charles 4937*, NY, P, S.

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## INTRODUCTION OF DR. REID MORAN

by DR. JOHN H. THOMAS

as the featured speaker at the Annual Dinner Meeting of the  
California Botanical Society, Inc., on Saturday evening, February 19, 1977  
in Emeryville, California.<sup>1</sup>

It is indeed a pleasure to be allowed to introduce our speaker, Dr. Reid Venable Moran. He is the third in a row of distinguished speakers at our annual dinner meetings from the land to which all our water flows. Last year, as you will recall, Dr. Harlan Lewis spoke to us, and the year before that, Dr. Sherwin Carlquist.

Reid is indeed in need . . . of introduction.

He was born, went to Stanford and received his A.B. degree in 1939. Cornell University with an M.S. in 1942 was next. World War II saw Dr. Moran as a stout defender of democracy in many parts of the world and in many heroic situations. After that, he continued his formal education at the University of California, Berkeley, and received his Ph.D. in 1951.

His dissertation was "A Revision of *Dudleya* Crassulaceae", and I would like to quote from page 4 of that most celebrated work:

"I am deeply indebted to Mr. Karl Jakob, without whose kind cooperation this thesis would have been submitted one hour and 35 minutes later.

While at Berkeley, and perhaps those were among the golden years there, he distinguished himself in many ways, and here the historical record may need some careful and detailed verification. But there are stories about an egg being mailed through the Post Office to Phyllis Gardner and the sword through his (Reid's) head at Halloween.

Following Berkeley, Dr. Moran did a number of good things in the contemporary commendable "post doctoral" tradition. And in 1957 he became Curator of Botany at the San Diego Museum of Natural History, a position which he has filled ever since. His long-standing interest in the flora and vegetation of Mexico, with emphasis on Baja California, began to blossom. For instance, his attention to details resulted in significant papers on range extensions. In 1962 he published his now classical paper on *Cneoridium dumosum*. The title of this paper is: "*Cneoridium dumosum* (Nuttall) Hooker f. collected March 26, 1960, at an elevation of about 1450 meters on Cerro Quemazón, 15 miles south of Bahía de los Angeles, Baja California, México, apparently for a southeastward range extension of some 140 miles." (Madroño 16:272. 1962.) The text of the paper is: "I got it there then(8068)". The acknowledgments go on for some 29 lines (8 pt. type), and I will quote only the last sentence: "Last but not least, I cannot fail to mention my deep indebtedness to my parents, without whose early cooperation this work would never have been possible." This cooperation would appear to have occurred in 1915!

Dr. Moran is also an expert in the families Cactaceae and Crassulaceae, and he recently described a new genus and species in the latter family with Jorge Meyrán: "*Tacitus bellus*, un nuevo género y especie de Crassulaceae de Chihuahua, México." (Cactácea y Suculentas Mexicanas 19:75-84. 1974.) I quote further: "The genus is named not for the Roman historian or emperor but for the peculiar form of the corolla—from the Latin word *tacitus*, meaning silent. The corolla is scarcely more silent than in most other plants; but compared with that of near relatives, it is very close-mouthed." (Page 82.) Is there perhaps something autobiographical in everything one writes? In the generic description itself, one finds a compelling example of Dr. Moran's compassion: "*Tacitus* Moran: genus novum mexicanum,

<sup>1</sup> The Editors of Madroño, with concurrence of Dr. Thomas and the Council of the California Botanical Society, take special pleasure in sharing with the membership this part of the annual meeting of the Society.—Eds.

*Graptopetalo* Rose proximum, a quo calycis segmentis reflexis, corollae ore clauso sementisque concoloribus basi angustatis enatioaibus ornatis, filamentis aetate non reflexis, stylis elongatis differt. Pax vobiscum. Herba perennis succulenta glabra. . . ." (Page 76.) And so on for 13 more lines of impeccable Latin prose.

Well, I would cite many more examples of Dr. Moran's contributions and philanthropies, but perhaps it is time to let him tell us about the "PLANT LIFE OF BAJA CALIFORNIA".

NEW OR RENOVATED POLEMONIACEAE  
FROM BAJA CALIFORNIA, MEXICO  
(IPOMOPSIS, LINANTHUS, NAVARRETIA)

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In collecting in Baja California I have found three Polemoniaceae that seem to be unnamed, three whose generic position needs changing, and a few otherwise worth noting. The first set of my specimens is in the herbarium of the San Diego Society of Natural History (SD); duplicates will be distributed. In this account, my field numbers are prefixed with "M". I am grateful to Drs. Alva Day and Charles H. Uhl for chromosome counts and to Dr. Day also for the drawings and for reviewing this paper. Also, I thank the curators at POM, RSA, UC, and US for the loan of specimens, and at GH for photographs.

IPOMOPSIS

In his reclassification of the Polemoniaceae, Grant (1959) maintained *Ipomopsis* Michx. as a genus distinct from *Gilia* R. & P., with the expanded limits he had proposed before (Grant, 1956). Between these two rather large and variable groups he found general differences in duration, leaf distribution, leaf texture and dissection, flowering season, corolla form and venation, seed size and shape, etc.; and despite some specific exceptions, the two genera appear distinct. He also found a supporting cytological difference: *Ipomopsis* has a basic chromosome number of  $x = 7$ , as in *Eriastrum* and *Langloisia*, whereas *Gilia* has  $x = 9$  as in *Navarretia*, *Leptodactylon*, and *Linanthus*. Thus *Ipomopsis* seems well maintained in this expanded sense.

Asa Gray named three species of *Loeselia* from the Sierra Juárez of northern Baja California: *L. effusa* (1876), *L. tenuifolia* (1876), and *L. guttata* (1885). He placed them in their own section, GILIOPSIS, "connecting with *Gilia*". Gray (1886) transferred all three to *Gilia* section IPOMOPSIS (Michx.) Benth.; but Brand (1907) and Standley (1924) kept them in *Loeselia*, and likewise Jepson (1943) and Mason (1951) kept in *Loeselia* the one species extending into Alta [upper] California. Grant (1959) defined *Loeselia* to exclude these species, placing *L. effusa* in *Gilia* section GILIASTRUM Brand, *L. tenuifolia* in *Ipomopsis* section

PHLOGANTHEA (A. Gray) V. Grant, and *L. guttata* in synonymy under *Ipomopsis tenuifolia*. Study of these plants suggests that Gray was right in recognizing three species and in placing them in one genus but that the genus now should be *Ipomopsis* rather than *Loeselia* or *Gilia*.

These three species appear to form a close natural group within *Ipomopsis*, distinct from other species of section PHLOGANTHEA but not different enough to be treated as a separate section. They might be called a subsection of PHLOGANTHEA, but without first-hand information about other members of the genus, I will not attempt a reorganization at this level. For convenience, therefore, I refer to them informally as the Giliopsis group, without proposing any change in nomenclatural status. The group may be described as follows.

IPOMOPSIS section PHLOGANTHEA, Giliopsis group

*Loeselia* section *Giliopsis* A. Gray, Proc. Amer. Acad. Arts 11:86. 1876.

*Loeselia* subgenus *Giliopsis* [attributed to Gray by] Peter, Nat. Pflanzenfam. 4(3a):54. 1891.

Annual with basal rosette and leafy stems or perennial with several leafy stems from woody base, glandular puberulent at least above, more or less pubescent with white multicellular hairs or glabrate in age, the herbage with odor recalling tomato plants. Leaves horny-mucronate, linear and entire or the lower pinnatifid with a few linear to ovate, mucronate lobes. Flowers cymose, erect to horizontal, borne spring to autumn. Calyx regular, with scarious intervals equalling or wider than herbaceous ribs, rupturing in fruit. Corolla either red and concolorous or white to pink and irregularly spotted, nearly regular to strongly irregular; when corolla irregular, the anterior (lower) one or two sinuses deeper than the others and the posterior or anterior segment respectively in plane of symmetry; throat (measured to base of deepest sinus) much shorter to slightly longer than tube, narrowly funnellform; segments variously spreading, oblong to linear, cuneate, truncate and irregularly tridentate, muricate-papillose ventrally especially near base of posterior segments. Stamens subequally inserted at base of throat, well exerted from throat, nearly equalling to well exceeding segments, declined with tips upcurved when corolla irregular; anthers versatile, lobed from base nearly to insertion; pollen blue. Seeds pale brown, mucilaginous when wet, oval, rounded on back and pitted, flattish on face; or when crowded, seeds irregularly angulate. Chromosome number:  $x = 7$ .

The type species of *Loeselia* section GILIOPSIS is *L. tenuifolia*, designated by Grant (1956).

In all three species of the Giliopsis group, the flowers range from nearly regular to strongly irregular; and when irregular, they follow either of two variable patterns. To some extent the variation is between individual plants, the flowers of one being generally more regular than those of another; but also, the flowers of one individual may vary markedly. The

attitude of the flowers varies from erect to horizontal, and the erect flowers tend to be more regular. In nearly regular flowers, the lower (anterior) sinuses of the corolla are scarcely deeper than the upper (posterior); the corolla segments are about equal and diverge about equally; and the stamens are not declined but equally spaced about the mouth of the corolla. In irregular flowers, either two lower sinuses of the corolla are conspicuously (to 6 mm) deeper than an uppermost one, or one lower sinus is conspicuously deeper than the upper two; the segments may be unequal, and they spread variously in bilateral symmetry; and the stamens are declined. Also, the two lateral sinuses vary in position and depth. When two lowest sinuses are deepest, the lowermost segment lies in the midplane of the flower, and the other four segments diverge from it to varying degrees, depending on the position and depth of the lateral sinuses: in extreme flowers the other four segments are within an upper arc of about  $180^\circ$ , thus forming an upper lip. When one lower sinus is deepest and marks the midplane, the two lowest segments diverge from it to varying degrees, again depending on the position and depth of the lateral sinuses: in extreme flowers all five segments are within an upper arc of  $180^\circ$ , thus forming an upper lip with no lower lip. Although the symmetry varies in all three species, the modes are different, the flowers of *I. tenuifolia* being more often nearly regular, those of *I. effusa* and *I. guttata* more often one- or two-lipped and seldom nearly regular.

The herbage of all three species has a characteristic odor, which on an early label I compared with that *Lantana camara* L. but which I settled on by comparing with that of *Lycopersicon esculentum* Mill.

The three species of the Giliopsis group differ from other members of *Ipomopsis* in their cuneate-truncate and irregularly tridentate corolla segments. No other thoroughgoing distinction from PHLOGANTHEA is evident. Whether the odor of the herbage is distinctive is not known since no comparable information is available for the other species. Like Giliopsis, the other five species of PHLOGANTHEA also have more or less irregular flowers; and floral symmetry is similarly variable at least in *I. havardii* (A. Gray) V. Grant, with the midplane of the flower passing through either a lower segment or a lower sinus. That species, of western Texas, is perhaps especially close to the Giliopsis group, as suggested by the treatment of Brand (1907).

***Ipomopsis effusa*** (A. Gray) Moran, comb. nov.

*Loeselia effusa* A. Gray, Proc. Amer. Acad. Arts 11:86. 1876.

*Gilia dunnii* Kellogg, Pacific Rural Press 17:354. 1879. (Based on specimen sent by G. W. Dunn "from the southern part of [California]").)

*Gilia effusa* Macbride, Contr. Gray Herb. 56:57. 1918.

Annual with basal leaf rosette and 1-several slender leafy stems, 0.5-3 dm high, moderately pubescent. Cotyledons basally connate, oblong to

linear-oblongate, acute, entire, 3–8 mm long. Rosette leaves 0.5–3 cm long, simple or mostly pinnatifid, with 2–10 oblong to ovate lobes mostly in upper half and sometimes crowded near apex, the rachis 0.5–1 mm wide, the lobes ca as wide and 0.5–2 mm long; cauline leaves similar, fewer-lobed and smaller upward, the upper entire, linear. Flowers May to October. Calyx 3–4 mm long, the lobes 0.5–1 mm long, the scarious intervals often marked with purplish red. Corolla commonly one-lipped, sometimes two-lipped, rarely nearly regular, pink and white, 9–14 mm long, the tube and throat white to pinkish with small darker pink spots, the tube 1.5–2 mm long, ca 1 mm wide (unflattened), the throat 1–1.5 (–3) mm long, ca 1.5 mm wide, the lower sinus(es) 0.5–3.5 mm deeper than upper, the segments deep pink, darker below, at base white with pink spots, 4–7 mm long, 2–4.5 mm wide above, 0.7–1.5 mm wide at base. Filaments white, 6–9 mm long, exerted 5–8 mm from throat and about equalling corolla segments. Style 5–10 mm long. Capsules 3–5 mm long, 1.5–2.5 mm thick. Seeds ca 1 mm long. Chromosome number  $n = 7$ .

Type: Tantillas Mountains, Lower California, [ca 10 September] 1875, *Edward Palmer 767* (GH, photo SD). This would be the Sierra Juárez, probably somewhere near El Progreso. On the same sheet is a later collection by C. R. Orcutt from nearby El Topo.

Distribution: On gravelly flats often with *Pinus quadrifolia* Parl. and in mountain meadows with *Pinus jeffreyi* Grev. & Balf., or occasionally in upper chaparral, at 1000–2600 m and straggling to lower elevations along streams, northern Baja California Norte: Sierra Juárez, 1000–1600 m; Sierra San Pedro Mártir, 875–2600 m.

Dr. Uhl reports a gametic chromosome number of  $n = 7$  probable for a collection of *I. effusa* (M17887) from Yerba Buena, in the Sierra San Pedro Mártir; and Dr. Day, from many clear cells, reports  $n = 7$  for a later collection (M18467) from the same place.

Grant (1959) placed this species in *Gilia* section GILIASTRUM Brand, but his criteria (1956: 351–352; 1959: 79) point to *Ipomopsis*. In *I. effusa* the stem is leafy, the leaves are simple or once-pinnate, and the segments are horny-mucronate. Flowering is in summer, from May to September. The flower is strongly irregular, the corolla is irregularly spotted, and its veins do not anastomose. The seeds are oblong, not small and spheroidal, and the chromosome number is  $n = 7$ . In all these respects, *I. effusa* is like *Ipomopsis*, not like *Gilia*. Although it is annual, like most species of *Gilia* and like no others of PHLOGANTHEA, both other section of *Ipomopsis* do include annuals. Thus there seems no reason to put it in *Gilia*. And finally, *I. effusa* agrees with the other two species of *Giliopsis* in types of pubescence, odor of herbage, and patterns of floral irregularity, and, most notably, in the cuneate-truncate and irregularly tridentate corolla segments.

From the other two members of the *Giliopsis* group, *I. effusa* differs in its annual habit and basal leaf rosettes, its more consistently pinnatifid

leaves, with more lobes, and its smaller flowers, with much shorter corolla tube. The corolla is often one-lipped and seldom nearly regular; hence it is generally more strongly irregular than that of *I. tenuifolia* and perhaps also than that of *I. guttata*.

***Ipomopsis guttata*** (A. Gray) Moran, comb. nov.

*Loeselia guttata* A. Gray, Proc. Amer. Acad. Arts 20:302. 1885.

*Gilia guttata* A. Gray, Syn. Fl. N. Amer. Ed. 2. 2(1):411. 1886.

Perennial with several slender leafy stems from woody base, 1–4 dm high, sparsely pubescent. Leaves mostly entire but the lower occasionally 1–3 lobed, 0.5–2.5 cm long, ca 0.5 mm wide or a little more, the lobes ca as wide, to 3 mm long. Flowers May to October. Calyx 3–5 mm long, the lobes 1–2 mm long, the scarious intervals purplish. Corolla commonly two-lipped or one-lipped but sometimes nearly regular, deep pink to white, lighter with age, irregularly spotted deep pink to purplish red, withering bluish to purplish, 12–25 mm long, the tube 5–11 mm long, ca 1 mm wide (unflattened), slightly wider at base, the throat 1–2 mm long, 1.5–2 mm wide, the lower sinus(es) 0.5–6 mm deeper than the upper, the segments 5–9 mm long, 2–3.5 mm wide above, 1–1.5 mm wide at base. Filaments white, 6–10 mm long, exerted 5–9 mm from throat and so about equalling corolla segments. Style 8–18 mm long. Capsules 3–5 mm long, 1.5–2.5 mm thick. Seeds ca 1.5 mm long. Chromosome number:  $n = 7$ .

Type: from "near Hanson's Ranch", 18 September 1884, C. R. Orcutt 1225 (GH, photo SD). Since Orcutt (1893) reported returning from Hanson's by San Rafael, and since another herbarium label puts him in San Rafael on 19 September, he could well have collected the type about 12–15 km southwest of Laguna Hanson, where the plant is known to occur.

Distribution: Openings in chaparral, with *Adenostoma fasciculatum* H. & A., and often also *A. sparsifolium* Torr., on the west slope of the Sierra Juárez and the Sierra San Pedro Mártir, Baja California Norte, at 800–1650 m. Apparently local, known only from two areas: 3–6 km W to SW of El Rayo, Sierra Juárez, 1450–1650 m, *M13536*, *13552*, *16636*, *18483*, *22738*; foothills of Sierra San Pedro Mártir from 1 mi S of Rancho Santa Cruz, 1050 m (*Wiggins 10031*), southward at intervals for 15–20 mi (*Wiggins 1944*); divide between Arroyos Santa Cruz and San Antonio, 1000 m, *M16417*, *23474*; 5.5 km W of Santa Cruz, 800 m, *M16280*.

Dr. Day reports a gametic chromosome number of  $n = 7$  for a collection (*M18483*) of *I. guttata* from west of El Rayo, in the Sierra Juárez. In some cells she found a ring or chain of four chromosomes, and in some the pairing appeared to be poor.

Grant (1959:137, 145) referred this species to synonymy under *I.*

*tenuifolia*, but it is clearly distinct. It is similar in size and habit, but with leaves a little narrower and more commonly entire. The flowers are strikingly different in color—white or pink and irregularly spotted rather than bright red; they are somewhat smaller, with narrower corolla tube and segments, much shorter throat, and much shorter stamens; and generally they are more markedly irregular. So far as known, the areas of the two species are distinct, but they are close enough that some overlap may occur.

Wiggins (1944) reported this species from the foothills of the Sierra San Pedro Mártir and gave notes about the flowers.

***Ipomopsis tenuifolia*** (A. Gray) V. Grant, *Aliso* 3:357. 1956.

*Loeselia tenuifolia* A. Gray, *Proc. Amer. Acad. Arts* 11:86. 1876.

*Gilia tenuifolia* A. Gray, *Syn. Fl. N. Amer. Ed. 2.* 2(1):411. 1886.

*Gilia truncata* A. Davidson, *Bull. S. Calif. Acad. Sci.* 22:72, pl. 19. 1923.

(Based on *Payne & Kessler 3572*, from near Jacumba, San Diego Co., Calif.)

Perennial with several slender leafy stems from woody base, 1–4 dm high, sparsely to moderately pubescent. Cotyledons basally connate, linear-oblongate, acute, horny-apiculate, ca 10–12 mm long and 1–2 mm wide. Leaves entire or lower often 1–4 lobed, 5–35 mm long, mostly 0.5–1 mm wide, the lobes ca as wide, to 7 mm long. Flowers March to December. Calyx 5–9 mm long, the lobes (1–)2–3 mm long, the scarious intervals reddish. Corolla nearly regular to two-lipped or sometimes more or less one-lipped, bright red except for irregular white guide-marks at very base of segment and continuous with white or light pink color within tube, (12–)16–28 mm long, the tube 5–10 mm long, 1.5–2 mm wide (unflattened), slightly wider at base, the throat 6–11 mm long, 2.5–3 mm wide, the lower sinus(es) 0.5–4 mm deeper than upper, the segments 4–9 mm long, 2–5 mm wide above, 1–2.3 mm wide at base. Filaments red above, white below, 14–22 mm long, exerted 8–14 mm from throat and so exceeding corolla segments. Style 20–30 mm long. Capsules 5–7 mm long, 2–3.5 mm wide. Seeds ca 2 mm long. Chromosome number:  $n = 7$ .

Type: from “northern borders of Lower California, Tantillas Mountains, especially at the entrance of the Great Canyon, W. Dunn, E. Palmer”, [ca 10 September] 1875 (GH, photo SD). Presumably this is near El Progreso, in the Sierra Juárez. Though not mentioned on the label, G. W. Dunn was on this trip (McVaugh, 1956).

Distribution: On open gravelly slopes and in arroyos, associated with pinyon–juniper woodland, chaparral, or desert scrub, from southern California to north-central Baja California (Baja California Norte) at 100–2300 m elevation: Mammoth Wash, Chocolate Mts., Imperial Co., [ca 100 m] *E. Gray* (SD); SW Imperial Co. and SE San Diego Co., Calif., ca 450–1200 m; Sierra Juárez at 1100–1600 m on the west slope,

with stragglers down to 700 m in eastside canyons; west slope of Sierra San Pedro Mártir, 800–2300 m; Cerro Matomí, 1375 m, *M20806*; Cerro San Miguel, 1125 m, *M19519*; Cerro San Luis, 1300 m, *Moran & Henrickson 10300*; Ubi [= Yubay, near 29°11'N, ca 650 m], *Brandegee in 1889* (SD, UC).

Grant (1959) cited a chromosome number of  $2n = 14$  for *I. tenuifolia*, based on a collection from Jacumba, California.

Grant and Grant (1965) reported that plants from Jacumba grown at Claremont, California, were commonly visited by hummingbirds: "Their bills slip easily into the tube as they hover and probe for nectar, and their heads become dusted with pollen at the same time." They concluded that hummingbirds are the animals best fitted to feed on and pollinate these flowers. This is the only species of section PHLOGANTHEA with flowers red like the hummingbird-pollinated flowers of section IPOMOPSIS. Grant and Grant (1965) found the Jacumba plants self-incompatible.

The corolla of *I. tenuifolia* is often nearly regular, as shown by Mason (1951: Fig. 4007), by Grant (1959: Fig. 45, from Brand), and by Grant and Grant (1965: pl. 2F); but it may also be markedly irregular. In the other two species of the Giliopsis group, presumably pollinated by insects, most flowers are markedly irregular. The red hummingbird-pollinated flowers of *Ipomopsis* section IPOMOPSIS are quite regular.

Like some other hummingbird flowers, *I. tenuifolia* is sometimes called "chuparosa" in Mexico. Also as common names, Martínez (1937) cited "ubi" and "agua bonita": clearly both are from Brandegee (1889), who gave them not as plant names but as place names.

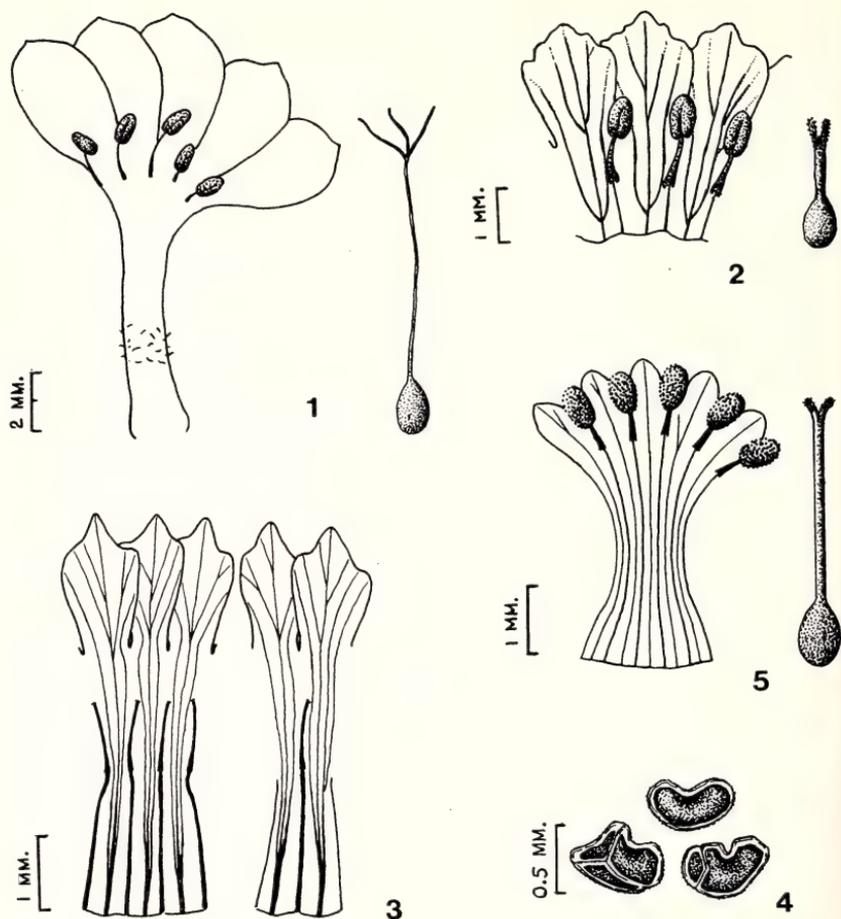
With *I. tenuifolia* in section PHLOGANTHEA, V. Grant (1956, 1959) placed the Baja California shrub commonly called *I. gloriosa* (Brandegee) A. Grant. However, Alva Day and I are studying this plant and consider that it probably does not belong to *Ipomopsis*.

*Ipomopsis sonora* (Rose) A. Grant ex V. Grant, of section MICROGILIA (Benth.) V. Grant, also occurs in Baja California: vernal moist depressions, sandy brush-covered flats north of the bay, San Quintín, 30 m, *Raven, Mathias, & Turner 12378* (UC), det. by V. Grant; La Bocana, east base of Sierra San Borja, 250 m, *M12494* (SD), det. by Alva Day.

#### LINANTHUS AND NAVARRETIA SPECIES

*Linanthus jamauensis* Moran, spec. nov. Fig. 1.

Planta annua hispidula supra glandulo-puberulenta 2–13 cm alta plerumque ramosa, internodiis infernis brevibus, supernis elongatis. Folia 1–9 mm longa 3–5 partita, segmentis linearibus spinuloso-apiculatis. Inflorescentia aperta, floribus terminalibus subsessilibusque vel axillariibus longae pseudopedicellatis. Calyx tubulo-campanulatus 3–4 mm



FIGS. 1-5. Drawings by Dr. Alva Day. Fig. 1. *Linanthus jamaicensis*, corolla, pistil; Moran 20930 (type). Fig. 2. *Linanthus uncialis*, part of corolla, pistil; Raven Mathias, & Turner 12528. Figs. 3, 4. *Linanthus viscaïnensis*, corolla, seeds; Moran & Reveal 19868 (type). Fig. 5 *Navarretia fossalis*, corolla, pistil; Moran 16014 (type).

longus  $\frac{1}{3}$  lobatus, tubo infra sinua scarioso. Corolla tubulo-infundibuliforma 10-17 mm longa, tubo gracillimo 6-10 mm longo intus supra basim puberulo-annulato, fauce 1-2 mm longa, lobis rubellis obovatis 3-6 mm longis. Filamenta sub sinubus inserta valde inaequilonga, brevissimis ca 0.3 mm longissimis 1.2-2.3 mm longis. Typus: Moran 20930 (SD 83887). Species staminibus valde inaequalibus notabilis, corollae tubo gracillimo calyce 2-3-plo longiore in sectione Dactylophylo praeterea distincta, *L. rattanii* et *L. ambigu* fors proxima qui autem foliis 3-7-partitis, calycibus grandioribus, corollis dissimiliter coloratis, et staminibus aequalibus valde exsertis differunt.

Much branched or rarely simple annual herb, 2–13 cm high and to 17 cm wide, hispidulous with stiff, tapering, whitish non-glandular trichomes to 0.15 mm long on stems and to 0.3 mm long or more on leaves, and glandular-puberulent with colorless 2–3-celled trichomes ca 0.1 mm long, each tipped with a yellowish globule to 0.05 mm thick, which shrinks and dries reddish. Hypocotyl papillose. Cotyledons subsessile and connate, elliptic, rounded at apex, 1.5–3 mm long, ciliate at base, otherwise glabrous. Stem reddish, to ca 1 mm thick at base, the main axis ca 2–6 cm high, with 3–10 nodes, in favorable years overtopped by 1–5 orders of axillary branches, hispidulous and scarcely glandular below, often closely leafy below, the basal internodes often only 1–3 mm long; branches mostly rebranching at each node; upper internodes more slender and elongate, commonly 0.5–3(–4) cm long, subglabrous except often glandular just below nodes, the ultimate to 0.2 mm thick. Leaves opposite and connate, palmate; lower 1–9 mm long, 1–12 mm wide, moderately hispidulous ventrally and on margins of segments, less so towards apex, scarcely glandular, mostly 5-parted (or lowermost pairs 3-parted or rarely simple), the segments linear, spinulose-apiculate, to 0.75 mm wide, ca half as thick or more, the middle 1–7 mm long, the lateral slightly shorter; upper leaves smaller, less hispidulous and more glandular towards base, mostly 3-parted. Flowers pink, diurnal, terminal and sessile or subsessile in a leaf pair or axillary on slender pseudopedicels to 15 mm long. Calyx tubular-campanulate, (2–)3–4 mm long, ca 1 mm wide, lobed ca one-third, moderately glandular throughout or at least in basal half, the tube with herbaceous ribs and scarious intervals about equally wide, the lobes equal, triangular-lanceolate, spinulose-apiculate, herbaceous, with scarious margins only at base. Corolla tubular-funnel-form, (7–)10–17 mm long; tube pinkish, slender, 0.3–0.5 mm wide (flattened), scarcely widened upward, 6–10 mm long, glabrous or commonly glandular-puberulent without, with puberulent ring ca 2 mm from base within; throat funnellform, 1–2 mm long, 1.5–2 mm wide above, glabrous; lobes pink, of various shades in different plants, drying blue-violet, narrowly obovate, rounded at apex, 3–6 mm long, 2–3 mm wide. Filaments subequally inserted in upper throat ca 0.3–0.6 mm below sinuses, markedly unequal, the shortest ca 0.3 mm long, the longest 1.2–2.3 mm long; anthers 0.8–1.0 mm long; pollen yellow. Ovary ca 1 mm long; style reaching corolla mouth, the stigma lobes exerted, 1–2.5 mm long. Capsules oblong, light tan, ca 2–3.5 mm long, 1–1.5 mm thick, with ca 2–3 seeds per cell. Seeds tan, irregular, verrucose, ca 1 mm long, mucilaginous when wet.

Type: Abundant on gentle north slope at 1250 m, with *Juniperus californica* Carr., *Pinus quadrifolia* Parl., and *Yucca schidigera* Roehl, ca 1 km W of Portezuelo de Jamau, Sierra Juárez, Baja California Norte, México (near 31°37'N, 115°39'W), 19 May 1973, *Moran 20930* (Holotype SD 83887).

Distribution: Known only from the southern Sierra Juárez. Other collections: gentle open north slope 3 mi NE of El Rincón, 1250 m, *M21257*; Portezuelo de Jamau, 1300 m, *M13886*; type locality, *M21221*; openings in chaparral, mesa 1 mi S of Portezuelo de Jamau, 1450 m, *M20937*, *21224*; flat divide 4 km NW of Cerro el Saiz, 1300 m, *M23282*.

Whereas plants collected in the relatively rainy year of 1973 (*20930*, *20937*) were bushy-branching, those collected at the same places (*21221*, *21224*) in the drier year of 1974 were mostly simple, with only 3–5 nodes and a single flower each. In May 1976, another dry time, I found no plants at either place.

This plant, with its short few-lobed leaves and open inflorescences, falls in the section *DACTYLOPHYLLUM* (Benth.) V. Grant (Grant 1959: 108, 109). It may have one to five generations of axillary branches, each of one elongate internode, or of very few, and ending with a leaf pair and a terminal sessile or subsessile flower. In the ultimate branchlets the upper leaf pair may be reduced or quite absent: with no leaves, the branchlet is like a pedicel and would commonly be called one. However, Grant used the term “peduncle” for the stalk of the flower in this section.

Within *DACTYLOPHYLLUM*, the new species falls in the group of species (*L. ambiguus* [Rattan] Greene, *L. aureus* [Nutt.] Greene, *L. bakeri* Mason, *L. bolanderi* [A. Gray] Greene, *L. lemmonii* [A. Gray] Greene, and *L. rattanii* [A. Gray] Greene) with glabrous filaments but with a puberulent ring within the corolla below the insertion of the stamens. From all these species, and apparently from all other members of the genus, it differs in its markedly unequal filaments, the longest about 4–8 times the shortest. Within the section it is remarkable also for its long slender corolla tube, 2–3 times the calyx and about  $\frac{1}{3}$  mm wide: in most other species the corolla is shorter or at least has a much shorter tube. Within the section, only *L. rattanii*, of the North Coast Ranges of California, and *L. ambiguus*, of the South Coast Ranges, have corollas that may be as long, though commonly they also are shorter. Both species differ further in their 3–7-parted leaves, their flowers more commonly borne on long pseudopedicels, their generally longer calyx, their differently colored corollas, and their exerted and more nearly equal stamens.

***Linanthus orcuttii*** (Parry & Gray) Jeps., Man. Fl. Pl. Calif. 804. 1925.  
*Gilia orcuttii* Parry & Gray, Proc. Davenport Acad. Nat. Sci. 4:40. 1884.  
*Linanthus pacificus* Milliken, Univ. Calif. Publ. Bot. 2:53. 1904.  
*Linanthus orcuttii* ssp. *pacificus* (Milliken) Masin, in Abrams, Ill. Fl. Pac. States 3:426. 1951.

The type of *G. orcuttii* is from a “high mountain ridge in Lower California, collected by C. R. Orcutt, June 1883”. From two accounts (Orcutt, 1883, 1893), it came from the north slope of the Guadalupe Mountains, “credited with an altitude of 4000 feet [ca 1200 m]” and with

*Pinus coulteri* near the summit, up valley from Rancho Guadalupe, 75 mi [120 km] from San Diego by road. This is the 1350-m peak now mostly called Cerro Blanco or Sierra Blanca, 8 km SE of Guadalupe (near 32°03'N, 116°30'W), with the only stand of *P. coulteri* within 50 km. *Linanthus orcuttii* is rather scarce in the open Coulter pine wood on the north slope, at ca 1000–1200 m (M16160, 23240). It also occurs, rarely, in the Sierra San Pedro Mártir (damp soil along streamlet, La Concepción, 1500 m, M15019; canyon of Río Santo Domingo, 950 m, I. L. Wiggins 10023A [DS]; Jeffrey pine forest, Santa Eulalia, 1850 m, M11137) and near the mouth of Río Santo Domingo (near Hamilton Ranch, J. H. Thomas 104 [DS]). (Dr. Day tells me of the two DS specimens, which I have not seen.)

Milliken (1904) described *L. pacificus* from Palomar Mountain, San Diego Co., without reference to *L. orcuttii*. It occurs also on Monument Peak, Laguna Mountains, 1800 m (Beauchamp & Williams 2754, SD). Jepson (1925, 1943) and Munz (1935) listed it in synonymy under *L. orcuttii*. Mason (1951) made it a subspecies of *L. orcuttii*, but with no comparison; and he was followed by Munz (1959, 1974). Grant (1959) referred *L. pacificus* to *L. orcuttii* with no comment as to subspecific status; but while he placed *L. orcuttii* in section DIANTHOIDES (Endl.) V. Grant, he named *L. pacificus* type of section PACIFICUS (Jeps.) V. Grant.

The specimens at hand show no basis for separating *L. pacificus* even subspecifically.

***Linanthus uncialis*** (Brandege) Moran, comb. nov. Fig. 2.

*Gilia uncialis* Brandege, Zoe 5:107. 1897.

Delicate annual 2–7 cm high, commonly simple,  $\pm$  lightly puberulent with slender several-celled trichomes 0.1–0.3 mm long, those of upper parts gland-tipped. Lower leaves opposite for 3–6 pairs, connate at base, simple, narrowly linear, horny-tipped, obtuse and apiculate, 3–18 mm long, ca 0.3–0.6 mm wide, channelled ventrally especially towards base, puberulent ventrally in lower half; upper few alternate, similar. Flowers February to April, terminal and solitary or also with 1–2 from upper axils on pedicels 5–10 mm long. Calyx 3–7 mm long, the tube 1–3 mm long, with scarious intervals slightly wider than herbaceous ribs, the sinuses V-shaped, the lobes linear, obtuse and apiculate, membranous-margined in lower ca 1 mm, channelled and puberulent ventrally, 2–5 mm long, in larger calyces often markedly unequal. Corolla white, 3–6 mm long, funnellform, glabrous within, the tube and throat each ca 1 mm long, the lobes obovate or narrowly so,  $\pm$  erose to irregularly rounded-toothed, ca 2–3 mm long. Filaments inserted at base of throat, equal, glabrous, ca 0.8 mm long; anthers oval, ca 0.3 mm long after dehiscence; pollen yellow. Style ca 0.5–1.0 mm long; stigmas ca 0.5–0.8 mm long. Capsules 3–4 mm long.

Type: Abundant on sides of gulches and in shade of bushes near summit of highest mountain [ca 1200 m], Cedros Island, Baja California Norte, México [near 28°08'N, 115°13'W], 7 Apr 1897, *T. S. Brandegee s.n.* (Holotype UC 125003).

Distribution: Near west coast of central and north-central Baja California at 500–1200 m. Other collections: Baja California Norte: Aguajito grade 2 km E of Aguajito, 540 m, *Raven, Mathias, & Turner 12528* (LA?, RSA, SD); 0.5 mi SW of southernmost pine grove, 1600 ft, Cedros Island (*Haines & Hale s.n.* (LA?, UC). Baja California Sur: upper N slope of Cerro Azul [ca 100 km SE of type locality], 700 m, *Moran & Reveal 19991*.

Brandegee wrote that this plant was closely allied to *Gilia dianthoides* Endl. [*Linanthus dianthiflorus* (Benth.) Greene], differing most obviously in its small corolla but not resembling the depauperate form of that species seen about San Diego in dry seasons. Grant (1959) kept it in *Gilia*, in section GILIASTRUM Brand, whose type is *G. rigidula* Benth. However, it does seem closer to *L. dianthiflorus* than to any species of *Gilia*, especially in view of the opposite leaves; and I place it in *Linanthus* section DIANTHOIDES (Endl.) V. Grant.

*Linanthus uncialis* resembles *L. dianthiflorus* in its leaves and calyx and its often pedicellate flowers. It differs in its glabrous filaments and its smaller and apparently unmarked corolla, glabrous within, with less prominent veins and no regular denticulations. Other species placed by Grant in this section have mostly palmately parted leaves (except *L. maculatus* [Parish] Milliken), sessile flowers, and calyx segments hyaline-margined over most of their length; and in some the calyx is more deeply divided. In most species the corolla is larger than in *L. uncialis*. The only other species with simple leaves and small flowers is *L. maculatus*, a rare endemic of the northwestern Colorado Desert, California. That is also a small plant but otherwise quite different: with compact branching habit; coarser pubescence; shorter, broader, thicker leaves; more flowers, on short pedicels; calyx divided to the base; corolla lobes spreading, subtruncate, maculate.

***Linanthus viscainensis*** Moran, spec. nov. Figs. 3, 4.

Planta annua 3–15 cm alta irregulariter multiramosa plus minusve villosa et glanduloso-puberulenta. Folia 5–18 mm longa, inferioribus oppositis linearibus, superioribus saepe alternis plerumque tripartitis, segmentis linearibus. Flores vespertini in cymulis vulgo trifloris conferti. Calyx tubularis 4–7 mm longus plus minusve ad medium lobatus, sinus acutis, tubo infra sinus et segmentorum marginibus inferioribus scariosis. Corolla calycem subaequans tubulo-infundibularis, segmentis albis 1–2 mm longis. Stamina inclusa brevia faucis basi inserta. Semina rubiginosa subreniformia irregulariter alboangulata foveolataque hilo constricta.

Typus: *Moran & Reveal 19868* (SD 92324). Species *L. arenicolae* affinis, sed ille parvior densiorque fere e basi dichotome ramosus, villosus sed non glandulo-puberulentus, foliorum segmentis altior insertis, seminibus sub aqua non mucilaginosus.

Erect bushy annual 3–15 cm tall and to 15 cm wide, glandular-puberulent with 2–3-celled trichomes mostly 0.05–0.1 mm long and each tipped with a yellowish globule, also more or less pubescent with multicellular white trichomes mostly 0.3–0.6 mm long. Stems slender, reddish, glandular, pubescent especially above, the main axis with ca 5–8 nodes, the lower internodes 1–3 mm long, the upper to 2 cm; lower branches also commonly with several nodes. Leaves opposite and basally subconnate below, often alternate above or at least with some pair-members well separated, 5–18 mm long, strongly nerved, pubescent ventrally at least near base, the lower simple, the upper simple or mostly 3-parted with lateral segments commonly ca half the mid-segment, the leaf or segments narrowly linear, 0.25–1 mm wide, horny-apiculate. Inflorescence cymose, the main axis and each branch ending in a flower, the main branches overtopped by 2–4 generations of axillary branchlets, each commonly of one internode, the lower elongate, to 4 cm, the ultimate very short, thus forming cymules of mostly 3 crowded subsessile or short-pedicellate flowers. Calyx tubular-campanulate, 4–7 mm long, 1–1.5 mm wide, sparsely glandular, pubescent at base and on pedicels, also in mouth and ventrally on lower half of lobes, the tube 2–4 mm long, with hyaline intervals equalling or slightly exceeding herbaceous ribs in width, the lobes erect or slightly outcurved, often unequal, subulate, hyaline-margined below, apiculate, 1–4 mm long, the sinuses sharply V-shaped. Corolla vespertine, tubular-funnelform, 4–6.5 mm long, the tube white, ca 2–3 mm long, ca 0.5 mm wide, the throat poorly delimited and scarcely wider, yellow, 1–1.5 mm long, the segments white (or light yellow?), narrowly obovate, subacute, 1–2 mm long, 0.5–1 mm wide. Stamens included, the filaments glabrous, 0.3–0.5 mm long, inserted somewhat unequally at base of throat, the anthers ca 0.25 mm long. Style 0.5–1 mm long; stigma lobes 0.5–1 mm long. Capsules oblong, light tan, 2–4 mm long, 1.5–2 mm thick, with ca 15–20 seeds per cell. Seeds red-brown, 0.4–0.6 mm long, subreniform, irregularly angled and pitted, notched and white at the hilum, the testa closely adherent but projecting as narrow whitish wings on some angles, mucilaginous when wet.

Type: Few and scattered in sandy bed of Arroyo Malarrimo 18 km S of mouth, at 75 m, Baja California Sur, México (near 27°39'N, 114°29'W), 6 Feb 1973, *Moran and James L. Reveal 19868* (Holotype SD 92324).

Distribution: Known only from sandy arroyo beds east and southeast of Bahía Tortuga, on the Viscaíno Peninsula, northwest part of Baja California Sur. Other collections: scarce in bed of Arroyo Largo 6.5 km

E of mouth, 110 m, *Moran & Reveal 19931*; scarce in arroyo bed 13 km by road NW of Asunción, 70 m, *Moran & Reveal 19786*.

At all three localities *L. viscaïnensis* was scarce, widely scattered along the sandy arroyo beds. Plants collected in mid-morning and early afternoon had no open flowers; only the late afternoon collection had any flowers open. These flowers had a white tube and segments and yellow throat; but closed ones at another locality looked as if the segments might have been light yellow.

The new species appears most closely related to *L. arenicola* (M. E. Jones) Jepson & Bailey, reported as a rare gypsophile occurring from the eastern Mojave Desert of California to southern Utah. That plant also has simple or 3-parted leaves, and it is similar in the size and form of the calyx and of the corolla, which again is vespertine. However, it is a smaller and more compact plant, branching dichotomously from near the base, the main axis having only one or two nodes, and flowering from even the lowest dichotomies. In *L. viscaïnensis* the main axis and its lower branches each have several nodes; and the upper branching is not regularly dichotomous because the leaves are not regularly opposite. *Linanthus arenicola* is similarly pubescent or more so, but it is not also glandular-puberulent; the lateral lobes of the leaves are inserted higher above the base; and the seeds are slightly larger and not mucilaginous when wet.

Mason (1938) considered *L. arenicola* (as *L. mohavensis* Mason) most closely related to *L. jonesii* (A. Gray) Greene, which it resembles in its vespertine flowers and its subreniform seeds, notched at the hilum. Likewise, Jepson (1943) placed *L. arenicola* in his subgenus EULINANTHUS, with *L. dichotomus* Benth. (generitype), *L. bigelovii* (A. Gray) Greene, and *L. jonesii*—all with vespertine flowers. Grant (1959) kept only *L. dichotomus*, *L. bigelovii*, *L. jonesii*, and *L. concinnus* Milliken in section LINANTHUS, characterized in part by flowers vespertine, calyx sinuses broad and more or less truncate, and filaments inserted on the corolla tube, i.e., below the throat. *Linanthus arenicola*, with sinuses V-shaped and filaments inserted low in the throat, he placed in section DIANTHOIDES (Endl.) V. Grant.

The vespertine flowers of *L. arenicola* and *L. viscaïnensis* do not alone necessarily show close relationship with the section LINANTHUS. However, the notched seeds are remarkably similar to those of *L. jonesii* and are different from those of section DIANTHOIDES. Furthermore, the calyx sinuses, though V-shaped, are not so deep as in most members of DIANTHOIDES. And other members of that section have broader corollas, mostly campanulate to funnellform (with a comparatively long tube and throat only in *L. killipii* Mason and *L. orcuttii* [Parry & Gray] Jepson) and mostly spotted at the throat. Thus there is reason to think that *L. arenicola* and *L. viscaïnensis* may belong in the section LINANTHUS.

**Navarretia fossalis** Moran, spec. nov. Fig 5.

Herba annua erecta prostratave 1–15 cm alta et lata plus minusve villosa et glanduloso-puberulenta, capitulo florali primario sessili caulescentive, vulgo ramos patulos in capitula simularia desinentes infra emitenti. Folia 1–5 cm longa remote pinnatifida infimisque integris. Bracteae 5–15 mm longae pinnatifidae, lobis acerosis. Calyx 4–8 mm longus, lobis inaequalibus integris, tubi ore arte ciliato. Corolla alba 4.5–6.5 mm longa, lobis uninervatis. Filamenta proxime infra sinua corollae inserta, 0.3–1.0 mm longa. Stigmata duo 0.2–0.3 mm longa. Capsula bilocularis diaphana indehiscens. Semina 5–25 rubiginosa 0.7–1.1 mm longa foveolata sub aqua mucilaginoso. Typus: *Moran 16014* (SD 70313). Ab aliis speciebus quarum stamina in sinibus corollae pariter inserta sunt calyce longiore (in illis plerumque 4–5 mm) filamentisque brevioribus (in illis plerumque 1.5–3 mm) differt. A *N. bakeri*, *N. pauciflora*, et *N. pleiantha* capsulis bilocularibus pluriseminalibus, a *N. prostrata* foliis basalibus parvioribus, calycis lobis simplicibus, corollaque parvioribus alba praeterea differt.

Annual 1–15 cm high and wide, the primary head sessile or caulescent, solitary or with 1–several spreading branches below, each bare below and ending in a similar head or also with several lateral heads; some parts pubescent with somewhat crinkly white pluricellular trichomes ca 0.5–1.0 mm long and glandular-puberulent with 2–3-celled trichomes ca 0.05 mm long, each tipped with a yellowish globule to ca 0.05 mm thick. Cotyledons connate at base, filiform, ca 5–13 mm long, bluntly horny-tipped. Stems whitish, retrorse puberulent or glabrous below. Leaves and foliaceous bracts soft-herbaceous when fresh, the bracts and upper leaves drying stiff and spinose. Lower leaves opposite, glabrous, 1–5 cm long, less than 0.5 mm wide, filiform and entire or remotely pinnatifid with linear or bifurcate lobes, the apices spinulose-apiculate. Middle leaves alternate, similar, remotely pinnatifid. Foliaceous bracts 5–15 or more mm long,  $\pm$  pubescent in lower half, the rachis oblong, 0.5–2 mm wide, several nerved, scarious margined and ciliate, with 1–7 pairs of simple or basally branching acrose lobes mostly below middle, the terminal lobe linear, acrose. Heads 1–2 cm wide, each a compact compound cyme of 15–50 subsessile flowers, flowering in May and June. Calyx 4–8 mm long, the tube 2–3 mm long, scarious between ribs,  $\pm$  pubescent and glandular, closely ciliate at mouth, the sinuses truncate, the lobes glabrous, linear, acrose, unequal by  $\pm$  2 mm, commonly 2 exceeding and 3 shorter than corolla, drying purplish. Corolla white, 4.5–6.5 mm long, in age circumscissile at base and pushed up by developing ovary, the tube 3–4 mm long, 0.2–0.4 mm wide, widened at base, the throat ca 0.5–1.0 mm long, the limb 3–4 mm wide, the lobes oblong, rounded at apex, 1–2 mm long, 0.4–0.7 mm wide, the single nerve sometimes with 1–2 ascending weak branches. Filaments inserted just below sinuses, 0.3–1.0 mm long; an-

thers oblong, sagittate, 0.5–0.9 mm long before dehiscence and 0.3–0.6 after. Ovary ovoid, green, ca 1 mm long, 2-celled; style slender, 2.5–4 mm long; stigma lobes 2, 0.2–0.3 mm long. Capsules 2–3 mm long, very narrowly attached, 2-celled, with diaphanous walls, indehiscent. Seeds 5–25, oval to irregular, 0.7–1.1 mm long, red-brown, finely pitted, mucilaginous when wet. Chromosomes:  $n = 9$ .

Type: Common in dry adobe soil, bank of ranch pond, Rancho Mesa el Tigre, 14.5 km SE of La Misión, Baja California Norte, Mexico, 375 m (near 32°00'N, 116°44'30"W), 31 May 1969, *Moran 16014* (Holotype SD 70313).

Distribution: Locally common in a few vernal pools and roadside depressions below 450 m, western Riverside and southwest San Diego Counties, California, and northwest Baja California. Other collection: Riverside Co.: 1 mi E of Perris, *R. Hoover 11152* (UC). San Diego Co.: 1 mi N of San Marcos, *F. Gander 3809* (SD); National Ranch, *D. Cleveland in 1882* (SD, UC), *Orcutt s.n.* (UC); Loma Alta, Otay Mesa, *F. Gander 217* (SD); Siempre Viva Rd., Otay Mesa, *R. M. Beauchamp 405* (SD); La Media Rd., Otay Mesa, 150 m, *Moran & Witham 16041, M23576*. Baja California Norte: Tijuana Airport, 150 m, *M16054, 16105*; mesa 5 km WNW of Ejido Matamoros, 150 m, *M17535*; 2.2 km SW of Redondo Sta., 220 m, *M17835*; mesa near canyon rim SE of La Misión, 250 m, *M15808a, 16004*; 18 km SE of La Misión, 325 m, *M14993, 14999*; 2 km NW of Ejido Ruben Jaramillo, 30 m, *M23503*; 2 km N of Rancho Ibarra, 50 m, *M22088*; 3.5 km E of old San Quintín, 10 m, *M23515*.

Dr. Day reports a gametic chromosome number of  $n = 9$  for a collection (*M23503*) of *N. fossalis* from near Ruben Jaramillo. This count agrees with earlier ones for *Navarretia* (e.g. Grant, 1959).

In view of the truncate and closely ciliate calyx sinuses, the one-veined corolla lobes, the indehiscent capsules, the minutely two-lobed stigma, and the vernal pool habitat, *N. fossalis* clearly belongs in section NAVARRETIA (= section FRAGILES Crampton) (cf. Crampton, 1954; Grant, 1959). Here it falls in the group of species (*N. bakeri* Mason, *N. pauciflora* Mason, *N. pleiantha* Mason, *N. prostrata* [A. Gray] Greene) whose filaments are inserted in or just below the sinuses of the corolla. *Navarretia bakeri*, *N. pauciflora*, and *N. pleiantha* all occur in northern California, in Lake County and *N. bakeri* also more widely. Like these three, *N. fossalis* has entire calyx segments; from them it differs in its two-celled capsules with more numerous seeds (5–25 vs. 1–5), its longer calyx (mostly 5–7 vs. 4–5 mm), and its shorter filaments (0.3–1.0 vs. 1–3 mm).

*Navarretia fossalis* has been confused with *N. prostrata*, which extends from Merced and Monterey to Los Angeles and Riverside Counties, California. Thus Jepson (1943) referred a San Diego County collection to *N. prostrata*, though he called it "a partial departure from the usual form" in its elongate main axis; and Mason (1957) also gave the range of *N.*

*prostrata* as south to San Diego County. *Navarretia prostrata* agrees with *N. fossalis* and differs from the three northern species in having two-celled capsules with more numerous seeds. Typically, *N. prostrata* has a distinctive aspect, with its main floral head sessile in a broad basal rosette, the leaves 3–8 or even 13 cm long, with a rachis often 1 mm and sometimes 3 mm wide, the long-stemmed lateral heads, when present, also subtended by conspicuous leaves; and few collections include caulescent plants. In *N. fossalis* the main floral head is more commonly caulescent, though in some populations often shortly so and in a few commonly sessile; and the leaves are mostly less than 3 cm long and 0.5 mm wide. In *N. prostrata* the calyx tends to be a little smaller (mostly 4–6 vs. 5–7 mm); and its larger segments often are tridentate, whereas in *N. fossalis* all are entire. Also, in *N. prostrata* the corolla is longer (6 or mostly 7–9 vs. 4.5–6.5 mm) and commonly blue or lavender rather than always white; the filaments are longer (1 or mostly 1.5–3 vs. 0.3–1.0 mm); and the anthers are longer (to 1.2 mm before dehiscence and 0.5–0.8 mm after vs. to 0.9 mm before and 0.3–0.6 mm after). Because of the longer corolla and shorter calyx, the corolla of *N. prostrata* typically is well exerted, whereas that of *N. fossalis* is included.

Jepson (1943) commented on the variation in vegetative characters in *Navarretia* and also on the variation in the calyx in some species and the similarity of calyx lobes to bractlets and leaves. In *N. fossalis*, so far as seen, the calyx segments are always entire. In *N. prostrata* the one to four largest segments often each have one or mostly two lateral teeth near the apex. Sometimes most flowers of one plant have tridentate calyx segments, sometimes relatively few, and sometimes none. Apparently, however, most if not all populations include plants with tridentate segments: for every herbarium sheet examined had such plants.

So far as noted on labels, the corolla color of *N. prostrata* is blue or violet, or blue or violet to white; but there is not enough information to surmise that all populations include blue or violet flowers.

So far as known from collections, *N. fossalis* occurred in relatively few of the many vernal pools formerly in San Diego County, and in just three areas. From two of these areas the vernal pools and the plant probably are gone, and on Otay Mesa it is now known only in a few of the few remaining pools; nor has it been found in artificial depressions. Possibly it survives also near Perris, Riverside County, but in any case it must be counted in Alta California a rare and endangered species. In Baja California, however, its future seems more hopeful. Although I found it there in only three areas of natural vernal pools, and some of these pools are since destroyed, it is well established in several rather widely scattered artificial depressions. Thus as the natural vernal pools disappear, it is becoming more a plant of roadside ditches; and I name it accordingly.

My three recent southern collections (22088, 23503, 23515), from 120 km or more below any of the northern, are all from ditches made during

construction of the highway completed about 1972—though the roadbed was started and these ditches perhaps dug several years before. The distribution of vernal-pool plants in these relatively new roadside ditches is still irregular and presumably unstabilized. An intriguing question is the source of these new colonists—whether from far to the north or from some unknown local population. With *N. fossalis* at one southern locality I was surprised to find *Orcuttia californica* Vasey, a very rare grass (cf. Moran, 1969) apparently known before in Baja California only from the type collection from San Quintín in 1886 and from my recent collections at Tijuana Airport. Having found neither the grass nor any natural vernal pools about San Quintín, I had wondered whether it persisted in that area. The recent collection suggests that it does and thus further suggests some refuge in the area where the *Navarretia* may also have persisted. Thus it seems reasonable to suppose that *N. fossalis* may be native as far south as San Quintín, even if it has perhaps not been found there by earlier collectors.

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## THE FLORAL ECOLOGY OF ASCLEPIAS SOLANOANA WOODS.

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Asclepiads possess a mechanism for pollen transfer which requires insects to remove discrete packets of pollen (termed pollinia) and later to insert these into receptive stigmatic chambers on other flowers. Several workers (Robertson, 1929; Grant, 1949; Woodson, 1954; Macior, 1965; Stebbins, 1970) have speculated that mechanical and ethological exclusion devices may be significant in the present reproductive isolation of certain *Asclepias* species. Stebbins (1974) further suggests that these exclusion devices, coupled with oligotrophy, may have been instrumental in the diversification of taxa throughout the Asclepiadaceae.

This paper is part of a study in which the floral ecology of a number of Californian and Mexican *Asclepias* species is being examined to determine pollination mechanisms and to assess the roles of insect behavior, floral morphology, and habitat specificity in reproductive success. The emphasis of this paper is to elucidate the life history and floral ecology of *Asclepias solanoana* as it occurs in the North Coast Ranges of California. Particular attention is given to the efficiency of the reproductive process with regard to flower, fruit, and seed production. Behavioral patterns and morphological adaptations both of the plant host and its insect vectors are analyzed in detail and correlated to the efficiency of the actual pollination process.

*Geography and Site Description:* *Asclepias solanoana* is endemic to northern California, occurring within the North Coast Ranges from Trinity County near Peanut in the north to Napa County near the Lake County boundary in the south (Fig. 1). It is known only from a few small

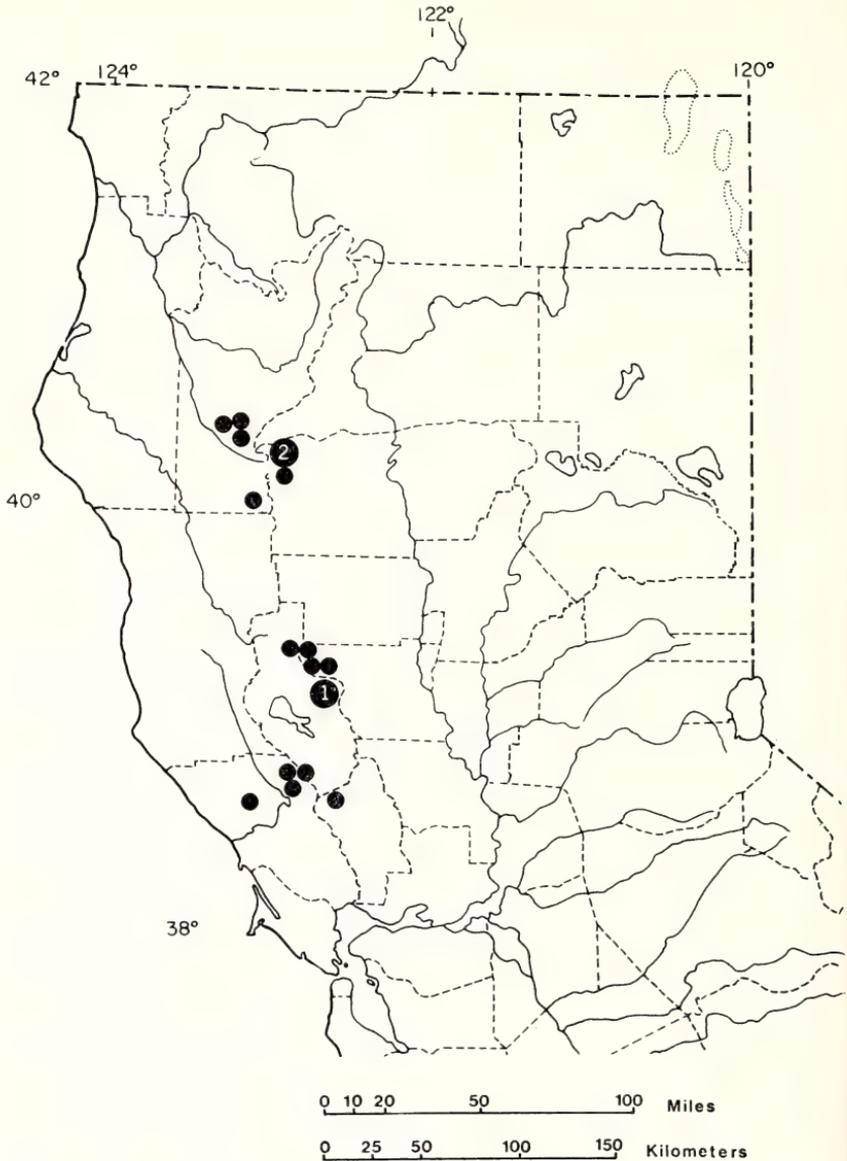


FIG. 1. Geographical distribution of *Asclepias solanoana* in northern California. Numbered dots correspond to study sites at Stanton Creek, Lake County (site 1), and at Tedoc Mountain, Tehama County (site 2).

local populations on ultrabasic soils formed from extrusive parent rock materials (serpentine). Each observed population is quite small, usually consisting of fewer than fifty plants confined to a single slope or clear-

ing on gently to steeply sloping hillsides with southerly exposures. Only two of the populations of *Asclepias solanoana* provided a sufficient number of plants for study. They are described as follows:

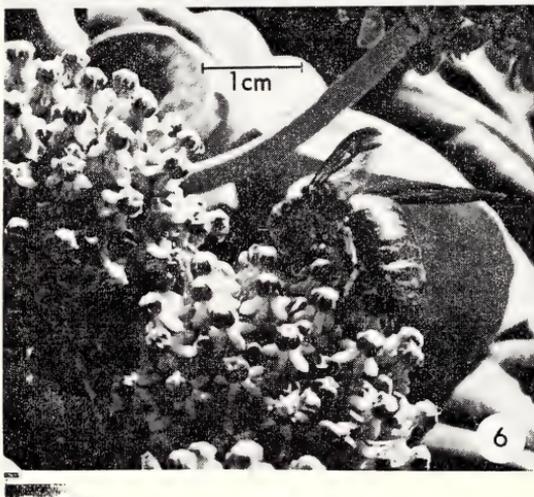
Site 1 (Fig. 2) is in Lake County along Stanton Creek just west of the Colusa County line near the northern edge of the new Indian Valley Reservoir at approximately 550 m. The population consists of about 45 plants on a south facing serpentine rock outcrop with a slope of 60–90%. The stony clay loam soil, developed from a mesozoic ultrabasic formation, belongs to the Henneke series of serpentine soils.

Vegetation surrounding the site is a foothill woodland–chaparral transition. Within the site, an area approximately 15 x 30 m, the only other perennials are two small leather oaks (*Quercus durata*); herbaceous species rarely occur within the confines of the site. Lack of competing vegetation in the proximity of the *A. solanoana* population is probably related to the chemical nature of the soil (Walker, 1964; Whittaker, 1954; Kruckeberg, 1954, 1969) as well as to slope and exposure.

Site 2 is on the southwestern slope of Tedoc Mountain in Tehama County at 1400 m. The study area, in a clearing in open jeffrey pine forest, encompasses the most extensive known *A. solanoana* population. The population consists of over 150 individuals covering several hundred meters square on a steep south facing slope (60–90%). The stony loam soil belongs to the Dubakella series of serpentine.

*Life History and Morphology:* *Asclepias solanoana* is a small, prostrate herbaceous perennial having one to several thin stems up to 2.5 dm long (Fig. 4). Each stem has one to several opposite pairs of firm, oval to ovate leaves 3–4 cm long and 2–3 cm broad. Flowers are arranged in terminal or subterminal umbelliform cymes with an average of 40 flowers per inflorescence.

All flowers in an inflorescence mature and open at approximately the same time, the entire inflorescence producing, in effect, an erect hemispherical blossom 3–4 cm in diameter. Individual flowers (Fig. 8) are small; the purplish–rose, 5-lobed and strongly reflexed corolla is approximately 6 mm in length and nearly obscures the small, 5 parted calyx. The five highly modified stamens are antisealous, and are adnate to the enlarged stigmatic head to form the gynostegium, a structure peculiar to all members of the Asclepiadaceae. The filaments are fused into a tube, the staminal column, and are adnate to the base of the corolla. The hoods, collectively termed the corona, are actually appendages of the filaments. They are cream to pink, saccate, and sessile, originating from the staminal column. Each hood is bifid dorsally, providing a protected entrance to the nectar stored in its hollow interior. The five bilocular brownish anthers are expanded laterally, the resultant “anther head” covering the enlarged stigma. Anther margins are bordered by leathery wings arranged parallel with the wings of adjacent anthers to form five slits around the



periphery of the anther head. Each slit is situated over a depression in the stigmatic head; the resultant "stigmatic chambers" contain the five receptive stigmatic surfaces or grooves of the gynoeceium. At the apex of each slit is a dark, notched body, the corpusculum, which is attached laterally to two thin, somewhat hyaline appendages, the translator arms. Each of these is attached through the apical pore of the adjacent anther locule to a discrete pollinium. The corpusculum, translator arms, and the two attached pollinia form a pollinarium.<sup>1</sup>

When an insect gathering nectar inadvertently introduces an appendage, hair, or spine into a slit, this body part may become attached to the notched corpusculum. In pulling free, the insect carries away the pollinarium which remains attached to its body (Figs. 5-7). The pollination process is completed when the insect, again inadvertently, inserts one, or rarely both, pollinia of the attached pollinarium into the basal region of a slit on a flower. As the insect pulls free, the pollinium becomes wedged into the stigmatic chamber and breaks away from the translator arm. After a pollinarium has been extracted, insertion of the pollinia into a slit is facilitated by twisting of the translator arms, which places the flattened planes of the pollinia in parallel (Fig. 8J illustrates the position of the pollinia on the pollinarium after twisting, which usually occurs one to several minutes after extraction).

The gynoeceium consists of two free, superior ovaries and two separate styles united only by the common stigmatic head. Each carpel contains numerous multi-seriate, anatropous ovules on a ventral placenta. While each carpel, once fertilized, is independently capable of maturing, usually only a single follicle is produced per flower. Follicles, when mature, lie prostrate on deflexed pedicels (Fig. 3). They are narrowly fusiform, reaching 10 cm in length, and producing an average of 50 flattened, comose seeds (Fig. 8). Mature seeds are dark brown, broadly oval, and approximately 6-7 mm long; the white, loosely attached coma is about 18-20 mm long.

<sup>1</sup> The term pollinarium is also commonly used to describe the pollinium apparatus in the Orchidaceae (Faegri and Van de Pijl, 1971; Proctor and Yeo, 1972). An orchid pollinarium, however, consisting of viscidium, caudicle, and pollinium is formed from the contents of a single anther; the two pollinia of the asclepiad pollinarium are produced by adjacent anthers.

FIG. 2-7. *Asclepias solanoana*. 2. Site of the study population at Stanton Creek, Lake County. Most plants occur in the clearing shown in the center of the photograph. 3. Mature follicles. 4. Habit of individual plant. 5. *Apis mellifera* worker searching for nectar on an inflorescence. 6. *Xylocopa californica* male on an inflorescence; note the position of the abdomen as the insect crawls over the flowers. 7. *Bombus vosnesenskii* foreleg with attached pollinaria.

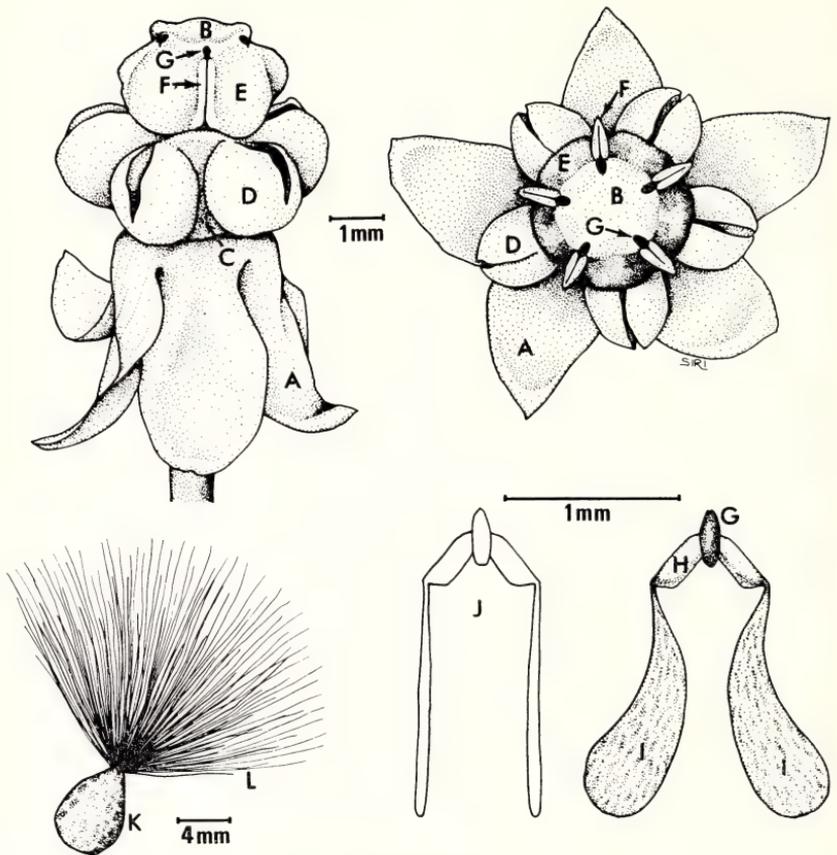


FIG. 8. *Asclepias solanoana* flower, pollinarium, and seed. A = corolla; B = gynostegium; C = staminal column; D = hood; E = anther; F = anther wings; G = corpusculum; H = translator arms; I = pollinium; J = pollinarium showing the orientation of pollinia after twisting of the translator arms has occurred; K = mature seeds; L = seed coma.

*A. solanoana* perennates through establishment of a subterranean caudex or "rootstock" derived from the hypocotyl (Woodson, 1954). Growth of established plants and seedlings commences in the spring, inflorescences being initiated early in the new growth phase. Seedlings do not normally flower in the first year; two or sometimes three years are necessary. Flowering commences mid-May to mid-June, most inflorescences within a given population opening within a two to three week period. Individual blossoms may retain their attractiveness to nectar-seeking insects for over a week, after which nectar production ceases and the flowers shrivel and become discolored. Several fruits may mature on a single inflorescence. At maturity the follicles dehisce along the ventral

suture. Seeds, loosely attached to their comas, usually fall near the parent plant. The few seeds which remain attached to their comas are wind dispersed. After follicle dehiscence the leaves and stems wither and dry, so that by mid-August to early September only the perennating rootstock remains.

The phenology of *A. solanoana* is influenced by numerous environmental factors and varies among populations and from year to year. In general, however, the population at Stanton Creek enters each phase of development much earlier than the population at Tedoc Mountain, which is much higher in elevation and usually experiences lower temperatures in the early spring.

#### METHODS

In each of the two study sites, experimental plants were selected and marked in the early spring of 1973. The distribution of milkweeds within each study area was mapped. Individually marked plants, 35 at each site, were then observed during selected stages of their development throughout the year. The Stanton Creek population was additionally observed through the entire 1974 and 1975 seasons and into the spring of 1976. The Tedoc Mtn. population was inaccessible from the winter of 1974 until mid-summer 1975, when the site was again visited.

Field observations included examination of each population to determine phenology, coordination of growth phases, establishment of new individuals, and the death of established plants. Individual plants were examined to determine stem number, inflorescence number, fruit initiation, and fruit maturation throughout each growing season. Further observations were made on pollinator activities, including frequency of visitation by each insect species, duration of visits, behavior of the insects in locating blossoms and obtaining nectar, and any activities of these insects in visiting other plant species in the vicinity.

Old inflorescences (those no longer attracting nectar-seeking insects) were examined to determine the number of pollinaria pulled per flower and the number and location of pollinia inserted into stigmatic chambers. Occurrence of double or triple insertions into a single stigmatic chamber and presence or absence of an intact (unremoved) pollinarium above an inserted pollinium were recorded. The species and sex of captured insect visitors were determined, as were the total number of pollinaria on each insect, the position of each pollinarium attached to the insect, and number of pollinaria attached indirectly by attachment to another pollinarium. Each pollinarium was scored as intact, missing one pollinium, or missing both pollinia. Insects of the same species visiting flowers of other plant species in the community were examined, but no attached pollinaria were observed.

Mature fruits were allowed to dry and dehisce at room temperature. Average numbers of seeds per pod were estimated from thirty or more

follicles for each year data were recorded. Average seed weights were established from 200 seeds randomly selected from 30 mature fruits. Ranges in seed weights were each established from 50 individual seeds in the average seed weight sample.

#### OBSERVATIONS AND DISCUSSION

*Plant Productivity:* In comparison with most milkweed species, *A. solanoana* produces a small biomass and averages fewer than four slender stems and 15 pairs of leaves per plant. The most robust plant observed produced 16 stems from its rootstock and had 34 inflorescences. Several plants at each site produced only a single stem and many had no flowers (of 118 plants at Tedoc Mtn., e.g., 35 were non-flowering). At the Stanton Ck. site no first-year plants produced flowers and only four of the eight produced flowers in the second year. Of these four plants, two set no fruit, one produced a single mature fruit, and one produced four. All plants observed in the third year of growth produced inflorescences. At Tedoc Mtn. in 1975 a late freeze damaged many stems and inflorescences. However, an area encompassing 83 plants in 1973 contained 107 in 1975; 16 new plants were found and eight established plants had failed to emerge. Of the 16 new plants nine flowered, producing eight fruit on four plants.

Table 1 summarizes vegetative and reproductive growth of the 35 marked plants at each site. There is a direct relationship between number of stems and number of inflorescences per plant, as well as between number of stems per plant and number of fruits matured. At each site, inflorescences matured in less than one month, the majority opening within a two-week period. The few late-maturing inflorescences in each population were often significantly smaller and had fewer flowers than those maturing earlier.

The number and average weight of seeds per fruit did not vary significantly from year to year or between sites. In 1973 the Tedoc Mtn. site produced .021 fruits per flower for a 2.1% fruit-set level and an estimated ratio of .742 seeds per flower. Fruit-set levels for the Stanton Ck. site include an estimated 2.7% for 1973, 2.4% for 1974, and 1.8% for 1975. The overall fruit-set level for the Stanton Ck. site was 2.3% and the seeds per flower ratio was .719, both remarkably close to the estimates for Tedoc Mtn.

*Flowers and Pollinia:* A total of 1000 flowers was examined for the number and position of pollinia pulled and inserted (Table 2). Data for the Stanton Ck. population in 1973 and 1975 are based on counts of 100 flowers picked randomly, ten each from ten different plants within the population. The 1974 data at Stanton Ck. and the 1973 data from Tedoc Mtn. are based on an examination of 400 flowers per site taken from 20 inflorescences picked randomly from 20 different plants in the

TABLE 1. PLANT PRODUCTIVITY OF ASCLEPIAS SOLANOANA AT STANTON CREEK AND TEDOC MOUNTAIN

Site and year	Stems per plant	Inflor per plant	Flowers per inflor	Mature fruits per plt	Seeds per fruit	Seed weight in mg	Number of new plants <sup>1</sup>	Number of deaths <sup>1</sup>
STANTON CK.								
1973								
Average (Range)	4.66 (1-16)	7.47 (0-34)	38.9 (12-63)	7.77 (0-29)	31.1 (20-42)	16.65 (15.4-25.0)	—	—
1974								
Average (Range)	5.17 (1-17)	8.08 (0-29)	47.2 (31-65)	9.19 (0-28)	—	—	4	0
1975								
Average (Range)	4.41 (1-18)	7.22 (1-28)	36.3 (8-58)	4.63 (0-19)	33.2 (21-43)	16.92 (12.2-24.4)	4	0
1976								
Average (Range)	3.19 (1-11)	3.58 (0-14)	—	—	—	—	10	0
TEDOC MTN.								
1973								
Average (Range)	3.42 (1-7)	5.75 (1-12)	45.5 (30-64)	5.61 (0-23)	34.6 (21-46)	17.20 (15.6-29.0)	—	—
1975								
Average (Range)	2.79 (1-6)	— <sup>2</sup>	— <sup>2</sup>	2.45 (0-8)	—	—	16	8

<sup>1</sup> Counts of seedlings and deaths were taken for the entire population of 35 plants at Stanton Creek. At Tedoc Mountain counts were taken for an

area including 83 plants.

<sup>2</sup> Counts were not taken due to freeze-damage during June.

TABLE 2. FREQUENCIES OF POLLINARIA REMOVED AND POLLINIA INSERTED IN ASCLEPIAS SOLANOANA FLOWERS.

Site and year	No. of inflor examined	No. of flowers examined	Pollinaria removed per flr	Extract acts per flower <sup>1</sup>	Pollinia inserted per flr	Slits inserted per flr	Prop of pollinia in intact slits <sup>2</sup>
STANTON CK.							
1973 TOTAL	10	100	3.85	7.35	1.61	1.30	.236
1974 TOTAL	20	400	4.43	10.86	1.81	1.66	.151
Peripheral	20	200	4.34	10.12	1.79	1.65	.182
Central	20	200	4.52	11.72	1.83	1.67	.120
1975 TOTAL	10	100	3.95	7.80	1.55	1.35	.194
SITE TOTAL	40	600	4.25	9.77	1.73	1.55	.170
TEDOC MTN.							
1973 TOTAL	20	400	2.91	4.36	1.23	1.12	.484
Peripheral	20	200	3.03	4.66	1.26	1.14	.478
Central	20	200	2.78	4.06	1.21	1.11	.489

<sup>1</sup> Mean number of extraction acts per flower which would yield an expected number of extractions equal to the observed number of extractions.  
<sup>2</sup> Proportion of pollinia inserted into stigmatic chambers of slit regions from which the flower's own pollinarium had not been extracted.

population. From each inflorescence, ten flowers from the periphery and ten from the central region were scored.

At both sites a rather high percentage of the pollinaria had been removed: at Tedoc Mtn., 58% and at Stanton Ck., 85%. In the 1974 season at Stanton Ck. 1772 of the 2000 pollinaria from 400 flowers (87%) had been extracted.

If we view the system of pollination of *Asclepias* flowers from the standpoint of behavior necessary to extract a pollinarium, it is obvious that the outcome of an event which might lead to extraction of a pollinarium from any given flower is not independent of the outcome of previous such events. If we define an *extraction act* as one which would remove a pollinarium if that pollinarium were still intact, then it follows that an initial extraction act on a given flower would have a 100% chance of extracting a pollinarium, leaving only four intact on that flower. A second extraction act on the same flower would have only an 80% chance of removing a pollinarium. The probability, therefore, that three consecutive extraction acts would remove three pollinaria is .48 ( $1.0 \times 0.8 \times 0.6$ ). If the second extraction act is performed on *the* slit from which the initial pollinarium was removed (a .2 probability) then no removal would occur, and a third extraction act would still have an 80% chance of removing a pollinarium. The probability of two pollinaria being removed through this sequence is .16 ( $1.0 \times 0.2 \times 0.8$ ).

The differences between pollinaria removed per flower among the sets of data are even greater when viewed in terms of insect behavior (extrac-

tion acts) required to pull pollinaria. When an increasing number of pollinaria is removed from flowers of a given population, an increasingly greater number of extraction acts must be performed to extract additional pollinaria. By appropriate calculations we can establish the mean number of extraction acts per flower which would yield an expected number of extractions. From an observed 2.91 pollinaria removed per flower at Tedoc Mtn., and 4.25 pollinaria removed per flower at Stanton Ck., we estimate it would take 4.36 and 9.77 extraction acts per flower, respectively, to pull an equivalent number of pollinaria. Seemingly small differences in extractions between yearly samples may be rather large when viewed from the standpoint of extraction acts. It would take, for example, an estimated 3.06 additional extraction acts per flower to produce the additional .58 extractions per flower observed for Stanton Ck. in 1974 as compared to 1975.

Unless otherwise stated, all correlations between pollinia and either inflorescences, flowers, or insects were statistically examined for goodness of fit using a  $\chi^2$  test at a level of significance of .05. All statistical tests followed the procedures and limitations outlined in Siegel (1956). Extraction data were subjected to several statistical tests to assess randomness of pollinarium removal among and within inflorescences. Under the assumption that any pollinarium is equally likely to have been removed, regardless of its position in the flower or in the inflorescence, and using actual data on the mean number of extractions per flower, we can calculate the expected numbers of flowers with zero through five pollinaria removed. No significant departure from randomness could be detected at the 5% confidence level for any of the observations.

Based on a  $\chi^2$  test, there are significant differences among inflorescences at each of the sites in terms of numbers of pollinia inserted per flower. In spite of this, using the Kendall Rank Correlation Coefficient, there was no significant correlation between number of flowers per inflorescence and either numbers of pollinaria extracted or numbers of pollinia inserted per flower. Using the same test, however, a significant direct correlation ( $P > 99.8\%$ ) can be demonstrated between the rate of insertion and extraction per inflorescence (Fig. 9). It seems likely, therefore, that inflorescences at each site differ in both insertion and extraction activity per flower, but that this is not closely related to inflorescence size.

A Fisher randomization test was used to examine the hypothesis that the number of pollinaria extracted from flowers is independent of position in the inflorescence. Extractions from peripheral flowers were compared with those from central flowers using inflorescences from both sites, but no significant departure from randomness was detected. Also, a binomial test demonstrated no significant departure from randomness for insertions as a function of position in an inflorescence.

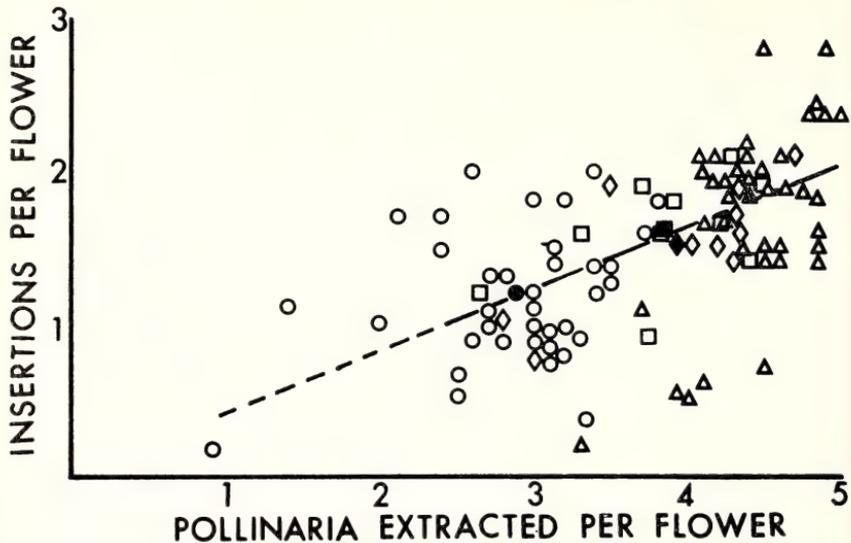


FIG. 9. Observed relationship between insertions per flower and pollinaria extracted per flower. Figures in outline each represent the mean values for ten flowers from one inflorescence. Solid figures represent the mean values for all flowers analyzed at a site for a given year. The yearly mean values were used to estimate the slope of the line. The key to the shapes of the various figures is as follows:  $\blacksquare$  = Stanton Ck., 1973;  $\blacktriangle$  = Stanton Ck., 1974;  $\blacklozenge$  = Stanton Ck., 1975;  $\bullet$  = Tedoc Mtn., 1973.

The number of pollinia inserted was significantly lower than the number extracted in all cases, averaging 1.73 per flower at Stanton Ck. and 1.23 per flower at Tedoc Mtn. The frequency distribution of rates of insertion of pollinia on a per flower basis indicated a significant deviation from expected frequencies for all but one set of observations, but no consistent pattern could be detected to explain this departure from randomness. Although the number of slits with multiple insertions was relatively low (10.1%) it is possible that the occasional insertion of two pollinia during a single insertion event accounts for some of non-randomness of the frequency distribution of insertions on a per flower basis. To assess the possibility that simultaneous insertions in adjacent slit regions might have occurred, flowers with two insertions in different slits were examined to determine whether they were positioned in adjacent or opposite slit regions. No significant departure from randomness could be detected, as an almost equal number occurred in both categories.

Perhaps more significant is the relationship between insertions and extractions for any given slit region. Correlations ranged from slightly negative, but not significant in all central flowers to significantly negative in all peripheral flowers. A disproportionately high number of inser-

tions were in stigmatic chambers of slit regions with intact pollinaria. This may indicate that pollinia inserted by insect visitors are more likely to remain inserted in a given slit region when the flower's own pollinarium is present and intact. This finding would at least partly concur with Wyatt's (1976) observations that, in *A. tuberosa*, the corpusculum of the intact pollinarium often serves as the point at which the translator arm to an inserted pollinium is broken, thereby allowing the pollinium to remain lodged against the stigmatic surface. My observations indicate that this may often be the case in *A. solanoana* flowers as well. Therefore, while increased numbers of extractions reduce the efficiency of additional extraction acts in producing additional extractions, they may also reduce the likelihood of additional insertions. The net effect is that the relationship between extractions and insertions is nearly linear (Fig. 9).

*Pollinator Behavior:* At both sites observations of pollinator activity were made through portions of each daylight hour. Days of visitation were arranged to span the flowering periods at each site. At Tedoc Mtn. the only floral visitor effective in extracting pollinia from *A. solanoana* flowers was a large carpenter bee, *Xylocopa californica* (Hymenoptera:Xylocopidae). At Stanton Ck., *X. californica* was also the principal floral visitor, but a bumble bee, *Bombus vosnesenskii* (Hymenoptera:Apidae), and the honey bee, *Apis mellifera* (Hymenoptera:Apidae) also visited flowers. No other floral visitors were observed to extract or carry pollinaria from *A. solanoana* flowers.

*Xylocopa* bees typically flew into the study areas at high speed, "buzzing" the population and making angling flight patterns over the area before sweeping in to hover above a plant. The bees sometimes repeated the entire sequence several times before landing on an inflorescence. After landing, they stayed on an inflorescence from one to 535 seconds (Fig. 6). Bees often flew from one inflorescence to another, hovering briefly before landing. More frequently, however, they visited another inflorescence on the same plant by crawling short distances along a leaf, the stem, or on the ground. Usually carpenter bees crawled over the surface of an inflorescence probing for nectar in a large number of hoods and then flew several feet from the plant before settling on another plant, re-entering a "buzzing" pattern, or flying off. Wariness of the insects and the terrain often prevented accurate determination of the sex of the insects, but field observations and captured specimens indicated a ratio of approximately 4:1 male:female visitations at both sites. No behavioral differences were observed in male and female carpenter bees visiting *A. solanoana*.

*Bombus vosnesenskii* males also visited *A. solanoana* inflorescences at the Stanton Ck. site, although at a consistently lower rate than that of carpenter bees. No worker or queen *Bombus* was observed or captured.

Bumble bees were consistently more direct in visitation behavior, flying into the study area and usually hovering briefly above a particular plant before landing. On the inflorescence bumble bees displayed the same behavior patterns as the carpenter bees. They flew from one inflorescence to another rather than crawling along foliage. Duration of the visit to each inflorescence varied greatly, ranging from two to 486 seconds.

Honey bee workers were observed as visitors only at the Stanton Ck. population in 1974. Frequency of visitation by the honey bees was less than 5% of the insect visits that year. Honey bees were quite direct in their approach to an inflorescence, flying much more deliberately than either *Xylocopa* or *Bombus*, and moving much more frequently and freely from inflorescence to inflorescence and from plant to plant. Visitation time varied greatly, ranging from a mere touchdown and take off to a stay of 225 seconds. Honey bees also used the entire inflorescence as a platform and crawled at random over the flowers searching for nectar (Fig. 5).

*Insects and Pollinaria:* Table 3 summarizes the analysis of location, condition, and attachment of 2706 pollinaria on insects captured on blossoms of *A. solanoana*. Of the three species visiting flowers at the Stanton Ck. site, *Apis mellifera* carried the greatest number of pollinaria per insect (48.4). On *Apis* all the observed pollinaria were attached directly or indirectly to hairs or spines on the legs. Nearly half of these were on the hind leg attached to the pollen-collecting apparatus of the tibia and to the enlarged first tarsal segment.

*Bombus* had fewer pollinaria per insect (29.1) than *Apis* and slightly fewer than the *Xylocopa* (32.4) at Stanton Ck. As with *Apis*, the only pollinaria attached to bumble bees were on the legs (Fig. 7), but these were nearly evenly divided among the three leg pairs. Approximately three fourths of all pollinaria on *Bombus* were attached to hairs and spines of the tibia. Nearly all remaining were on various tarsal segments or the claws.

At both sites *Xylocopa* males and females collected many pollinaria not only on their legs but also on the fringe of hairs along the posterior portion of the abdomen. The number of pollinaria per insect at Tedoc Mtn. was significantly higher (163.0 for females and 74.2 for males) than for the *Xylocopa* at Stanton Ck. Greater numbers of pollinaria on females are attributable to the additional pollinaria attached to the longer and more plentiful hairs and spines of the hind tibiae. The number of pollinaria on the abdominal brush of females was not significantly different from that of males. Ratios of pollinaria found on each leg pair of male carpenter bees from either site and bumble bees from Stanton Ck. were not significantly different. Both *Xylocopa* females and *Apis* workers, however, had a significantly greater percentage of pollinaria on their modified hind legs than did male pollinators.

TABLE 3. FREQUENCY AND LOCATION OF POLLINARIA ON INSECTS COLLECTED VISITING ASCLEPIAS SOLANOANA. TI = Total number of insects; TP = Total number of pollinaria; API = Average number of pollinaria per insect; FL = Front leg; ML = Middle leg; HL = Hind leg; ABD = Abdomen; TAR = Tarsi; TIB = Tibiae; FEM = Femora; A = Pollinaria with two pollinia; B = Pollinaria with one pollinium; C = Pollinaria with no pollinia left; IND = Proportion of indirectly attached pollinaria. FL through IND read as percent of total pollinaria observed.

Study site and pollinators	TI	TP	API	Position on body						Position on legs			Condition of pollinaria										
				FL	ML	HL	ABD	TAR	TIB	FEM	A	B	C	IND									
STANTON CK.																							
♀ <i>Xylocopa</i> <i>californica</i>	2	39	19.5	51.2	10.3	15.4	23.1	12.8	61.5	2.5	35.9	7.7	56.4	0.0									
♂ <i>Xylocopa</i> <i>californica</i>	18	610 <sup>1</sup>	33.9	22.1	20.3	18.2	38.9	11.0	48.0	1.6	30.7	25.7	43.6	5.6									
♂ <i>Bombus</i> <i>vosnesenskii</i>	17	495	29.1	30.5	36.2	33.3	0.0	27.2	72.5	0.2	17.7	18.0	64.2	2.2									
♀ <i>Apis</i> <i>mellifera</i>	5	242	48.4	26.4	24.7	48.8	0.0	41.7 <sup>2</sup>	58.3	0.0	44.6	21.5	33.9	5.4									
TEDOC MTN.																							
♀ <i>Xylocopa</i> <i>californica</i>	4	652	163.0	18.7	14.2	44.7	22.4	4.8	71.4	1.4	12.4	17.3	70.2	0.9									
♂ <i>Xylocopa</i> <i>californica</i>	9	668	74.2	16.6	11.7	12.1	59.6	3.9	35.0	1.4	33.4	24.9	41.6	13.3									
<b>TOTAL</b>	55	2706	49.2	22.3	19.9	28.5	29.2	13.5	56.1	1.1	25.9	21.4	52.6	5.6									

<sup>1</sup> Includes two pollinaria on thoracic hairs and one pollinarium on mouthparts.

<sup>2</sup> 43.6% of these were attached to the enlarged first tarsal segment of the hind legs.

Pollinaria were examined to determine whether the "slit" or corpusculum was attached directly to the insect's body or indirectly to another pollinarium carried by the insect. The proportion of indirect attachments was low, ranging from 13.3% in *Xylocopa* males from Tedoc Mtn. to .9% for females of the same species at the same site. In all, only 5.6% or 152 of 2706 pollinaria were attached indirectly, 58% of these on the male carpenter bees at Tedoc Mtn.

The condition of pollinaria, intact (condition A), one pollinium removed (condition B), or both pollinia removed leaving only the corpusculum (condition C), were also examined. On *Apis* workers and *Xylocopa* males the ratios among A, B, and C pollinaria were roughly similar, honey bees tending to have slightly more A pollinaria, and the male carpenter bees more C pollinaria. Both *Bombus* males and *Xylocopa* females, however, had significantly higher percentages of C pollinaria. In *Bombus* these C pollinaria were evenly divided among the three leg pairs, while in the female carpenter bees more C pollinaria were on the pollen-collecting hairs of the hind legs. This may indicate that the insects actively remove pollinia by their cleaning behavior in addition to inserting them into stigmatic chambers. Also of note was the existence of a small number of A pollinaria with pollinaria attached to them. This indicates that the introduction of a pollinium into a slit or the attachment of the translator arm of that pollinium to the corpusculum of the flower's pollinarium does not necessarily result in a successful insertion.

*Plants and Insects:* Accounts of observations of pollinators on other species of *Asclepias* (Robertson, 1929; Woodson, 1954; Macior, 1965; Willson and Rathcke 1974), as well as personal observations in California, Arizona, and Mexico, have shown that the majority of *Asclepias* species attract numerous kinds of floral visitors, many of which are effective in extracting pollinaria. With *A. solanoana*, however, only two native insect species were observed to pull pollinia from the flowers.

The inflorescences of *A. solanoana* are rather compact, the individual flowers being tightly clustered into a hemispherical head. Each inflorescence is erect on its peduncle, providing a dome-shaped platform for visiting insects. The gynostegium of each flower is situated well above the hoods so that, upon landing, the insects utilize the gynostegia as footholds as they crawl about the flowers gathering nectar. Situated as they are, the slit regions are easily accessible to hairs and spines on the legs of insects. The large, hairy carpenter bees seem particularly well suited for the removal of pollinaria since they also drag their abdominal brush across the exposed slit regions (Fig. 6). Bumble bees did not make appreciable body contact with the exposed gynostegia and collected no pollinaria on their abdomens. The bodies of honey bees, nearly devoid of hairs or spines, also collected no pollinaria.

Significantly fewer pollinaria were pulled per flower at Tedoc Mtn.

than at Stanton Ck. Therefore, it would be expected that the Tedoc Mtn. pollinators would tend to pick up more pollinaria per visit than those at Stanton Ck. The *Xylocopa* at Tedoc Mtn. did, in fact, carry more pollinaria per insect than those at Stanton Ck.

The presence of *Apis* at Stanton Ck. in 1974 may be important in the explanation of the slightly but significantly greater number of extractions per flower that year than in previous or following years. Since, theoretically, three additional extraction acts per flower would be necessary to extract the additional pollinia, the introduction of an additional source of pollinators (*Apis*) could account for this difference. Another consideration is that the number of available pollinators at the Tedoc Mtn. site may have been smaller in proportion to the number of plants available at Stanton Ck. The population size at Tedoc Mtn. was much larger, numbering over 150 plants, as compared to an initial total of about 35 plants at the Stanton Ck. site. Also, while two other populations of *A. solanoana*, totaling an additional 100 or more plants, were located within three miles of the Tedoc Mtn. study site, extensive explorations near the Stanton Ck. site revealed fewer than 15 additional plants.

Additional sources of nectar and pollen may be significant in limiting pollinator activity on *A. solanoana*. Female *Xylocopa*, for example, carried pollen of other plant species. Male and female carpenter bees visited *Arctostaphylos viscida* flowers early in the spring at the beginning of flowering of *A. solanoana* at Stanton Ck., and a few *X. californica* and several *X. tabaniformis* ssp. *orpifex* visited *Penstemon breviflorus* ssp. *glabripetalis* near the study site. No pollinaria, however, were found on the three *X. californica* captured and examined. Carpenter bees at the Tedoc Mtn. site were not observed visiting other plant species in the vicinity of the study site.

Only males of *Bombus vosnesenskii* were observed on *A. solanoana* at Stanton Ck., but numerous other individuals of the same species, both males and workers, and several *Xylocopa tabaniformis* ssp. *orpifex* obtained nectar and pollen from *Phacelia imbricata* less than 100 m from the study site. However, there were no pollinaria on any insects collected on *Phacelia*. These observations suggest that the floral constancy of the insects may limit the number of visitors to *A. solanoana* blossoms. For example, while *X. tabaniformis* was present near the Stanton Ck. study site and could have been an effective pollinator of *A. solanoana*, no individuals were observed visiting any *Asclepias* plants.

Field observations of insect visitation indicated that plants within each study population were not visited equally, but that microrelief, number of open inflorescences, and general position of particular plants within the population seemed to affect pollinator preference. Analysis of extraction and insertion data for the sites, however, indicated that frequency of insect visitation and subsequent pollen transfer did not limit mature fruit production. In all inflorescences examined, the number of insertions

far exceeded the number of fruits produced per inflorescence. Furthermore, it appeared that no more than one pollinium per flower was necessary to effect fruit set and full seed production. In an examination of flower parts from tips of healthy, rapidly maturing follicles at Tedoc Mtn., three of ten contained only a single pollinium in one of the five stigmatic chambers, a percentage similar to that found in flowers which did not set fruit.

Insertion of pollinia into flowers of the same plant from which they were produced might partially account for the high number of pollinia inserted for each fruit produced. If *A. solanoana* is largely or completely self sterile, a condition assumed for most milkweed species (Woodson, 1954; Wyatt, 1976), then pollinia inserted in self pollinations should be discounted in any estimate of successful pollen transfers. However, excessive numbers of pollinia inserted in comparison with numbers of fruit set and the presence of many abortive fruit argues strongly against the hypothesis that insufficient pollination is the cause of relatively low fruit set in both populations. Galil and Zeroni (1969) observed that, in *A. curassavica*, pollen tube germination occurred only where the convex margin of the pollinium contacted the stigmatic surface. Nearly all the inserted pollinia of *A. solanoana* examined, however, were oriented with the convex margin in contact with the stigmatic surface. Partially inserted pollinia were not counted in this study.

In experimenting with populations of *A. syriaca* in Illinois, Willson and Rathcke (1974) hypothesized that selection favored a balance between energy allocated to production of pods and seeds and energy allocated to production of surplus flowers which increase the output of pollinia, though at the expense of decreasing efficiency of seed production per flower. This model may well be applicable to *A. syriaca*. In *A. solanoana* however, the lack of correlation between the number of flowers in an inflorescence and rates of extraction or insertion, the relatively narrow range of variation in inflorescence size, and the seeming "overkill" in terms of numbers of pollinia inserted per inflorescence, make this hypothesis untenable. The relatively large number of small flowers produced may be important in attracting insects and in providing sufficient quantities of nectar to maintain a constant rather than occasional relationship with them. The majority of *Asclepias* species I have studied show a distinct seasonal variation in number of flowers per inflorescence with larger inflorescences with more flowers produced early in the season. The size of inflorescences may be correlated with vigor and rate of growth of the whole plant which may affect the size of floral apices which produce inflorescences. If this were so, numbers of flowers per inflorescence would not only vary throughout the year, but from year to year. Fruit production might also vary from year to year, not as a direct consequence of inflorescence size, but rather in response to greater allocation of energy for reproduction during periods of vigorous growth.

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## VARIATION IN THE HELIANTHUS EXILIS-BOLANDERI COMPLEX: A REEXAMINATION

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In his classic monograph on the evolution of *Helianthus annuus* L. and *H. bolanderi* Gray, Heiser (1949) analyzed variation in natural populations as well as artificial hybrids that led him to the following conclu-

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sions: "Of the entities comprising *H. bolanderi*, the one Gray designated *H. exilis* appears to be confined almost exclusively to areas of serpentine outcrops in many of the foothills regions of California, whereas true *H. Bolanderi* occurs in the valleys as a weed. The two races of *H. Bolanderi* conform to the definition of the "ecotype" of the experimental taxonomist." Heiser (1949) discussed the role of introgressive hybridization between *H. annuus*, an introduction into California by the American Indian in recent times, and *H. bolanderi* (native foothills race). Accordingly, he provided a taxonomic key for the two races of *H. bolanderi*, *annuus* x *bolanderi* hybrid swarms, and for the western races of *H. annuus*. A hybrid swarm between *H. annuus* and *H. bolanderi* was extensively studied by Stebbins and Daly (1961) in which a hybrid index based on six morphological traits was used to analyze population changes over an eight-year period. Although Heiser (1949) raised issues about the definition of species boundaries and the tentative nature of his conclusions regarding the role of introgression, and later (Heiser, 1973) concluded that "no additional evidence has appeared to support or to reject the hypothesis of the origin of the weedy race of *H. bolanderi* through introgression," the sunflower story is frequently cited as an outstanding example of introgression (e.g. Grant, 1971; Briggs and Walters, 1969).

Here we shall briefly reexamine evidence from population studies of two races of *H. bolanderi* (the *exilis-bolanderi* complex) and weedy *H. annuus* in relation to certain systematic, genetic, and statistical aspects of introgression. Morphological variation for a wide range of characters and in three new collections of *H. exilis* provided the basis of a multivariate analysis of these taxa. Preliminary data from the electrophoretic assays of allozyme variation are presented as a test of specific gene transfers through introgression. Two other lines of study, namely, the cytogenetics of hybrid swarms and the ecological tests of the adaptive role of gene exchange, will be discussed in another paper. It should be noted that introgression resembles the common backcross method of plant breeding, and therefore detailed analyses of introgressive hybridization are of wide interest in both evolution and crop genetics.

#### MATERIALS AND METHODS

Fourteen populations were sampled during the summers of 1973, 1974 and 1975 by harvesting 50-100 individuals along two or three linear transects per population (Table 1). Twenty to 75 plants were scored for plant height\*, branching index (1 = none to 5 = extensive branching), stem diameter, stem pubescence\*, stem color (1 = green to 4 = red), number of opposite leaf pairs, number of unpaired leaves\*, leaf length\*, and width\*, leaf shape index\* (1 = linear, 5 = cordate), leaf margin

\* Characters marked by an asterisk were also scored by Heiser (1949).

TABLE 1. SPECIES AND PROVENIENCE OF THE POPULATIONS STUDIED.

Species	Locality	Code	No. of plants studied
<i>annuus</i>	1. <i>H. annuus</i>	Yolo Bypass; 0.5 mi. S of 1st bridge of I-80 from Davis to Sacramento.	DVS 1 24
	2. <i>H. annuus</i> and <i>H. annuus</i> x <i>H. Bolanderi</i>	40 meters N from site DVS 3, across the railways.	DVS 2 33
<i>exilis</i>	3. <i>H. Bolanderi</i>	About 3 mi. NW of Knoxville (located N of Lake Berryessa), off Berryessa-Knoxville Road and along Cedar Creek Road.	KNX 1 20
	4. <i>H. Bolanderi</i>	1.5 mi. W of KNX 1, near Hunting Creek.	KNX 2 42
	5. <i>H. Bolanderi</i>	Patch located near the Campground, about 50 meters from KNX 2.	KNX 2a 20
<i>valley bolanderi</i>	6. <i>H. Bolanderi</i>	4 mi. S of Williams Colusa Co., along Rd. 15.	WLS 32
	7. <i>H. Bolanderi</i>	4 mi. W of West Butte, Sutter Co., along Pass Road.	WBT 46
	8. <i>H. Bolanderi</i>	2.5 mi. NW of Sutter, Sutter Co., along Pass Road.	STR 39
<i>foothills bolanderi</i>	9. <i>H. Bolanderi</i> and <i>H. Bolanderi</i> x <i>H. annuus</i>	5.4 mi. E of Davis, Yolo Co., in ditch area between railways and Frontage Road along 180.	DVS 3 75
	10. <i>H. Bolanderi</i>	About 7 mi. NW of Knoxville, off Morgan Valley Road.	KNX 5 36
	11. <i>H. Bolanderi</i>	About 5 mi. NW of Knoxville, along Morgan Valley Road.	KNX 7 33
	12. <i>H. Bolanderi</i>	3 mi. NE of Middletown, Lake Co., along S29.	MTW 1 26
	13. <i>H. Bolanderi</i>	4 mi. NE of Middletown, Lake Co., along S29.	MTW 2 28
	14. <i>H. Bolanderi</i>	ca. ½ mi. N of KNX 2, along Hunting Creek.	KNX 3 22

dentation (1 = none, 3 = extensive), head diameter\*, disk diameter\*, number of ray flowers\*, ray width, ray flower shape, floret length, floret tube length, basal floret shape index\* (1 = not swollen to 3 = largely swollen), floret color (1 = yellow, 2 = light red, 3 = dark red), stigma apex color (1 = yellow, 2 = orange, 3 = red), lateral and central palea

cusplength, palea apex color, involucre bract number, bract length\* and width\*, bract pubescence\*, achene length\* and width\*. Numerical taxonomic analyses of vegetative and floral characters were carried out with a BMD principal component analysis program.

Samples of populations KNX 1, KNX 2, DVS 1, and DVS 2 were grown during 1975 summer in the greenhouse in 18 cm pots and UC soil mix, and scored for a subset of 15 characters to study population differences under a common environment. To measure the genetic similarities among different groups of populations, electrophoresis for isozyme variation was carried out using standard horizontal starch gel techniques described by Shaw and Prasad (1970), with minor changes to adapt to our materials. Three- to four-week-old seedlings were used for sample extracts. Three enzyme systems (leucine aminopeptidase, phosphoglucosyltransferase, phosphoglucose isomerase) were scored. Data on the allelic composition at two alcohol dehydrogenase loci were kindly supplied by Dr. A. Torres of the University of Kansas on a small set of samples. For present purposes, a phenotypic analysis of variation is presented in terms of the presence vs. absence of well-developed and consistent bands within populations, rather than gene frequencies, since genetic analyses using progeny tests are not yet completed for most of the loci. Accordingly, data are summarized in terms of the number of different alleles present in several populations, and estimates of similarity are based on Jaccard's index,

$$J = \frac{c}{a + b - c}$$

where  $c$  = number of common alleles between populations A and B;  $a$  and  $b$  are total numbers of alleles in populations A and B respectively.

#### RESULTS AND DISCUSSION

Means were determined for 15 characters and ten selected populations based on the field samples (Table 2). Heiser (1949) had noted that important taxonomic distinctions were based on the shape of involucre bracts, the nature of the palea or chaff (length, texture and angle of awn of the palea or chaff), and the overall size of the plants. Leaf shape, disk diameter, ray number, and achene length were included in his "taxonomic key features" (Heiser's Table 1). Our data confirm his observations on these characters for describing the two *H. bolanderi* "ecotypes" and weedy *H. annuus* (Table 2). However, it should be noted that our *H. exilis* populations are a distinct group based on the same characters and in fact represent an extreme below the following ranges for the foothills *H. bolanderi*:

TABLE 2. ESTIMATES OF CHARACTER MEANS FOR 10 SELECTED POPULATIONS

Character	H. bolanderi											
	H. annuus			valley			foothills			H. exilis		
	DVS 1	DVS 2	WBT	STR	DVS 3	MTW 1	MTW 2	KNX 5	KNX 1	KNX 2	KNX 1	KNX 2
Plant height (cm)	87.5	108.8	60.7	55.6	30.3	65.3	50.6	39.1	24.4	24.1		
Branching index	2.6	2.5	2.1	2.6	1.3	3.1	2.1	2.6	2.7	2.2		
Leaf length (mm)	89.0	88.5	50.0	49.6	26.0	64.0	48.6	52.0	28.0	40.0		
Leaf shape index	4.7	4.2	3.4	2.8	3.1	2.5	2.9	3.0	3.8	3.9		
Head diameter (mm)	62.9	64.7	49.0	47.0	38.7	41.7	44.8	42.4	29.7	26.1		
Disk diameter (mm)	17.6	18.6	15.5	13.8	9.4	13.6	12.3	11.4	7.7	7.1		
Ray number	13.3	13.9	12.3	11.4	9.3	10.8	10.7	9.6	6.8	7.7		
Floret length (mm)	7.5	6.9	6.3	6.3	5.8	5.7	5.8	6.1	5.3	4.6		
Basal floret shape index	3.0	2.7	2.0	1.8	1.9	1.4	1.4	1.3	1.6	1.3		
Apical stigma color index	3.9	3.7	2.4	2.0	1.7	1.0	1.0	1.1	1.0	1.2		
Bract length (mm)	12.3	11.6	12.3	11.9	9.6	11.4	11.2	12.4	8.8	8.5		
Bract pubescence index	1.4	1.7	2.5	2.7	2.6	2.8	2.9	3.0	3.2	2.6		
Seed length (mm)	5.4	5.1	4.1	4.3	3.8	2.9	3.2	3.3	2.8	2.5		
Seed width (mm)	2.6	2.4	2.1	2.1	2.0	1.5	1.6	1.8	1.6	1.3		

	plant height	disk diameter	bract width	ray number	achene length
serpentine, foothill race (á la Heiser)	30–100 cm	15–20 mm	30–40 mm	10–13	3.0–4.0 mm

All three populations from new locations for what we have designated as *H. exilis* group are homogeneous, different, and fall below the ranges given for the foothills *bolanderi* populations (cf. Jain et al., 1977 for agronomic traits in *H. exilis*). Apparently, these localities were not visited by Heiser; the access road to these populations on the Bureau of Land Management land was completed ten years ago. Several of the localities described on the University of California, Berkeley herbarium specimens for *H. exilis* were revisited in 1974. A majority have very small populations and showed a variation pattern in agreement with that described by Heiser (1949) for the *H. bolanderi* group.

Analyses of intrapopulation variation are of particular interest. A nested analysis of variance showed that (1) the *H. annuus* and *H. bolanderi* populations are significantly different ( $P < .05$ ) for 20 out of 21 characters tested; and (2) populations of each of the two species are also significantly different for 18 characters at  $P = .01$  and two characters at  $P = .05$  levels. Estimates of the coefficients of variations (CV) for a majority of characters were higher in the valley *H. bolanderi* and weedy *annuus* groups than for the foothills *H. bolanderi* or the *H. exilis* populations.

Figure 1 compares the means and ranges (as well as the estimates of standard deviations) for *H. exilis* vs. the two *H. bolanderi* groups pooled together. The ranges overlap considerably but the *H. exilis* means were consistently different from those of *H. bolanderi*. Diagnostic keys in such cases would clearly require a numerical taxonomic approach as well as a further search for certain qualitative genetic traits.

Principal component analysis for vegetative and floral characters respectively reveals that populations 3, 4 and 5 representing *H. exilis* form a separate group, DVS 1 and DVS 2 representing *H. annuus* as a second distinct group, and the remainder *H. bolanderi* populations form a continuum between them (Figs. 2, 3). Populations 10–14 represent the foothills race of *H. bolanderi* which are separated from the valley race (represented by the populations WLS, WBT, STR). Population 9 (DVS 3) represents a hybrid swarm studied by Stebbins and Daly (1961) which was recently fragmented by cultivation and road construction. It seems to be differentiated from all others in its vegetative characters. Overall, the multivariate analysis confirms the observations of Heiser and ours on the four overlapping groups identified in these collections (Table 1). Moreover, data from greenhouse materials of KNX 1, KNX 2

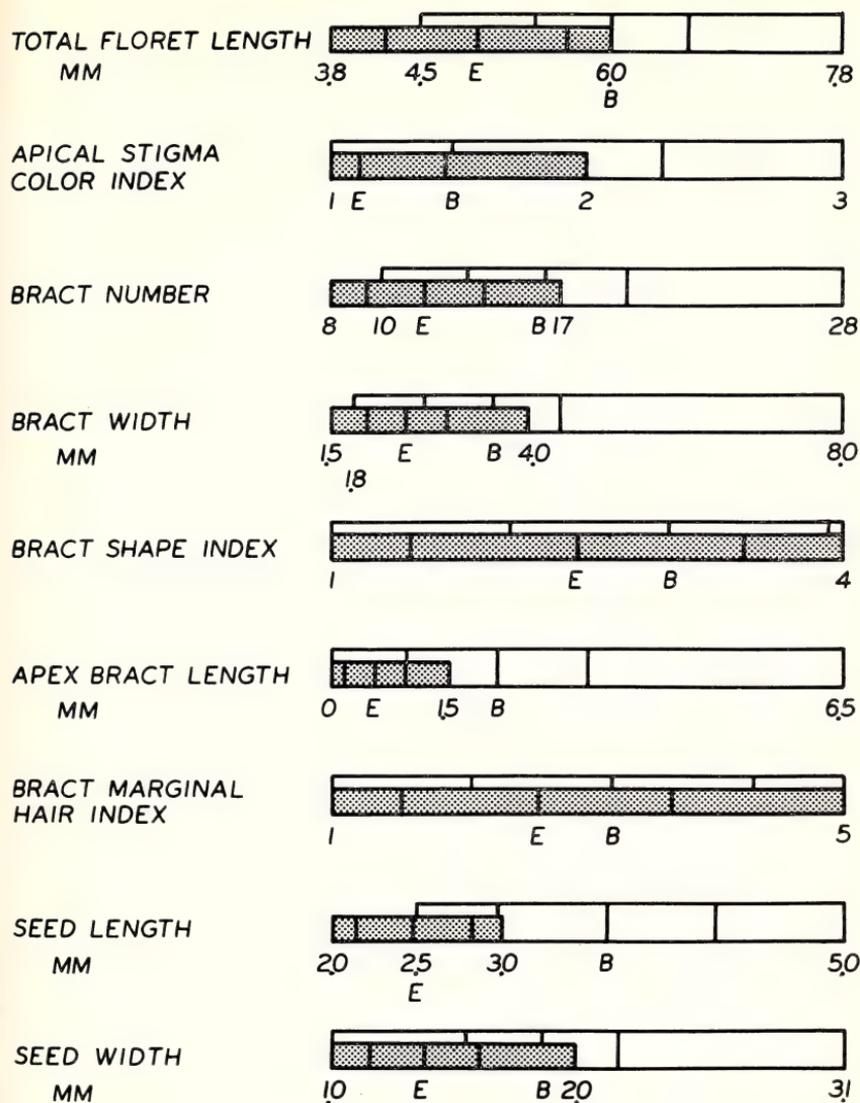


FIG. 1. Range of variation in *H. exilis* (E, stippled area) vs. *H. bolanderi* (B, nonstippled area). Bars near E or B indicate the means and the two bars placed on each side of the means indicate standard deviations. Note the distinctness of *H. exilis* on the basis of range as well as the lower extremes for several characters.

vs. BGS vs. DVS 1 and DVS 2 gave significant intergroup differences in a majority of the same characters. Thus, populations as grouped here seem to represent genetically differentiated clusters. Introgression, on the other hand, is neither supported directly nor ruled out by these observations. Valley *H. bolanderi* and weedy *H. annuus* are most likely connected by a

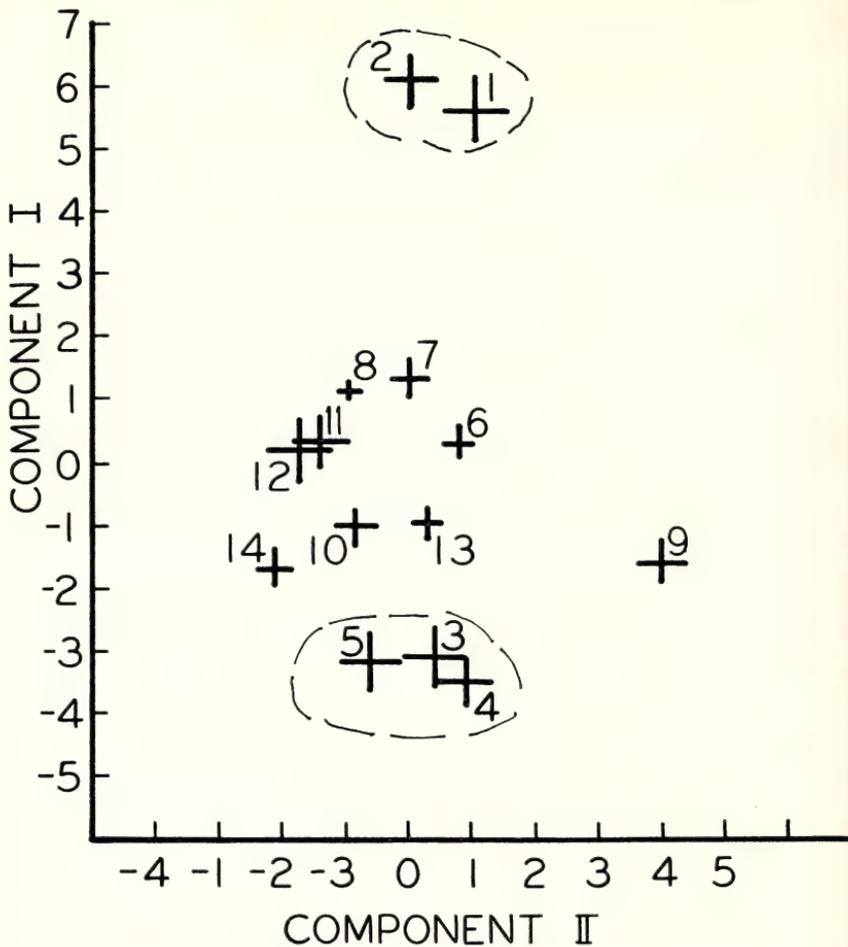


FIG. 2. Principal component analysis of 14 OTUs (Operational Taxonomic Units) using stem, leaf, and seed characters. The codes of locations (1 to 14) are given in Table 1. Dotted boundaries around the four groups of OTUs are drawn simply to match with the four "taxa" as noted in Table 1. No. 9 is an outlier (see text).

series of gene exchange events, and *H. bolanderi* and *H. exilis* in the foothills probably represent another series of populations connected by a two-way introgression underlying the origin of variation in *H. bolanderi*. On the other hand, native *H. exilis* might have been highly variable and could have colonized some disturbed areas on its own. A complete description of parental forms uncontaminated by hybridization is a prerequisite to the "proof" for introgression, and as noted by Heiser (1973) in a recent review, reliance on simply circumstantial evidence is not sufficient.

The so-called hybrid index method is often used to establish introgression (e.g. Keeley, 1976). In this method a set of diagnostic charac-

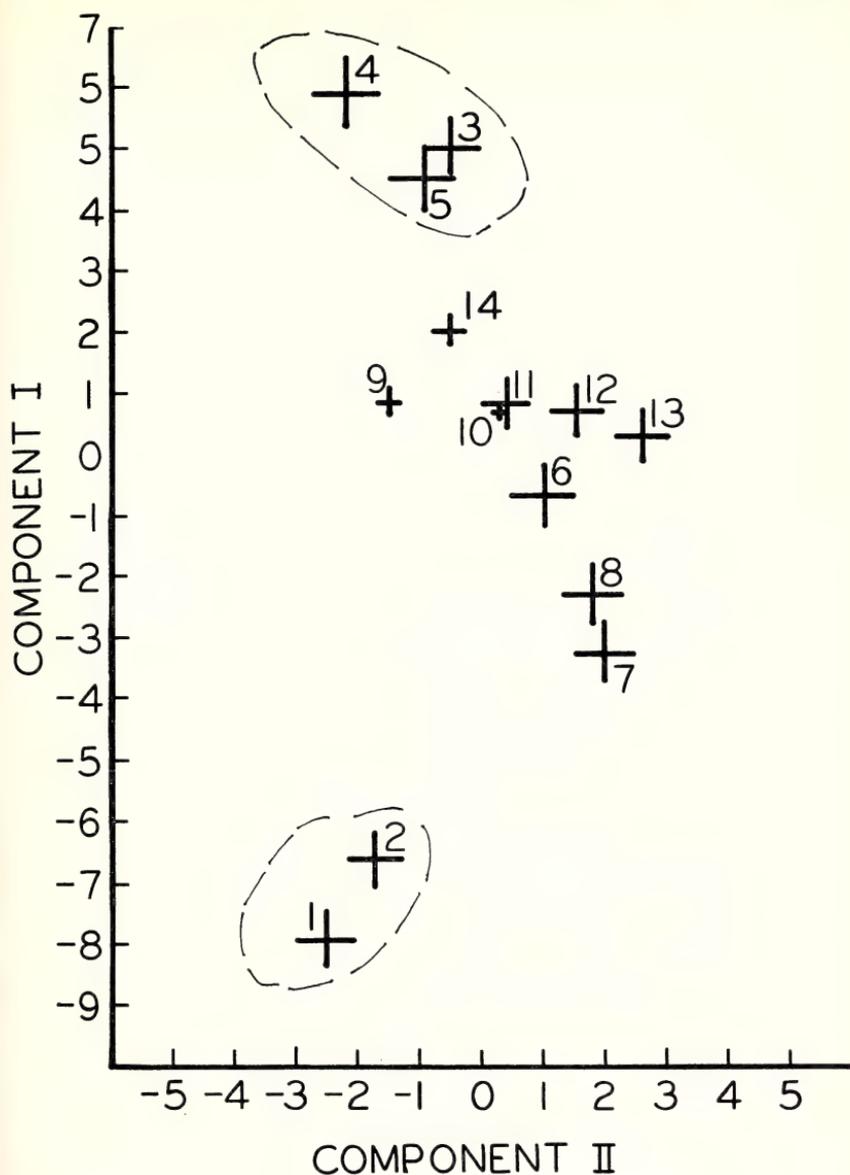


FIG. 3. Same as in Fig. 2 except for the use of floral characters. Note the same four groups, in particular, the separation of *H. annuus* (1,2) and *H. exilis* (3,4,5) from each other.

ters are often selected to pictorialize the variation in putative hybrid swarms. If they vary in a way to show a large amount of overlap with one of the parents but with a few characters from the other parent, introgression is assumed. Many of the examples perhaps show this con-

vincingly, but as noted recently by Namkoong (1966), several statistical and genetic assumptions are rarely stated, much less tested. For example, the number of populations required and the statistical differentiation of hybrid index scores are fairly stringent conditions. Additive genetic variation, independence of different traits, etc. are also assumed. We developed hybrid indices (or what we prefer to call "species identity scores" (SIS) since hybridity need not be presumed) using nine characters chosen to include the six characters (Fig. 4) used by Heiser (1949) and Stebbins and Daly (1961) in their studies and to represent a highly heritable and more or less correlated set of nine traits (Fig. 5) in which case the distributions of DVS 1 and DVS 2 become wider and so also for the WBT population of *H. bolanderi*. The overall gradient across four groups still remains consistent. Use of *t*-test for significance showed SIS means to be significantly different among various groups, with a larger difference when we used SIS based on the nine correlated traits (Fig. 5). Further weighting by their respective heritability estimates obtained from a greenhouse study (Olivieri, 1976) confirmed that differentiation is at least partly genetic. Use of more characters with known genetic control should improve the interpretation of the SIS scores.

Electrophoretic assays provided a series of isozyme markers (presence vs. absence of bands on gels). Zymograms are drawn to derive the allelic designations for various phenotypes. For alcohol dehydrogenase, surprisingly, *H. exilis* and two cultivated varieties of sunflower had the same alleles whereas *H. bolanderi* showed two unique alleles (A. M. Torres, pers. comm.). For the other three enzyme systems our data are summarized in Table 3. *H. exilis* (KNX 1 and KNX 2) have unique alleles at four out of the eight loci whereas *H. bolanderi* populations have a great deal of variability in both foothills and valley populations but with fewer "unique" alleles. The estimates of Jaccard's index based on the shared alleles between groups taken pairwise are as follows: (a) *H. exilis* vs. foothills *H. bolanderi*: 0.63; (b) *H. exilis* vs. valley *H. bolanderi*: 0.57; (c) valley vs. foothills *H. bolanderi*: 0.69. These estimates are based on very small samples (20 plants per population, two populations per group) and should be considered preliminary. However, so far there is no convincing evidence to reject or accept the hypothesis that the foothills race of *H. bolanderi* is more similar to *H. exilis* due to gene exchange. With further genetic work on allozyme loci and extensive enzyme assays of our collections, this method might yield a crucial test for the postulated gene exchanges between different taxa.

For genetic variation analyses to be useful in a specific test of introgression hypothesis, the key criteria, as outlined by Heiser (1973), include increased hybridity and genetic variation, frequently through the occurrence of a few alleles characteristic of species A in the populations of species B living in the areas of sympatry and habitat changes in recent past. Experimental hybrids and backcrosses could provide some clues to

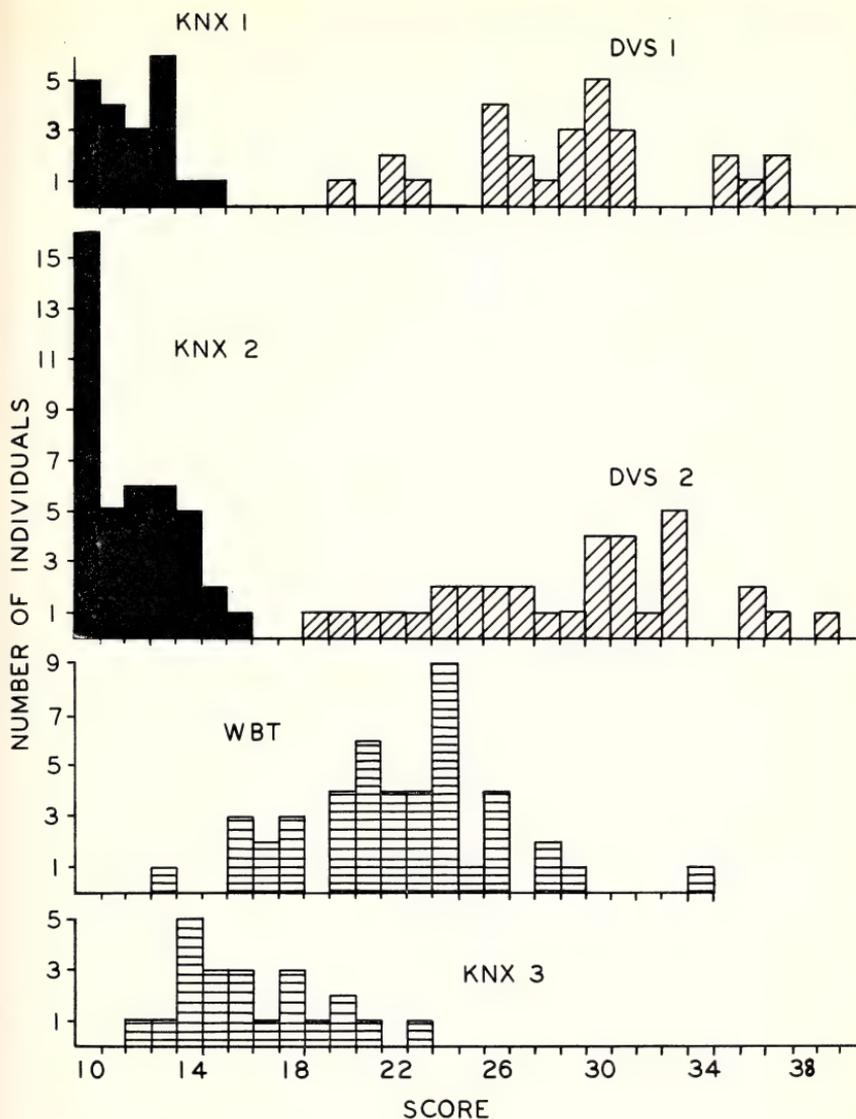


FIG. 4. Histograms showing the frequency distributions of "species identity scores" (= hybrid indices) based on the six characters used by Heiser (1949) in his earlier studies.

the potential for gene exchange as well as to the genetics of species differences. For example, Rick (1969) developed a test for controlled introgression in tomato (*Lycopersicon-Solanum*) crosses using recombination data in the marked regions of three chromosomes. Wall and Wall (1975) developed an experimental test in *Phaseolus* species based on allozyme

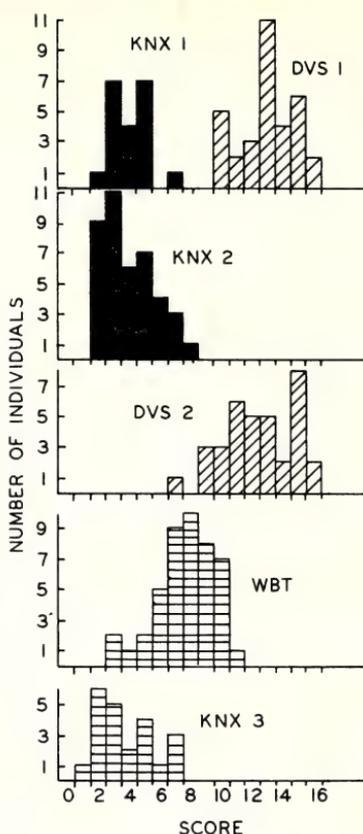


FIG. 5. Same as in Fig. 4 except for the use of nine most highly correlated traits, namely, plant height, leaf shape, stem diameter, diameter of head and disk, ray number, bract number, bract length and bract width. Note that the pattern of distribution is slightly changed toward a wider range and less overlap between the scores for *H. annuus* (DVS1, DVS2) and *H. exilis* (KNX1, KNX2).

TABLE 3. GENETIC VARIATION AT ALLOZYME LOCI.

Enzyme locus	Number of alleles					
	exilis		foothills bolanderi		valley bolanderi	
	total	"unique"	total	"unique"	total	"unique"
*Pgm-1	2	1	1	0	1	0
Pgm-2	2	0	2	0	2	0
Pgm-3	3	1	2	0	2	0
*Lap-1	3	1	3	0	3	1
Lap-2	1	0	1	0	2	1
Lap-3	3	1	3	1	4	0
*Pgi-1	1	0	1	0	1	0
Pgi-2	1	0	2	1	2	1

surveys. Several other recent reports (e.g. *Sorghum-Saccharum*; maize-teosinte) have recently appeared in the crop science literature. The results of this study show that evidence for introgression needs to be examined in relation to morphology, Mendelian loci, quantitative genetics of distinguishing characters, and appropriate statistical tests of differences among various taxa. Hopefully, the sunflowers will provide some very exciting materials for population studies on the role of hybridization in plant evolution.

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A NEW COMBINATION IN CYMOPHORA  
(COMPOSITAE: HELIANTHEAE: GALINSOGINAE)

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Specimens of *Tridax* L. and *Cymophora* B. L. Robins. were examined by the author during studies of the generic and specific relationships of *Galinsoga* Ruiz & Pavon (Canne, in press a, b). A recent, additional study of several specimens of the relatively poorly known *Tridax venezuelensis* Arist. & Cuatr. indicate that this species falls within the concept of *Cymophora* as discussed by Turner and Powell (1977). The transfer of *T. venezuelensis* to *Cymophora* is made here and comments are included concerning interspecific relationships in *Cymophora*.

*Tridax venezuelensis* shares features of the pappus, achenes, and capitulescence with *T. dubia* Rose and *Cymophora accedens* (S. F. Blake) Turner & Powell while resembling *Galinsoga* in several vegetative and floral features (Aristeguieta, 1964; Powell, 1966). However, both *T. venezuelensis* and *C. accedens* possess additional features that do not occur, or occur only rarely, in *Tridax* and *Galinsoga*. These are the white to creamy yellow corolla color; paniculate capitulescence; angular disc achenes; and the cylindrical to subcampanulate involucre that characterize *Cymophora*. *Tridax venezuelensis* differs from *Tridax* proper in achenes glabrous to strigose, not densely long villous or pilose; pappus of fimbriate scales rather than plumose bristles; and heads less than 8 mm diameter. The transfer of *T. venezuelensis* to *Cymophora* is made on the basis of these morphological comparisons.

***Cymophora venezuelensis* (Arist. & Cuatr.) Canne, comb. nov.**

*Tridax venezuelensis* Aristeguieta & Cuatrecasas, Flora de Venezuela 10:694. 1964. TYPE: VENEZUELA: MIRANDA, La Providencia, Sep 1936, *H. Pittier 13754* (HOLOTYPE, VEN; ISOTYPES, F! US!; PARATYPES, *V. M. Badillo 271, 772*, VEN; *H. Eggers 13508*, US!; *H. Pittier 11152*, GH! NY! P! US!).

Additional specimens examined: VENEZUELA: DISTRITO FEDERAL, between Naiguatá and Hacienda Cocuizal, 7 Oct 1966, *J. Steyermark 97465* (F); above Chichiriviche, 1 Jul 1966, *J. Steyermark & L. Aristeguieta 122* (NY, US). State and locality unknown, 9 Aug 1891, *H. Eggers 13568* (US); 1865, *Moritz s.n.* (BM).

*Cymophora venezuelensis* is distinguished from the other three species in the genus by its pistillate ray florets with corollas having short inner lobelets. The peripheral florets of other species are perfect and have inconspicuously ligulate corollas. *Cymophora venezuelensis* differs in distribution as well, being known only from northern Venezuela, whereas other species of *Cymophora* occur in south central Mexico.

The four species of *Cymphora* fall into two rather well-defined morphological groups that presumably reflect closeness of relationship. *Cymphora venezuelensis* and *C. hintonii* Turner & Powell have ovate to trullate leaves with coarsely serrate margins, petioles 2–5 cm long, phyllaries with 15–20 veins, and, in *C. venezuelensis*, pales with 8–16 veins but pales absent in *C. hintonii*. In contrast, *C. accedens* and *C. pringlei* B. L. Robins. have ovate to ovate-lanceolate leaves with sub-entire to serrate margins, petioles to 2 cm long, phyllaries with 4–9 veins, and pales with 3–5 veins. Nomenclatural recognition of these species groups seems unnecessary in such a small genus until warranted by additional knowledge of the biology of the species.

#### ACKNOWLEDGMENTS

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#### REVIEW

*California Mushrooms, a Field Guide to the Boletes*. By HARRY D. THIERS. vii + 261, 4 figs., colored microfiche with 54 figs. Hafner Press, New York. 1975. \$15.95.

Californians interested in the boletes now have a treatise prepared by an internationally recognized student of this taxonomically difficult group. Previous comprehensive treatments of this group in North America have emphasized eastern species. Various popular mushroom books have included a few bolete species, but the identification of all but the most common and unique California bolete species was essentially impossible, except for the specialists. It is perhaps a bit optimistic to expect that everyone, even with the aid of Professor Thiers' book, will be able to identify bolete species without a good compound microscope and a good deal of effort and experience. Nevertheless, this book provides a means, regardless of previous training, for anyone to learn the California bolete flora.

Recent taxonomic studies, including this work, in the Boletaceae and of other groups of fungi strongly suggest that there is a greater diversity of fungal species than previously thought. Thus, regional taxonomic treatments rather than worldwide, or even continental, monographs will probably become the objective of the fungal taxonomist, especially those working with the taxa of the saprobic basidiomycetes. Professor Thiers' publication on the Boletaceae of California places this group among the few fungal taxa that are *relatively* well known in any region in North America. Even so, as the author emphasizes, this publication probably represents only a firm starting point for an understanding of the bolete species in California.

The author has wisely based his species descriptions on those specimens housed

in his herbarium. The vast majority of these specimens were collected by the author or his students.

In the introduction (19 pp.) Professor Thiers briefly describes the somatic, or vegetative, phase of the boletes and discusses in more detail the bolete fruiting structures, especially those features of the basidiocarp that are of taxonomic importance. He introduces the necessary terminology in such a manner that a serious student will be able to use the book. Four figures are provided to supplement the explanations given in the text. Techniques of study of the basidiocarps and methods of collecting boletes are subjects that are also covered. The author describes the probably mycorrhizal association of 36 species in table form. This emphasizes the necessity of noting the trees associated with the various bolete species when making collections and of the probable importance of the Boletaceae as mycorrhizal formers with forest trees. In California all bolete species occur only in forested habitats; therefore, they are probably all mycorrhizal formers.

Professor Thiers also provides a brief history of bolete taxonomy and points out the unique features of the species of boletes in California; i.e., the relatively high percentage of endemic species and the absence of representative species of the genera *Strobilomyces* and *Boletellus*.

After a synopsis of the species and subspecies of Boletaceae known from California, a formal description of the family is provided followed by a key to the genera (7) represented in California. Each genus description is followed by a key to the species within each section.

Each species description lists the accepted name of the species as well as several other synonyms and a list of illustrations to the species in other publications. Fifty-four of the eighty California taxa are also illustrated in the colored microfiche. The species or subspecies descriptions consist of a discussion of the macroscopic features of the pileus and stipe, especially the color and texture. The context of both the stipe and pileus are described as are the microscopic features of the tube trama, basidia, and spores. Included here also is the spore print color, still an important taxonomic character in the Agaricales, followed by a description of the reactions of various parts of the basidiocarp to the several chemical tests outlined earlier in the introduction. An appealing feature here, which is often overlooked in other taxonomic treatments of the Agaricales, is that the author cautions the reader that the nature and significance of these chemical tests are essentially unknown.

The author concludes the taxonomic description of the basidiocarps with a discussion of the habitat and distribution of each species in California. He then lists the specimens studied and comments on certain unique features of the species, including its known edibility properties.

The book closes with a field key to the genera, species, and subspecies treated, a list of references, and an index to the various taxa.

This publication is designed for both the professional and amateur mycologist. It is reasonable to expect, in my opinion, that a serious amateur, equipped with a good compound microscope, would be able to identify bolete specimens using this text. While field keys are useful for both the amateur and specialist, mycological taxonomy has long since reached the stage at which microscopic examinations are essential for correct determinations. Among the Agaricales this is probably especially true for the Boletaceae, which are taxonomically notoriously difficult.

There is little doubt but that this publication is an important contribution to the taxonomy of the Agaricales. It will certainly be an essential acquisition for all those interested, for whatever reason, in the mushrooms of California and for all mycological taxonomists. It would, in my opinion, have been desirable to present the 54 color photographs as colored plates rather than in a microfiche; however, this would no doubt have drastically increased the cost, which by today's standards is reasonable. In any case, I, and many others, now eagerly await Professor Thiers' publications on the other families of the Agaricales.—KENNETH WELLS, Department of Botany, University of California, Davis 95616.

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# MADROÑO

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# HYBRIDIZATION OF FOXTAIL AND BRISTLECONE PINES

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The pines have been more successful than most of their coniferous relatives in occupying marginal habitats at the upper and lower edges of the forest zone in western North America. Among the groups restricted to such habitats is subsection *Balfourianae* of *Pinus*, comprising the foxtail and bristlecone pines. These pines characteristically grow on cold dry sites at high elevations, and in most places have few tree associates. Perhaps because of their inaccessibility and limited economic importance, not much was known about them until E. Schulman's discovery in the mid-1950's that some bristlecone pines reach greater ages than other higher organisms (Ferguson, 1968). Since then, much has been learned about the *Balfourianae*, and investigations of natural variation have generated two taxonomic proposals in the group. Bailey (1970) named the western populations of bristlecone pine *P. longaeva*, restricting the older name, *P. aristata* Engelm., to the eastern populations. Mastrogiuseppe (1972) proposed the subdivision of foxtail pine (*P. balfouriana* Grev. & Balf.) into two subspecies.

The first attempts to cross bristlecone and foxtail pines were made in 1940 by the U.S. Forest Service's Institute of Forest Genetics (IFG) at Placerville, California, but most of our exploratory crossing of the *Balfourianae* pines with each other and with other pines was carried out between 1963 and 1971. This paper summarizes the results of these crosses, examines variation in several characteristics of the *Balfourianae*, and relates this information to recent investigations of the systematics and evolution of the group.

## THE TAXA OF *Balfourianae*

Subsection *Balfourianae* is a morphologically and geographically coherent group, with no close affinities to any other group of white pines in subgenus *Strobus* (*Haploxylon*). The needles mostly number five per fascicle, but this common feature of white pines is accompanied by the absence of marginal teeth on the needles, cone scales with dorsal umbos terminating in a mucro or spine, and seeds with long detachable wings—a combination of characters that readily differentiates the *Balfourianae* from other subsections of *Strobus*.

Among the named taxa in the *Balfourianae*, foxtail pine is the most limited in distribution. This Californian endemic grows only in the Klamath Mountains of northwestern California and a portion of the southern

Sierra Nevada centered on Sequoia National Park. The northern and southern stands are separated by more than 500 km. They differ in turpentine composition (Haagen-Smit, Wang and Mirov, 1950) and in morphology, particularly quantitative characteristics of cones and seeds (Mastrogiuseppe, 1972; Mastrogiuseppe and Mastrogiuseppe, 1975). Mastrogiuseppe (1972) summarized the evidence supporting their recognition as separate subspecies.

The bristlecone pines are much more widely distributed, ranging from California to the southern Rocky Mountains. The Colorado River separates eastern *P. aristata* from western *P. longaeva*. Eastern bristlecone pine grows in the mountains of Colorado and New Mexico, with a disjunct population more than 500 km west in the San Francisco Peaks of northern Arizona. Western bristlecone pine is widely distributed in the mountains of Utah, Nevada, and eastern California. At its western limits in the White and Inyo Mountains of California, it grows only about 25 km from the nearest foxtail pine stands on the east slope of the Sierra Nevada.

The eastern and western bristlecone pines differ in morphology (Bailey, 1970) and turpentine composition (Zavarin and Snajberk, 1973; Zavarin, Snajberk and Bailey, 1976). Bailey noted differences in cone morphology and color, resin odor, needle retention, and other features, but his separation of eastern and western bristlecone pines was documented primarily by characteristics of the needle resin canals. He found that most needles of western bristlecone and foxtail pines had two externally visible resin canals and ungrooved needle surfaces. In the needles of eastern bristlecone pine, the resin canals were located beneath shallow grooves in the needle surface, and Bailey estimated the number and distribution of resin canals by counting grooves. About half of the needles had only one groove. The rest had two or more, but in more than half of these needles all but one groove terminated below the apical quarter of the needle.

The resin canals of the eastern trees are also much smaller and closer to the needle surface. They often burst, exuding resin onto the surface. The dried resin forms a white fleck, and the eastern and western trees differ greatly in the incidence of these flecks. Only 5 percent of the needles Bailey sampled in western stands had flecks. In the east, flecks were present on 92–94 percent of the needles from Colorado and New Mexico and 47–63 percent of the needles from Arizona (Bailey, 1970; Zavarin et al., 1976).

Bailey also observed differences between eastern and western bristlecone pines in the shape of the cone base, stoutness and length of the cone bristles, and color of ripe pollen-cones and maturing seed-cones. Measurements of the length of bristles on cones in the IFG herbarium substantiate his statement that eastern bristlecone pines often have longer bristles. Cones from eastern trees averaged about 5 mm in bristle length,

and ranged from 3–8 mm. Cones from western trees had bristles averaging about 3 mm long (range 1.5–6 mm).

Polymorphism in the color of maturing reproductive structures is one of the most distinctive characteristics of western bristlecone pine, differentiating it from all other elements of the *Balfourianae*. The seed-cones of most western trees are dark purple during their second season of development, and the pollen-cones of the same trees are nearly always deep red at maturity. A minority of trees have green seed-cones and yellow (sometimes pink-tipped) pollen-cones. The green-cone trees lack an anthocyanin pigment that is present in the others (Mastrogiuseppe, 1976). This color variant is more common in some western stands than Bailey's (1970) estimate of less than 1%. We found that about 20% of the trees in the White Mountains had green cones (Johnson and Critchfield, 1974), and on Telescope Peak in the Panamint Mountains about 4% had green cones (Unpub. data, IFG). Eastern bristlecone pine and foxtail pine are not known to be polymorphic in cone color. Both have purple or greenish-purple seed-cones and yellow pollen-cones. Thus nearly all western bristlecone pines differ from the other *Balfourianae* pines in the color of either the ripening seed-cones (green) or the mature pollen-cones (deep red).

Bailey's classification of the bristlecone pines was supported by the results of the first detailed investigation of turpentine composition in the group (Zavarin and Snajberk, 1973). With a single exception in each region, turpentine of 37 eastern trees was mostly 3-carene (63–92%); that of 30 western trees was almost entirely  $\alpha$ -pinene (95–97%).

A more complex picture has emerged from further work in which Zavarin et al. (1976) used larger samples and analyzed needle resin as well as the turpentine fraction of wood resin. Between 10 and 26% of the trees sampled in Arizona and the White and Inyo Mountains of California were chemically deviant in turpentine composition. The most remarkable finding of these authors was the turpentine composition of a California stand of *P. longaeva* recently discovered on Sentinel Peak in the Panamint Mountains (Johnson, 1976). All ten trees sampled were higher in 3-carene content than most eastern bristlecone pines. Needle resin composition showed three main groups: Arizona, Colorado–New Mexico, and west of the Colorado River. Arizona trees were closer to Colorado–New Mexico trees in a quantitative measure of chemical similarity, but in several constituents they were intermediate or resembled western trees. Foliage from the single Sentinel Peak tree sampled was most like Colorado–New Mexico trees in resin composition, but in some constituents it was apparently outside the range of other bristlecone pines. Thus there are four chemically identifiable groups of bristlecone pines: Colorado–New Mexico, Arizona, Utah–Nevada, and the highly variable California stands.

## METHODS

*Parent trees.* Access is a problem in the controlled pollination of foxtail and western bristlecone pines, and all parent trees were in a few relatively accessible native stands. No arboretum trees of these taxa were used; none has survived to reproductive age in the warm foothill climate of Placerville.

The first crosses on western bristlecone pine were made in 1940 and 1948 at Telescope Peak in the Panamint Range (plot location: 36°10'N, 117°05'W, 3330 m). In the same years, crosses were made on foxtail pine at Onion Valley, on the east slope of the southern Sierra Nevada (36°46'N, 118°20'W, 2790 m). The fate of the seed harvested from these early crosses is not fully documented and they are not included in the summarized data. Two 1940 crosses of *P. monticola* females and Telescope Peak pollen are included in the data summary (Table 1).

In 1963 and 1971 crosses were made on six and five bristlecone pines about 1.5 km north of Schulman Grove in the White Mountains (plot location: 37°24'N, 118°11'W, 3095 m). Five of the trees were used as females in both years. Pollen was collected from other stands within 1.5 km of Schulman Grove at elevations of 2990–3200 m. All crosses with foxtail pine as female parent were made in 1965 on four trees at Onion Valley. Pollen was collected in several seasons within 0.5 km of Onion Valley at elevations of 2775–2955 m. Pollen from northern foxtail pine was collected in 1961 and 1964 on North Yolla Bolly Mountain at elevations of 2195–2285 m (40°12'N, 122°59'W). Pollen of eastern bristlecone pine was collected in 1970 by D. K. Bailey in three stands west of Denver, Colorado. The stands were 13–27 km apart, and ranged in elevation from 2990–3290 m (39°40'–52'N, 105°34'–44'W).

Crosses of western bristlecone and foxtail pines with other species utilized trees in natural stands and the IFG arboretum. Female parents of *P. bungeana* and *P. flexilis* were old arboretum trees, mostly of unknown origin. *Pinus monticola* and *P. monophylla* females grew in native stands in the central Sierra Nevada, *P. monticola* at 2130 m and *P. monophylla* on the east side at 1615 m. Arboretum trees supplied all pollen except *P. flexilis*, which was collected near Schulman Grove in the White Mountains.

*Techniques and Terminology.* Standard breeding and seed-processing techniques were used (Critchfield, 1963). Pollen was collected during the season before pollination and deep-frozen, unless otherwise noted. The data summaries (Tables 1–4) include all crosses for which we have complete information: numbers of strobili pollinated, cones harvested, and sound and hollow seeds.

An *attempt* is the pollination during a single season of a female parent with pollen from a single male parent (Tables 1–4) or with a mixture of pollen from more than one male parent (Table 1 only). *Crossability* is

TABLE 1. CROSSES OF *Balfourianae* WITH OTHER WHITE PINES.

Female parent	Male parent	
	<i>monticola</i>	<i>longaeva</i>
<i>monticola</i>	2 (-) / 2	1 / 2 (2) / 0
	79: 43	38: 87
	76.8 / 94.4	0 / 92.2
<i>flexilis</i>	<i>flexilis</i>	<i>balfouriana</i>
	2 (2) / 2	2 (2) / 0 2 /
	17: 59	18: 0
	38.0 / 65.4	
<i>balfouriana</i>	3 (3) / 2	3 (5) / 3
	18: 78	44: 93
	0.2 / 42.8	46.4 / 55.4
<i>bungeana</i>	<i>bungeana</i>	<i>balfouriana</i>
	1 (1) / 1 3 /	1 (1) / 0
	8: 100	3: 67
	4.0 / 6.0	0 / 0.5
<i>balfouriana</i>	3 (3) / 0	3 (5) / 3
	15: 73	47: 85
	0 / 13.0	53.6 / 62.3
<i>monophylla</i>	<i>monophylla</i>	<i>balfouriana</i>
	2 (4) / 2	2 (6) / 0
	25: 44	34: 29
	9.4 / 11.6	0 / 8.5

nd pollination  
 llen frozen for 2 years  
 f pollination

number of attempts.....

number of female strobili.....

number of sound seeds per cone.....

0	(0)	0
0	0	
0.0	/	0.0

.....Number of tree x tree combinations

.....Number of attempts producing sound seeds

.....Percent of strobili producing cones

.....Mean total number of seeds per cone

the mean yield of sound seeds per cone from crosses between two taxa, expressed as a percent of the yield from control crosses within the seed-parent taxon. All control crosses summarized in Tables 1-4 were made on the same seed parent in the same season as crosses between taxa.

The following abbreviations are used: northern foxtail pine—NFO, southern foxtail pine—SFO, western bristlecone pine (*P. longaeva*)—WBR, and eastern bristlecone pine (*P. aristata*)—EBR.

*Seedling Observations.* Seedlings of the *Balfourianae* are slow-growing, and do not regularly produce secondary leaves (needles in fascicles) until the third growing season. Needles were sampled at the end of that season. Comparisons of needle characteristics were based on five fascicles from each of five seedlings from each of these groups: WBR (White Mountains); EBR (Colorado); EBR (Arizona); WBR x EBR, and SFO (Onion Valley). The seedlings were as diverse as possible in origin and parentage.

Counts of grooves on the needle surface did not provide reliable data on the number and distribution of resin canals in the needles of EBR seedlings. All needles were hand-sectioned at one-fourth of the distance from the tip to the base of the needle, and about half were also sectioned at one-half and three-fourths of this distance. All resin canals were external, and with a few exceptions were adjacent to the abaxial face of the needle. Resin canal diameters were measured perpendicular to the abaxial surface. Measurements were made between the outer walls of the epithelial cells, since the cells in this layer were highly variable in degree of flattening.

*Other observations.* Several unnoticed or poorly documented characteristics of the *Balfourianae* pines were observed in California stands of fox-tail and western bristlecone pines or in herbarium collections and stored seeds at the IFG. The materials available limited comparisons to major groups within the *Balfourianae*. Cone specific gravity was determined from volume, measured by water displacement, and oven-dry weight. Measurements were made of single cones from ten trees in each of the following groups: NFO (trees scattered throughout range); SFO (all but two trees in Onion Valley area); WBR (three trees in Utah, one in Nevada, two in Panamint Range, and four in White and Inyo Mountains); EBR (Arizona); and EBR (Colorado/New Mexico: two in New Mexico, eight in four Colorado stands). Seed-wing length was measured on four seeds from each of ten trees or mass collections in these groups: SFO and NFO combined (two SFO, eight NFO); WBR (three Utah, two Nevada, one Panamint Range, four White and Inyo Mountains); and EBR (seven Arizona, two Colorado, one New Mexico). De-winged, air-dried seeds in cold storage were weighed to the nearest milligram. Five seeds were measured from each of eight trees or collections in these groups: SFO and NFO combined (five SFO, three NFO); WBR (two Utah, six White Mountains); and EBR (Arizona); and four trees or collections of EBR (Colorado/New Mexico: three Colorado, one New Mexico). Tree means were analyzed for seed weight and wing length. Stratification requirements were determined for seed samples of EBR (Kenosha Pass, Colorado); WBR (White Mountains); and SFO (Onion Valley). Samples of 100 seeds received one of three treatments (stratification for 45 or 90 days, or no stratification). All seeds were placed in

germinators at the same time, and germination was observed for four weeks.

#### RESULTS

*Reproductive Phenology and Capacity.* Bristlecone and foxtail pines flower later in the season than any other North American pines. Flowering (pollen shedding and/or maximum opening of ovulate strobili) was observed in natural stands of these pines during 12 seasons between 1940 and 1974. All observations fall within a narrow range of calendar dates: a three-week period beginning in mid-July and peaking during the last week in July. Western bristlecone pine flowers later than *P. flexilis* in the White Mountains, and foxtail pine is later than *P. flexilis* or *P. albicaulis* at Onion Valley. In Tilden Park, near Berkeley, California, planted western bristlecone pines were observed in two seasons to flower in mid-June, about six weeks earlier than in their native habitat.

The *Balfourianae* pines flower at almost the same time. In four years of observations on successive days in stands of foxtail pine at Onion Valley and bristlecone pine in the White Mountains, we found no differences in flowering time, nor are there any indications of differences between eastern and western bristlecone pines. Pollen was collected in three Colorado stands between July 25 and August 2, 1970. In an Arizona stand at 2925 m, pollen was shed on July 22-27, 1969 (Schubert and Rietveld, 1970), and on July 31, 1975 (Rietveld, pers. comm., 1975). More generalized dates for pollen shedding in Arizona at 3050 m, based on three seasons of observations, were July 20 to August 20 (Pearson, 1931).

Northern foxtail pine has been observed to flower later than southern stands. In 1963 and 1964, observations were made 3-4 days apart at Onion Valley and North Yolla Bolly Mountain. In 1963 the North Yolla Bolly stand was estimated to be at least a week behind the Onion Valley stand, but in 1964 flowering was nearly simultaneous. Western bristlecone pine stands at different elevations have also been observed to peak a few days apart. With these exceptions, there appear to be no substantial differences in flowering time in the *Balfourianae*.

These pines are also uniform in the timing of cone-opening. Cones of foxtail pine at Onion Valley and western bristlecone pine in the White Mountains open in a two-week period starting about September 20. Arizona cones mature at about the same time. Schubert and Rietveld (1970) found that seeds of Arizona trees matured (were germinable) between September 24 and October 2, 1969, and the cones opened between September 27 and October 10. They concluded that cone maturation is not complete until just before the cones open, and our experience with western bristlecone pines confirms this. Some control-pollinated cones of White Mountains female parents, still closed when they were collected at the end of September, failed to open and had to be discarded.

In crosses where genetic barriers were not encountered, controlled pol-

ination of western bristlecone pine produced more sound seeds per cone than wind pollination. Wind-pollinated cones from the bristlecone female parents yielded a mean of 38 sound seeds per cone (range 25–65)—close to the 36 sound seed per open-pollinated cone reported for Arizona trees (Schubert and Rietveld, 1970). Cones from controlled pollination of the White Mountains trees averaged about 30% more sound seed than wind-pollinated cones, and the most successful controlled crosses on individual parents averaged 70 sound seed per cone. A potential source of bias in these comparisons is the possibility that seed extraction was more complete for control-pollinated cones.

The reproductive capacity of bristlecone and foxtail cones can be conservatively estimated from these seed yields, together with available data on numbers of cone scales. Bailey (1970) estimated that western bristlecone pine averages 117 scales per cone. Since the most successful controlled crosses produced 70 sound seeds, a minimum of 30% of the scales can bear two sound seeds. Foxtail pine, averaging only 81 scales per cone (Bailey, 1970; Mastroguseppe, 1972), had a mean of 58 sound seed per cone in the most productive controlled crosses. Thus at least 35 or 36% of its cone scales can bear two sound seeds. Wind pollination utilizes only a fraction of this potential reproductive capacity—54% in our bristlecone pine female parents. Comparable data are not available for the foxtail female parents, but a few estimates of sound seed per cone in bulk collections suggest that about 40% of the cone's reproductive capacity is exploited by wind pollination.

*Crossing the Balfourianae with other Pines.* Like most other subsections of *Pinus* (Critchfield, 1975), the *Balfourianae* appear to be isolated from the rest of the genus by genetic barriers. With one doubtful exception, our limited attempts to cross them with members of other white pine groups failed (Table 1). Representatives of other groups include *P. monticola* and *P. flexilis* (subsection *Strobi*), *P. monophylla* (*Cembroides*), and *P. bungeana* (*Gerardianae*).

In two instances there were indications of strong barriers acting early in the reproductive process. *Pinus balfouriana* x *P. bungeana* and the species-reciprocal cross yielded very few hollow seeds in either direction (Table 1). Since seed coats form early in the second season of cone development, at about the time of fertilization, this drastic reduction in hollow seeds indicates a developmental breakdown before fertilization. Another suggestion of early barriers is the abortion of all *P. flexilis* strobili pollinated with *P. balfouriana* pollen, but here a genetic interpretation is confounded by pollen age (Table 1).

Of the crosses summarized in Table 1, only *P. balfouriana* x *P. flexilis* produced any sound seed. Two *P. balfouriana* parents crossed with the same *P. flexilis* pollen parent produced a total of three sound seeds with normal embryos (determined by X-ray radiographs). Only one of the

three seeds germinated. In its germination time and three-year height the seedling was similar to sibling *P. balfouriana* seedlings in adjacent nursery rows, but before its non-hybrid identity could be firmly established the seedling was accidentally destroyed.

*Crossing Northern and Southern Foxtail Pines.* Northern and southern stands of foxtail pine were almost fully crossable (Table 2). Onion Valley females pollinated with North Yolla Bolly pollen produced 84% as much sound seed as they did in combination with Onion Valley males. The reduction in seed yield was not statistically significant (four pairs,  $0.20 > p > 0.10$ ) but it was consistent among female parents. Individual trees averaged 5–27% less sound seed in hybrid combinations than in control crosses.

The hybrid seedlings did not differ appreciably in size or other features from their non-hybrid siblings in the nursery, and it is doubtful whether they will be morphologically identifiable as hybrids until they reach reproductive maturity.

*Crossing Foxtail and Western Bristlecone Pines.* White Mountains bristlecone pine and Onion Valley foxtail pine were fully compatible in both directions (Table 3). Foxtail pine females produced nearly identical

TABLE 2. CROSSES BETWEEN SOUTHERN AND NORTHERN FOXTAIL PINES.  
(See Table 1 for legend.)

Female parent	Male Parent	
	balfouriana (northern)	balfouriana (southern)
balfouriana (southern)	12 (12)/ 12 99: 84 43.4/ 55.4	7 (7)/ 7 63: 87 51.6/ 60.6

TABLE 3. CROSSES BETWEEN FOXTAIL AND WESTERN BRISTLECONE PINES.  
(See Table 1 for legend.)

Female parent	Male parent		
	balfouriana (northern)	balfouriana (southern)	longaeva
longaeva	1 (1)/ 1 1/ 7: 43 5.3/ 21	23 (23)/ 23 191: 54 52.4/ 68.5	13 (13)/ 13 2/ 96: 65 36.9/ 47.3
balfouriana (southern)		7 (7)/ 7 63: 87 51.6/ 60.6	3 (3)/ 3 31: 90 52.9/ 65.4

1/ pollen frozen for 2 years

2/ fresh pollen used in 1971

amounts of seed in combination with bristlecone pines and with other foxtail pines (52.9 and 51.6 sound seeds per cone). And bristlecone females produced more seed when foxtail pine was the pollen parent than they did in control crosses with other bristlecone pines (52.4 and 36.9 sound seeds per cone). Single-tree combinations ranged from 40–66 sound seeds per cone in SFO x WBR crosses, and 4–116 in WBR x SFO crosses.

Although the reduced seed yield of crosses within bristlecone pine was not significant (eight comparisons,  $0.10 > p > 0.05$ ), it was consistent in both breeding seasons. Within-bristlecone crosses averaged 40.6 and 30.9 sound seeds per cone in 1963 and 1971, compared to 49.1 and 57.8 seeds from crosses with foxtail pine. The 1971 reduction may have been due to the use of slightly abnormal bristlecone pine pollen, which formed enlarged pollen tubes when it was germinated in the laboratory, but the 1963 difference is unaccounted for. This anomalous reduction cannot be attributed to inbreeding between closely related neighbors: in both seasons the bristlecone pollen was collected in stands 1–2 km from the female parents.

A single cross between northern foxtail pine and western bristlecone pine yielded fewer sound seeds (5.3 per cone) than other crosses on the same bristlecone female (x foxtail pines: 34.8 seeds; x other bristlecone pines: 25.8). Although the foxtail pollen had been frozen for two years and its viability may have been slightly reduced, this cross provides the only suggestion in our data that the crossing behavior of northern and southern foxtail pines may differ in combination with western bristlecone pine.

By the end of three growing seasons most of the hybrids could be distinguished from their western bristlecone siblings. At this age most bristlecone pines (both western and eastern) resembled cushion plants, lacking an emergent leader. If a leader was present it usually lacked a definite terminal bud, and the stem was mostly concealed by branches, fascicles, and closely appressed primary leaves. The slightly taller hybrids and much taller foxtail pines of the same age nearly all had emergent leaders, and much of the stem was visible. This was due partly to fewer primary leaves on the third-season stems and partly to slightly longer internodes—1.2–1.5 mm compared to 1.0 mm for bristlecone seedlings. Many hybrids and nearly all foxtail pines had well-developed terminal buds at this stage.

*Crossing Eastern and Western Bristlecone Pines.* Unlike the combinations described above, crosses between California and Colorado bristlecone pines were relatively unsuccessful. Although 19 or 20 combinations produced filled seeds, the mean of all 20 crosses was only 6.1 filled seeds per cone, and the maximum for a single cross was 18.7 seeds. The filled seeds were routinely X-rayed before most of them were planted in the

nursery. The rest were later germinated in petri dishes. Germination was low in the nursery and only slightly higher in the laboratory. A total of 69 seeds from 11 crosses germinated. The mean number of germinated seeds per cone for all hybrid crosses was 1.6, compared to 19.8 for non-hybrid combinations (Table 4)—a crossability of 8%. This could be an overestimate because of the possibly abnormal pollen used in the non-hybrid crosses (see above); 4-6% may be a more realistic estimate of crossability.

X-ray radiographs of the seeds provided an explanation of the low germination. Most "filled" seeds contained fully developed or slightly shrunken female gametophytes, with well-defined embryo cavities extending almost the full length of the gametophyte. Nearly one-fifth of the filled seeds had empty cavities, another one-fifth contained embryo-like objects too small to identify with certainty, and the others contained identifiable embryos. Most of these embryos were smaller than the embryos of germinable seeds from control crosses, which ranged in size from about two-thirds to the full length of the embryo cavity. Although the hybrid seeds were not handled individually, a few that germinated must have had embryos as small as 35-40% of the length of the cavity. But the great majority of germinable seeds from hybrid combinations had embryos from 45-65% of the cavity length. Embryos of this size showed about 80% germination.

Nine of the 20 hybrid combinations failed to produce any germinable seeds. All but one produced filled seeds, but the embryos were mostly vestigial, with a few ranging in length up to a third of the embryo cavity. Only two of the nine failed crosses (both on the same female parent) produced ungerminable embryos in the 45-65% size range.

Third-year hybrid seedlings resembled unrelated Colorado and Arizona seedlings more closely than their western bristlecone siblings, although all of the seedlings were similar in size and appearance. The

TABLE 4. CROSSES BETWEEN WESTERN AND EASTERN BRISTLECONE PINES.

Female parent	Male parent	
	aristata	longaeva
aristata	20 (20)/ 11	5 (5)/ 4
longaeva	113: 37 1.6/ 49.6	14: 79 19.8/ 35.1

Number of attempts.....	0 (0)/0	Number of tree x tree combinations
Number of female strobili.....	0, 0	Number of attempts producing germinable seed
Mean number of germinable seeds per cone.....	0.0 / 0.0	Percent of strobili producing cones
		Mean total number of seeds per cone

needles of the hybrids were more like those of eastern seedlings in having grooves overlying the resin canals and in the small size of the canals. The needles of western seedlings, like those of older western trees, lacked grooves. The mean diameter of resin canals in western, eastern, and hybrid seedlings was 0.138, 0.085, and 0.105 mm.

The expression of other needle characteristics was quite different in the seedlings than in older trees, as it often is in other pines. Two of the needle characteristics that Bailey (1970) found most useful in distinguishing *P. aristata* and *P. longaeva*—resin flecks and number of resin canals—were much more similar in seedlings than in the older trees he observed in natural stands.

Seedlings from (a) Colorado, (b) Arizona, and (c) the White Mountains had resin flecks on (a) 61, (b) 58, and (c) 27% of their needles. Corresponding percentages in the older trees that Bailey sampled were (a) 92–94, (b) 47–62, and (c) 3. Only 9% of the hybrid needles had flecks—fewer than either parental group of seedlings.

Eastern and western bristlecone pine seedlings were also more similar in resin canal number than the older trees that Bailey sampled in natural stands. Only 3% of the needles of eastern (and hybrid) seedlings had single canals extending the length of the needle, compared to 49% in older trees. Arizona and Colorado seedlings had single resin canals in the apical quarter of only 20 and 8% of their needles, compared to 84 and 87% in older trees (Bailey, 1970).

The presence of three or four resin canals per needle was fairly common in eastern bristlecone seedlings and occasional in hybrids, but none of the needles of western bristlecone or foxtail pine seedlings had more than two canals. Only 3 and 5% of Colorado and Arizona seedling needles had three canals near the tip, but near the base the frequency of three or more canals was 30 and 48%. The mean number of canals in Colorado and Arizona seedlings increased from 2.0 and 1.8 per needle near the tip to 2.3 and 2.6 near the base. Four resin canals—the highest number observed—were present in 15% of the needles of eastern seedlings. Where three or four canals were present, they were crowded together and often shared grooves. In seedlings, at least, the number of resin canals would be underestimated by counts of the grooves.

*Variation in Morphological and Other Characteristics.* Closer attention to the *Balfourianae* pines in recent years has turned up an array of differences that merit more detailed study:

Tree form—Most old foxtail pines have single, erect stems even under severe timberline conditions (Arno, 1966), although exceptions have been noted on dry sites (Bailey, 1970). Old bristlecone pines in the desert ranges of California have what Arno described as an “ungainly, weedy” form, usually twisted and multi-stemmed. To what extent this multi-stemmed form is characteristic of old bristlecone pines farther east is uncertain, although it is present in Colorado (Bailey, 1970; Fig. 1).

Bark—Young trees of eastern bristlecone pine differ from the other *Balfourianae* pines in having the smooth, blistered cortical bark and delayed onset of periderm formation that is characteristic of the firs and many white pines (Zavarin and Snajberk, 1973; Zavarin et al., 1976). Old foxtail pines in southern stands have thick, reddish-brown bark in squarish plates, a combination that has not been observed in other *Balfourianae* pines (Bailey, 1970; Mastrogioseppe, 1972).

Foliage—A vegetative difference noted by LeRoy C. Johnson (pers. comm., 1974) distinguishes living trees, including seedlings. The needles on a foxtail pine twig are painfully sharp to the touch; those of eastern and western bristlecone pines are not. This difference, difficult to quantify but useful in identification, appears to be due partly to sharper points but primarily to the greater stiffness of foxtail pine needles.

Cones—Eastern and western bristlecone pine cones project abruptly from the branch, and their straight axes form right or acute angles with the distal part of the branch. The cones of foxtail pine are pendent to varying degrees. This visually striking difference in orientation is due primarily to a difference in peduncle length. The peduncles of mature bristlecone pine cones in the IFG herbarium were usually flush with the basal cone scales, but occasionally extended beyond them a maximum of 4–5 mm. Intact peduncles of foxtail pine cones in the herbarium were 7–16 mm long, and several trees growing at Onion Valley had cone peduncles 14–16 mm long. An associated feature is the curved axis of 21–23% of foxtail pine cones (Mastrogioseppe, 1972).

The cones of foxtail pine have somewhat “fleshy” apophyses (Bailey, 1970; Mastrogioseppe, 1972), and are softer and more fragile than cones of the bristlecone pines. This difference can be expressed quantitatively in terms of cone specific gravity. Northern and southern foxtail pine cones did not differ significantly in specific gravity, nor did the western, Colorado–New Mexico, and Arizona samples of bristlecone pine. But the combined data showed a significant difference ( $0.05 > p > 0.01$ ) between the less dense cones of foxtail pine (mean specific gravity 0.45) and the cones of the bristlecone pines (mean 0.49).

Seeds—Our data confirm Uyeki's (1927) observation that foxtail pine seeds have longer wings than seeds of bristlecone pine. His measurements of a few seeds of unspecified origins showed ranges of 18–20 mm and 8–11 mm for the two pines. In our samples, wing length was almost identical in eastern and western bristlecone pines: the means were 10.7 and 10.0 mm, and ranges were 7–15 mm in both samples. Seeds of foxtail pine have much longer wings (mean 17.2 mm), and the differences between it and the bristlecone pines were highly significant ( $p = < 0.01$ ). Foxtail pine's range in wing length (13–24 mm) just overlapped that of the bristlecone pines. In disagreement with these data is Mastrogioseppe's (1972) observation that southern foxtail pine has rather short seed wings. His large samples of seeds from single localities of northern (Lake

Mountain) and southern (Timber Gap) foxtail pines had mean wing lengths of 17.4 and 11.5 mm, a highly significant difference. Timber Gap may be poorly representative of southern stands, however. The two southern foxtail pines in our sample, both collected by Mastrogioseppe (XIV-7, Onion Valley, and XI-5, Silliman Crest), had average (17.5 mm) or long (23.3 mm) seed wings—the latter the longest wings of any tree in the sample.

The *Balfourianae* pines were much more variable in seed weight. Foxtail and Arizona bristlecone pines had the heaviest seeds, with means and ranges of 25.4 mg (13–39) and 26.4 mg (18–38). The small sample of Colorado–New Mexico trees had somewhat lighter seeds (mean 20.8 mg, range 11–25), the difference between it and the Arizona sample approaching statistical significance ( $0.10 > p > 0.05$ ). Western bristlecone pine seeds were by far the lightest—less than half the weight of the others (mean 8.8 mg, range 6–15). The differences between this and the other samples were highly significant ( $p = < 0.01$ ).

A difference in seed color has been noted by Zavarin et al. (1976), eastern bristlecone pines having darker seed coats than western trees.

Stratification requirement—Bristlecone pine seeds germinate promptly without stratification, but the germination of foxtail pine seed—like that of most other white pines—is slow and incomplete without this pretreatment (Forest Service, 1974). Unstratified seed of Arizona bristlecone pine showed 75% germination within eight days (Schubert and Rietveld, 1970); untreated Colorado seed germinated 75–80% in 4–10 days (Reid, 1972); and untreated White Mountains seed showed 90% germination within six days (Wright, 1963). In foxtail pine, Mastrogioseppe (1972) obtained only 29–63 and 50–55% germination in three-month tests of unstratified seed from northern and southern stands. In germination tests at the IFG, 45 or 90 days of stratification reduced mean germination time of Colorado and White Mountains seed by 2–3 days (unstratified: 11.3 and 7.9 days; stratified: 8.3–8.4 and 5.5–5.8 days), but did not increase the amount of germination. The same pretreatments increased the germination of Onion Valley foxtail pine seed from 41 to 100% and reduced mean germination time by 8–9 days (unstratified: 11.9 days; stratified: 2.6–3.5 days).

#### DISCUSSION

The ability of pines to hybridize is generally restricted to taxa that are considered to be related on other grounds. Within groups linked by the ability to hybridize, however, the degree of crossability is sometimes highly discordant with other evidence of relationship. Among the pines, *P. muricata* (bishop pine) provides the closest parallel to the *Balfourianae* in this respect. The three races of this coastal Californian species—northern, central, and southern—exhibit little correspondence between crossability and other indicators of relationship (Critchfield, 1967). The

northern race differs morphologically from the other two, and all three are chemically distinct. These distinctions are nearly absolute except in the narrow zone where the northern and central races meet. Crossability is complete between northern and central races (the only two in contact), low between central and southern races, and close to zero between northern and southern races.

Among the *Balfourianae*, the crossing behavior of northern and southern foxtail pines is an exception. Their crossability of 84% is fairly typical of segments of a species that have diverged sufficiently to warrant taxonomic recognition. In *P. ponderosa*, the western (var. *ponderosa*) and eastern (var. *scopulorum*) races had an average crossability of 52% in small-scale reciprocal tests (Krugman, 1970). The coastal and Sierra Nevada races of *P. contorta*, usually given subspecific or varietal status but still occasionally considered two species (*P. contorta*, *P. murrayana*), has a crossability of 93% in an extensive series of reciprocal crosses (unpublished data, IFG).

No macrofossils of foxtail pine have been described from the Tertiary, although Axelrod (1976) noted that a fossil pine in the Thunder Mountain, Idaho, flora (Eocene age) resembles this species. Pollen identified as *P. balfouriana* was present in several pollen floras in and near the southern Sierra Nevada during the first recorded Pleistocene glaciation (Axelrod and Ting, 1961), but one problem with this identification is the assumption that the dimensions of the pollen have remained constant since then. Foxtail pine cones have recently been found near Clear Lake, California, in late Pleistocene (probably Illinoian) deposits (J. Wolfe, pers. comm., 1977). At this site, more than 100 km south of and more than 1000 m below the present northern distribution of foxtail pine, the abundance of cones suggests that this species was a major component of a high-elevation mixed-conifer forest.

Mirov (1967), Bailey (1970), and Mastrogioseppe (1972) have speculated—apparently on the basis of geological history—that the northern and southern stands of foxtail pine have been separated since the end of the Tertiary or the early Pleistocene. If so, the accumulation of genes influencing crossing ability has been very slow in the two or three million years these groups have been isolated from each other. However, the recent Clear Lake find raises the possibility of contact between them as recently as one of the last major glacial episodes of the Pleistocene.

The most striking instance of discordance between genetic and other evidence of relationships in the *Balfourianae* is the complete crossability of western bristlecone and southern foxtail pines. This combination is also by far the best supported by crossing data; it is the only combination made in both directions and in more than one season. This level of crossability is remarkably high for pine species, although it is approached by the 69–85% crossability of the California closed-cone pines *P. attenuata*

and *P. radiata* (Critchfield, 1967) and a few other less fully investigated combinations.

Although genetic barriers to interbreeding are nonexistent in the White Mountains and Onion Valley stands, the morphological and other differences between foxtail and western bristlecone pines are of the same magnitude as those distinguishing most other closely related pine species. Two cone characteristics have traditionally been emphasized: foxtail cones have minute mucros but lack conspicuous bristles, and have fewer scales—about 80–81, compared to 117 for western bristlecone pine. But they also differ in peduncle length and the complex of associated characters (cone orientation, curvature), cone density, seed weight, seed-wing length, stratification requirement, foliage stiffness, and probably tree form.

The morphological distinctions between eastern and western bristlecone pines are less conspicuous, with the notable exception of the resin flecks on the needles. The principal differences between the two are in the complex of characters associated with the needle resin canals and in resin composition, but they also differ in cone color, bristle length, seed weight and color, bark, and other features noted by Bailey (1970). These taxa are also far less crossable than foxtail and western bristlecone pines, with a crossability of only a few percent, estimated from crosses made in one direction in a single season. A smaller number of crosses made by Bailey in the opposite direction in the same season were even less successful (Zavarin et al., 1976).

The reproductive barriers between the two bristlecone pines resemble those of many other white pine combinations in acting mainly or entirely after fertilization (Kriebel, 1975). The seed coats, which form at about the time of fertilization, showed no reduction in numbers in western x eastern combinations (Table 4). Post-fertilization barriers are also indicated by the many seeds with fully developed female gametophytes and embryo cavities, but lacking embryos or with very small embryos. Embryo cavities form after fertilization (Sarvas, 1962), and the female gametophyte usually degenerates rapidly after the death of the last developing embryo (Sarvas, 1962; Plym Forshell, 1974). Mature or nearly mature seeds with empty embryo cavities have been reported in only a few instances: in *P. sylvestris* by Ehrenberg et al. (1955), Sarvas (1962), and Plym Forshell (1974); and in the cross *P. jeffreyi* x *P. coulteri* by Krugman (1970). These authors interpreted such seeds as indicators of breakdown at a relatively late stage of embryo development. Another unusual feature of the cross between western and eastern bristlecone pines was the germination of seeds with embryos less than half the length of the embryo cavity. This has also been reported in *P. sylvestris* (Ehrenberg et al., 1955).

The *Balfourianae* group is an old lineage in western North America. Macrofossils resembling contemporary bristlecone pines have been found

in Eocene and Oligocene deposits in Nevada, New Mexico, Colorado, and Montana. Most of these fossils have been described under the name *P. crossii* Knowlton.

The oldest *P. crossii* fossils were part of the Eocene Copper Basin flora of northern Nevada (Axelrod, 1966), which has an estimated age of about 40 million years. Copper Basin is 120 km north of the present northern limits of western bristlecone pine. The five-needled fascicle illustrated by Axelrod (Plate 6, Fig. 6) has needles only 13 mm long—much shorter than most needles of contemporary *Balfouriana*. Needles this short were not observed on specimens of eastern bristlecone pine and were very rare on foxtail pine, but bristlecone pines in the White Mountains occasionally produce fascicles of this size on slow-growing branches. I have examined the Copper Basin fascicle (University of California Museum of Paleontology hypotype 8873), and one of the needles shows two linear impressions suggestive of resin canals extending the length of the needle.

According to Axelrod (1976), a mid-Oligocene flora at Hillsboro, New Mexico, was dominated by a pine that closely resembles contemporary *P. aristata* in its cones and fascicles. The nearby Hermosa flora, also mid-Oligocene, consists mostly of a “five-needled pine allied (distantly) to *P. aristata*.”

A pine resembling *P. aristata* is also abundantly represented in a fossil flora deposited near Creede, Colorado, near the end of the Oligocene, about 27 million years ago. This pine (*P. crossii*) is represented by a conelet, seed wing, and many needle impressions (Fig. 34–37, Bailey, 1970). Bailey and earlier authors consider it nearly identical with *P. aristata*, which grows nearby today.

A single fascicle that can probably be assigned to *P. crossii* was found in late Oligocene deposits in the Ruby Basin of southwestern Montana (Becker, 1961). It consists of three needles and the base of a fourth. These needles are also shorter (16–17 mm) than those of contemporary *Balfouriana* pines.

Impressed by the characteristics shared by foxtail and western bristlecone pines and by the similarity of the Creede fossils to eastern bristlecone pine, Bailey (1970) proposed a polyphyletic origin for the bristlecone pines. According to this scheme, two lineages arose in northwestern North America at the start of the Tertiary or earlier, and migrated south into the Rocky Mountain and Pacific regions. The eastern line—substantially unchanged since at least the late Oligocene (Creede flora)—is modern *P. aristata*, and the Arizona population is a Pleistocene offshoot. The western line resembled *P. balfouriana*. It gave rise to *P. longaeva* at the end of the Tertiary and beginning of the Pleistocene as the major uplift of the Sierra Nevada produced increasing aridity in the Great Basin.

A principal reason for rejecting Bailey's polyphyletic hypothesis is the

burden it places on convergent evolution, which must account for all of the diverse ways in which eastern and western bristlecone pines resemble each other and differ from foxtail pine. These include, in addition to cone-scale number and bristles, several characteristics noted above—peduncle; orientation and density of the cone; seed wings; absence of a stratification requirement; foliage stiffness; and perhaps tree form. Nor does recent chemical evidence (Zavarin et al., 1976)—particularly the chemical intermediacy of Arizona stands and the similarity of Sentinel Peak to Colorado–New Mexico trees—support the view that western bristlecone pine evolved from a foxtail–pine–like ancestor.

The tendency of western bristlecone pine to resemble foxtail pine in some respects (needle resin canals, chemistry) and eastern bristlecone pine in others can be explained more simply in other ways. Western bristlecone pine could be the product of ancient hybridization between eastern (*P. aristata*) and western (*P. balfouriana*) ancestral lines. One difficulty with this hypothesis is that western bristlecone pine is not intermediate in most respects (bristle length is an exception). Instead, it closely resembles either eastern bristlecone pine or foxtail pine. And in a few characteristics it resembles neither (cone-color polymorphism, seed size, great longevity). A more critical objection is the asymmetrical crossing behavior of western bristlecone pine in combination with its presumed parents. The hypothesis of a hybrid origin is difficult to reconcile with the complete absence of crossing barriers on the one hand (*P. balfouriana*) and the presence of strong barriers to interbreeding on the other (*P. aristata*).

An alternative—and more acceptable—hypothesis is that all of the elements of the *Balfourianae* are segregates of a single ancestral line most closely resembling western bristlecone pine (Eocene Copper Basin fossil). By the middle or late Oligocene a Rocky Mountain lineage split off and developed some of the distinctive attributes of contemporary eastern bristlecone pine (Hillsboro and Creede floras). Arizona bristlecone pine could have arisen as a very early offshoot of this lineage, or it could be (as Zavarin et al., 1976, suggested) the product of later contact between eastern and western bristlecone pines. It is uncertain when foxtail pine originated from the western bristlecone pine lineage, although separation must have been complete before the late Pleistocene (Clear Lake fossils). Foxtail pine has undergone pervasive changes in morphological and other characteristics, but divergence has apparently been too recent for the accumulation of genes influencing its ability to cross with the closest modern equivalent of its ancestor.

The crossing data summarized in this paper are incomplete in many respects. The exploratory hybridization of the *Balfourianae* should be extended to include Arizona *P. aristata*, *P. longaeva* of the Panamint Range, the untried combination of *P. balfouriana* and *P. aristata*, and more combinations of *P. balfouriana* and *P. longaeva*. Crosses between

*P. aristata* and *P. longaeva* also need to be repeated and extended, but our preliminary finding of very low crossability between these taxa provides tentative support for Bailey's (1970) proposal to recognize them as species.

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### A NEW GYPSOPHILOUS SPECIES OF PHACELIA (HYDROPHYLLACEAE) FROM COAHUILA, MEXICO

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Floristic studies of the Cuatro Ciénegas Basin in central Coahuila, Mexico, have revealed a new species of *Phacelia* growing on gypsum dunes and flats. This taxon is apparently restricted to the basin, adding to the list of gypsophiles only known from there: *Dyssodia gypsophila* Turner (1972a), *Gaillardia gypsophila* Turner (1972b), *Haploesthes robusta* I. M. Johnston (1941), *Machaeranthera gypsophila* Turner (1973a), and *M. restiformis* Turner (1973b).

***Phacelia marshall-johnstonii*** Atwood and Pinkava, sp. nov. Plantae perennes 1.5–2.5 dm altae, caudicibus ligneis usque ad 1.5 cm diametro; caules 1–plures e basi erecti vel ascendentes ramificantes supra saepe viscidis et dense canescentes, pilis patulis 1–2 mm longis et pilis brevior et mollior 0.3–0.8 mm longis; folia aggregata diminuta sursum, petiolis 0.2–2.0 cm longis, laminis ovatis ad elliptica 0.8–5.5 cm longis 0.5–2.5 cm latis, margine grosse crenatis ad duple crenatis vel leviter lobatis, apicibus obtusis, basibus rotundatis ad subcordatis, utrinque dense hirsutis-viscidis; inflorescentiae terminales in axibus principalibus et ramis magnis cymarum compositarum scorpioidarum, cymae usque ad 13 cm longae in fructum; flores numerosi subsessiles; sepala elliptica ad oblanceolata usque ad 4.5 mm longa et usque ad 2 mm lata in fructum dense et grosse hirsuta-viscida; corollae caesiae albae ad extremum 5 mm longae infundibuliformia, tubis 4 mm longis glabris, lobis 1 mm longis hirsutis extis subtiliteris; antherae globosae ca 0.5 mm diametros exsertae-longae, filamentis purpureis ca 1 cm longis glabris 0.8 mm supra basim corolla insertis, appendicibus basalibus auriculiformibus 0.7 mm longis; styli longo-

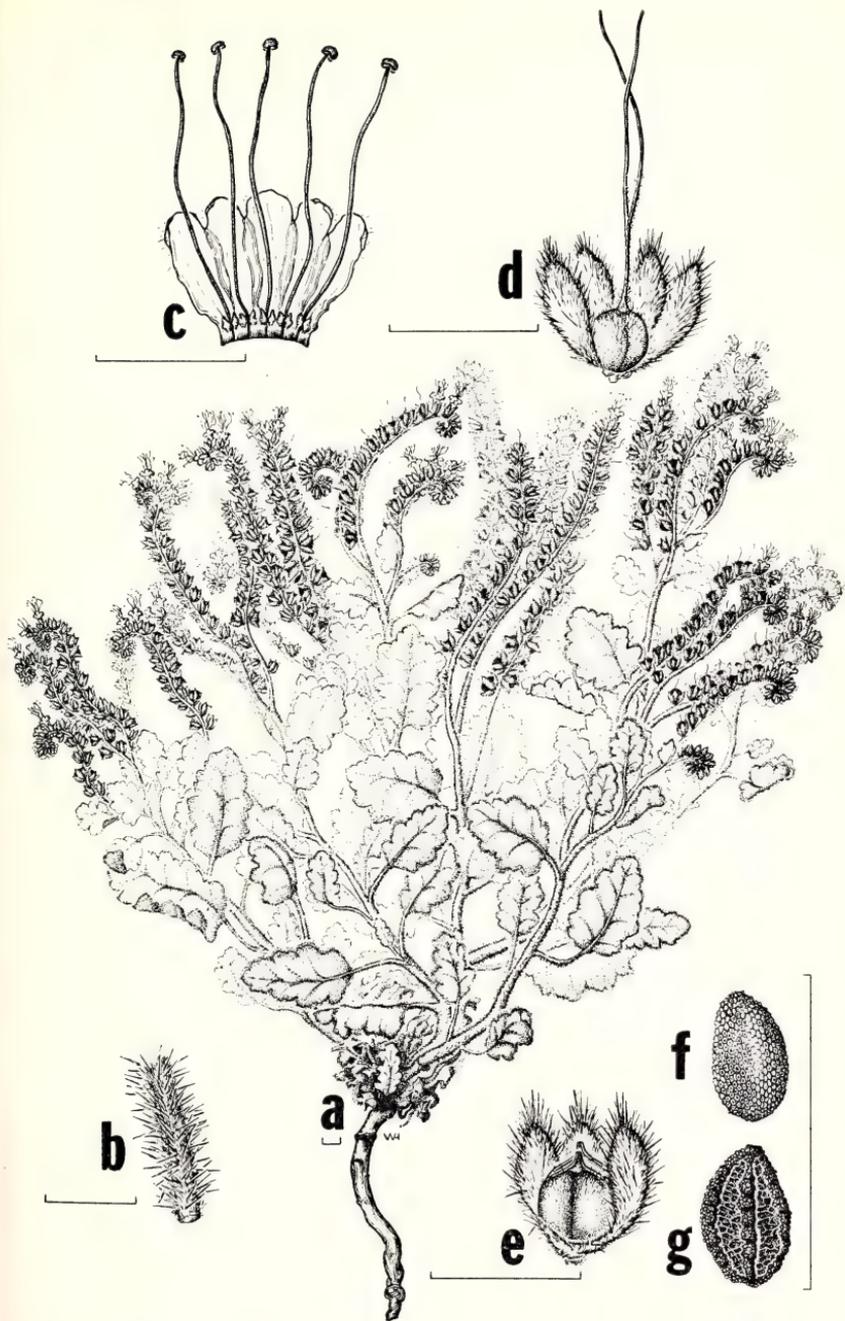


FIG. 1. *Phacelia marshall-johnstonii*. a, habit; b, stem segment enlarged; c, corolla and androecium; d, calyx and gynoecium (at flowering); e, fruit in calyx; f, seed, dorsal view; g, seed, ventral view. Illustration based on holotype. Scale line = 5 mm.

exserti stamina equantes purpurei subti pubescenti grosse pilis 0.2–0.5 mm longis; capsulae ovoidae ad subglobosae 3.0–3.5 mm longae 2.5–3.0 mm latae apice subtiliter puberulentae; semina 4 elliptica 2.0–2.5 mm longa 1.1–1.3 mm lata fusca irridescentia leviter, pagina dorsali foveolata, pagina ventralis excavata reticulata, marginibus et crista centralie ventralis corrugatis leviter.

TYPE: MEXICO: COAHUILA: Cuatro Ciénegas Basin, along new road to gypsum dunes, 0.3 miles S of Poso de la Becerra, gypsum flats with *Atriplex*, *Nama*, and *Sporobolus*, 15 Aug 1975, *Reeves & Pinkava P13100* (Holotype: ASU; Isotypes: BRV, ENCB, GH, MEXU, NY, LL-TEX, UC, US).

Additional materials examined: MEXICO: COAHUILA: Poso de Escobeda, grassy banks, 17 Aug 1967, *Cole, Minckley & Pinkava P4086* (ASU); Julio's Canal, 4.5 miles SSW of Cuatro Ciénegas, along roadside, 15 Aug 1967, *Cole, Minckley & Pinkava P3812* (ASU); stabilized dunes W of headwaters of El Chiqueros, 15 Aug 1967, *Cole, Minckley & Pinkava P3953* (ASU); stabilized dunes S of Laguna Grande, 8 Jun 1968, *Lehto, Keil & Pinkava P5024* (ASU); gypsum dunes, 16 km S of Cuatro Ciénegas, ca. 2 km SW of Poso y Balneario La Becerra, 26° 52' N, 102° 09' W, 770 m, 22 Mar 1973, *Johnston, Wendt & Chiang 10334* (LL-TEX); 19 km SW of Cuatro Ciénegas, gypsum dunes, with *Petalonyx*, *Sporobolus*, *Dasyllirion*, 26° 52' N, 102° 09' W, 700 m, 11 Jun 1972, *Chiang, Wendt & Johnston 7649* (LL-TEX).

*Phacelia marshall-johnstonii* (Fig. 1) is apparently closely related to *P. pallida* I. M. Johnston of the *Phacelia crenulatae* group (Atwood, 1975), but is distinguished from that taxon by the densely canescent, harsh spreading hairs, only sparsely glandular pubescence and smaller seeds.

This species is named in honor of Professor Marshall C. Johnston, University of Texas, Austin, devoted scholar of the floras of Texas and the Chihuahuan Desert.

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# ROOT:SHOOT BIOMASS RATIOS IN SHRUBS IN SOUTHERN CALIFORNIA AND CENTRAL CHILE

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One characteristic of vegetation in mediterranean-type climates is an abundance of deep-rooted shrubs (Hellmers et al., 1955; Sacchori et al., 1967). The deep rooting patterns correspond with the cool, wet winter and hot, dry summer climatic pattern in which water is available deep in the soil when surface layers are dry and temperatures are favorable for photosynthesis and growth (Miller and Mooney, 1974). Where evergreen, sclerophyllous shrubs predominate, annual precipitation is about 400–650 mm (Aschmann, 1973; Miller et al., 1977). Deep rooting patterns imply an investment of carbon resources by the plants in the root system, but there are few data on the root:shoot biomass ratios for shrubs in mediterranean regions, probably because of the difficulty in obtaining these figures (Kummerow et al., pers. comm.). At the beginning of this study we expected to find that root-shoot biomass ratios of shrubs in the mediterranean climatic regions of southern California and central Chile would be greater than one and that the biomass of absorbing roots, identified by small root size, would be correlated with the transpiring leaf area of the shrub. Our field study tested these hypotheses on selected shrubs in the 2 regions. We excavated 14 individual shrubs of 6 species: 8 in southern California and 6 in Chile. The main comparison involved 2 Californian species: *Adenostoma fasciculatum* (4 shrubs excavated) and *Ceanothus greggii* (2 shrubs excavated); and 2 species of similar areal stature in Chile, *Satureja gilliesii* (4 shrubs) and *Colliguaya odorifera* (2 shrubs). In addition, one plant of *Heteromeles arbutifolia* and one of *Arctostaphylos glauca* were excavated in California.

## DESCRIPTION OF STUDY SITES

In California roots of all plants except the *Heteromeles* and one *Adenostoma* (*Adenostoma* 4) were excavated at Echo Valley in San Diego County (32°54'N, 116°39'W). These 2 plants were excavated near the Viejas Road, 15 km southwest of the Echo Valley site. In Chile all the plants were obtained by excavating back from a road cut at the Fundo Santa Laura site (33°04'S, 71°00'W). We used hydraulic excavation to remove roots from the soil. This requires large volumes of water, a high pressure pump, and suitable drainage away from the root washing site. Rapid drainage of water and soil was necessary during excavation

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to keep the root system exposed and allow its extraction. Therefore, plants near road cuts or on steep banks were chosen. However, the center of the excavated plant was always more than 1 m from the road cut. Roots were excavated at comparable sites in California and Chile: approximately 55 km from the coast at about 1,000 m. Annual precipitation in both regions is about 550 mm, with about 60% during the winter 6 months in California and 83% in the analogous months in Chile (Miller et al., 1976). The annual mean temperatures at the research sites are about 17C in California and 15C in Chile. The Californian site burned in 1950. The Chilean site was subjected to wood cutting prior to 1959, although the species measured are not used for firewood (Aschmann and Bahre, 1977). Root excavations in both countries were made during the respective summer when surface layers of soil were dry but subsurface layers were still moist. Roots were excavated in June, July, and August, 1971 in California and in February, 1972 in Chile. Precipitation through the winter preceding the excavations was about 250 mm at the site in California. A complete precipitation record prior to excavations is not available in Chile; however, in California there was no precipitation during the 2 months preceding excavations, and in Chile none during the 4 months preceding excavations. Average soil moisture at 0.3–1.2 m depth decreased from 0.25 to 0.09 cm<sup>3</sup> water per cm<sup>3</sup> soil during the excavations in California; thus, the soil was presumed to be dry at excavation in both countries.

Shrubs excavated from the Echo Valley site were growing near recent road cuts; those from the Viejas site were adjacent to recent excavations for land fill. Slope inclinations were 10°–15° for each site. Slope exposure of the plants at Echo Valley was north; *Adenostoma* 4 was on a south-facing, and *Heteromeles* on an east-facing exposure. The soils at both excavation sites are sandy loams, underlain by decomposed granite from weathered Bonsall Tonalite, without much vertical stratification and, although of variable depth, more than 0.5 m deep. The soils at the Viejas site were much rockier than those at Echo Valley. *Ceanothus* and *Adenostoma* were excavated in a mixed stand of these species. *Adenostoma* 4 was in a pure *Adenostoma* stand. *Arctostaphylos* was associated with *Quercus agrifolia* and *Quercus englemanni*, and *Heteromeles* was associated with *Q. agrifolia* and *Salvia apiana*. No herbaceous cover occurred on the plots excavated.

The excavation site in Chile was predominantly northwest facing. The slope inclination was highly variable but was 10°–25° where excavations were made. The surrounding vegetation was dominated by *Satureja gilliesii* and *Colliguaya odorifera*, with occasional *Lithraea caustica*, *Trevoa trinervis* and *Cryptocarya alba*. The site had a definite herbaceous layer. Soils were generally coarse textured but not underlain by decomposed granite. The absence of decomposed granite facilitated the excavation.

## METHODS

For hydraulic excavations in California a 400-gal tank truck and a Barnes impeller type pump were used. The pump was capable of putting out 15 gal min<sup>-1</sup> at 100 lbs in<sup>-2</sup> pressure. A similar pump configuration was assembled in Chile where two 50-gal drums provided water storage. The relatively low outflow rate was important because the water supply was limited and sites were remote from the source. A variable nozzle regulated the pressure of water from a narrow, high pressure stream to a fine spray. The fine spray minimized loss of root material during excavation, but the narrow high pressure stream was necessary to remove the soil.

For selected plants, maximum height and radial extent of the crown were measured, and the foliage was tied. Three metal reference stakes were placed in the ground, two in the upper and lower edges of the plot 0.5–1.0 m from the plant, and the third as close as possible to the plant, without piercing its burl (lignotuber). The stakes served as depth gauges while washing the soil and to support the plant as it was undercut. As soil was washed away, exposed roots were marked according to depth. Depth was recorded every 0.2 m in California and every 0.1 m in Chile. Excavation stopped when an impenetrable layer of soil or rocks was reached, when the drainage became insufficient because the level of the road was reached, or when the root system was exposed as completely as possible. Maximum radial extent of the root system was measured. The entire plant was then brought into the laboratory and separated by level for oven drying for 24 hr at 85C.

In California, unbiased estimates of the biomasses of different sized roots, total root length, and root area could not be made because of the nature of the excavation. The decomposed granite washed away in 0.5–1.0 cm<sup>3</sup> chunks, which probably contained most of the fine roots. Therefore, only dry weights of all roots in each stratum were measured. In Chile the soil particles disintegrated more readily with the application of water and fewer fine roots were lost. The retention of small roots allowed those of each plant to be divided into size classes of different diameters within different soil depths. The dry weights of roots in each class were measured. Roots were randomly subsampled from similar size classes and their total length and weight were measured to obtain a length:weight ratio for each size class. The length:weight ratio times the weight and diameter were used to estimate the area of each size class of roots.

## RESULTS AND DISCUSSION

Even with the variable size of shrubs of the same species, the measured root:shoot biomass ratios were less than one for all individuals (Table 1). The largest root:shoot ratio of an individual was 0.93 and the smallest, 0.25. *Ceanothus greggii*, a shallow-rooted species, had the smallest root:shoot ratios (0.25 and 0.39), while *Adenostoma fasciculatum*, a deep-rooted species, had root:shoot ratios of 0.49–0.69. *Heteromeles*, which is

TABLE 1. SUMMARY OF SHRUB SIZE MEASUREMENTS. Diameter, area, and volume refer to the areal extent of the shoot and root systems, not to an individual shoot or root.

Plant part	Species and number of individual															
	<i>Ceanothus greggii</i>				<i>Adenostoma fasciculatum</i>				<i>Heteromeles arbutifolia</i>		<i>Arcto-staphylos glauca</i>		<i>Satureja gilliesii</i>		<i>Colliguaya odorifera</i>	
	1	2	1	2	3	4	1	1	1	1	1	2	3	4	1	2
<b>Shoot</b>																
Height (m)	1.10	0.71	0.40	—	0.54	0.95	1.79	1.05	1.00	0.95	0.90	0.85	0.60	0.20		
Diameter (m)	0.40	0.35	0.25	—	0.15	0.93	0.75	1.00	0.70	1.25	0.60	0.80	0.32	0.14		
Area (m <sup>2</sup> )	0.13	0.10	0.05	—	0.018	0.67	0.45	0.78	0.39	1.23	0.28	0.50	0.08	0.015		
Volume (m <sup>3</sup> )	0.14	0.07	0.012	—	0.001	0.63	0.80	0.82	0.39	1.16	0.25	0.42	0.05	0.003		
Biomass (g)	249.0	30.0	17.0	15.0	14.0	506.0**	342.0	215.0	355.0	357.0	67.0	117.0	47.0	7.0		
Stem biomass (g)	151.0	18.0	—	—	—	—	263.0	559.0**	—	—	—	—	—	—		
Leaf biomass (g)	97.0	12.0	—	—	—	—	79.0	215.0	—	—	—	—	—	—		
<b>Root</b>																
Depth (m)	0.3	0.3	0.3	0.8	1.0	1.0	0.3	0.3	0.4	0.6	0.7	0.85	0.3	0.6		
Diameter (m)	0.6	0.4	0.3	—	0.4	2.4	0.6	1.2	1.2	2.0	—	1.4	—	—		
Area (m <sup>2</sup> )	0.28	0.13	0.07	—	0.13	4.52	0.28	1.64	1.64	3.14	1.2*	1.54	—	—		
Volume (m <sup>3</sup> )	0.085	0.038	0.021	—	0.13	4.52	0.085	0.49	0.63	1.88	0.84	1.30	—	—		
Biomass (g)	63.0	11.0	8.4	11.0	9.0	250.0	254.0	670.0**	125.0	260.0	62.0	90.0	28.0	5.0		
Mean biomass density (g m <sup>-3</sup> )	740.0	290.0	400.0	—	69.0	55.0	3000.0	1370.0	198.0	138.0	74.0	69.0	—	—		
<b>Burl</b>																
Biomass (g)	—	—	—	—	—	—	—	—	152.0	207.0	34.0	108.0	11.0	0.0		
TOTAL BIOMASS (g)	311.0	41.0	25.0	26.0	23.0	756.0	596.0	1444.0	480.0	617.0	129.0	207.0	75.0	12.0		
<b>ROOT:SHOOT BIOMASS RATIO</b>																
	0.25	0.39	0.50	0.69	0.63	0.49	0.74	0.87	0.35	0.73	0.93	0.77	0.60	0.89		

\*\* Includes weight of burl.

\* Area was oblong, 2.4 × 0.5 m<sup>2</sup>.

considered deep-rooted, and *Arctostaphylos glauca*, *Satureja*, and *Colliguaya*, which are all considered shallow-rooted, had similar root:shoot ratios, usually 0.60 to 0.93.

Except for *Heteromeles*, the ground surface area underlain by the roots of an individual was larger than the vertical projection of the crown (Table 1) (Hellmers et al., 1955). The ratios of the ground surface underlain by roots to the vertical projection of the crown were: *Ceanothus*, 1.9–2.0; *Adenostoma*, 6.7–7.2 in two deeper-rooted plants and 1.4 in the shallow-rooted plant; *Arctostaphylos*, 2.1; and *Satureja*, 2.6–4.4.

Roots were concentrated in the upper 0.3 m of soil (Table 2). In *Ceanothus*, *Heteromeles*, *Arctostaphylos*, and one *Adenostoma* all of the root biomass was in the upper 0.3 m. In the other *Adenostoma*, 50–55% of the biomass was in the upper 0.3 m and over 94% in the upper 0.8 m. Roots of *Adenostoma* extended to at least 1 m on large plants. In *Satureja* 83–100% of the root biomass was in the upper 0.3 m, with maximum root depths between 0.4 and 0.84 m. In *Colliguaya* over 84% of the root biomass was in the upper 0.3 m, with roots of one individual extending to 0.6 m. Rooting depth appeared independent of root weight both within a species and with all species combined, but was directly related to shoot height in *Satureja* and *Colliguaya*. Root biomass densities of 100–1400 g dry weight  $m^{-3}$  in the 0–0.3 m depth (Table 3) compare with values for crop plants of 300 g  $m^{-3}$  (Penning de Vries, pers. comm.), and tundra plants of 1,000 g  $m^{-3}$  (Dennis and Tieszen, 1972). Root biomass densities at the surface were less with deeper-rooted individuals, indicating a trade-off between high exploitation of the surface and exploitation of the deeper soil.

Mean root diameters decreased with depth in *Satureja* and *Colliguaya*, the only species for which root weights could be measured by diameter class (Table 4). At each depth the length of the roots in the smallest diameter class was larger than that for the other diameter classes. Roots smaller than 0.5 mm diameter comprised 10–25% of the total root biomass and 40–50% of the total root length. The weight of the small roots decreased with both shoot and root biomass. Percentage of the total root biomass which was small roots decreased with increasing root biomass because of the increasing diameter of roots with age and did not correlate with the shoot biomass in the measurements.

Our excavation underestimated the root biomass because of the loss of fine roots in excavation (Caldwell and Fernandez, 1975) and because of the death and sloughing of fine roots as the soil dried in early summer, but a correction for this loss does not increase root:shoot ratios greatly. The correction is based on concepts of absorbing root densities required for the absorption of phosphorus, nitrogen, and water. Chaparral soils are generally considered to be nitrogen and phosphorus deficient (Hellmers et al., 1955; Christensen and Muller, 1975) and are dry during the

TABLE 2. PERCENTAGES OF SHOOT BIOMASS AND OF ROOT BIOMASS IN DIFFERENT LEVELS ABOVE AND BELOW THE SOIL SURFACE.

Plant part	Species and number of individual													
	<i>Ceanothus greggii</i>		<i>Adenostoma fasciculatum</i>			<i>Heteromeles arbutifolia</i>		<i>Arcto-staphylos glauca</i>		<i>Satureja gilliesii</i>		<i>Colliguaya odorifera</i>		
	1	2	1	2	3	4	1	1	1	2	3	4	1	2
Shoot														
1.5-1.8														
1.4-1.6							6							
1.2-1.4							10							
1.0-1.2							5							
0.8-1.0	15					11	10	1	1	1	3	1		
0.6-0.8	26	3				38	9	10	5	9	16	7		
0.4-0.6	10	43		8	22	21	12	18	21	12	17	21	15	
0.2-0.4	11	34	24	54	42	29	17	19	26	17	23	23	30	
0.0-0.2	10	20	76	38	36	*	13	22	47	61	41	48	56	100
Root														
0.0-0.1	**	**	**	***	***	***	***	**	**	48	49	51	38	68
0.1-0.2	100	100	100	41	44	37	100	100	28	39	17	24	24	30
0.2-0.3				20	21	33			24	5	21	21	2	14
0.3-0.4									*	4	4	6	9	7
0.4-0.5				27	16	17			2	2	4	2	2	5
0.5-0.6				13	14	10			1	1	1	2	2	4
0.6-0.7											*	2	2	
0.7-0.8												2	2	
0.8-0.9												2	2	
0.9-1.0					6	3						*	*	

\* Indicates percentage is less than 0.5%.

\*\*\* Sampling level 0.0-0.3 m.

\*\*\*\* Sampling levels are 0.2 m thick.

TABLE 3. LEAF BIOMASS DISTRIBUTION, ROOT BIOMASS DENSITY, AND LEAF:STEM BIOMASS RATIOS IN DIFFERENT LEVELS ABOVE AND BELOW THE SOIL SURFACE. Measurements were not made on *A. fasciculatum* 2 and *C. odorifera*.

Height (m)	Species and number of individual											
	<i>Ceanothus greggii</i>		<i>Adenostoma fasciculatum</i> *			<i>Heteromes arbutifolia</i>		<i>Arctostaphylos glauca</i>		<i>Satureja gilliesii</i> *		
	1	2	1	3	4	1	1	1	2	3	4	
Root biomass density (g m <sup>-3</sup> )	**	**	**	***	***	***	**	**	**	**	**	
0.0-0.1	740	290	400	150	102	3000	1370	362	412	265	220	
0.1-0.2				72	92			215	325	88	138	
0.2-0.3								182	46	108	121	
0.3-0.4								2	30	29	54	
0.4-0.5				53	47				18	22	12	
0.5-0.6									1	6	12	
0.6-0.7				46	28					1	12	
0.7-0.8											12	
0.8-0.9				20	7						1	
0.9-1.0												1
Leaf:stem biomass ratio												
1.6-1.8						6.14						
1.4-1.6						1.68						
1.2-1.4						0.50						
1.1-1.2						0.71			2.63			
1.0-1.0						0.28			3.04			
0.6-0.8						0.21			1.12			
0.4-0.6						0.05			0.50			
0.2-0.4						0.02			0.12			
0.0-0.2						0.0			0.03			

\* Leaves were not separated from stems.

\*\* Rooting level 0.0-0.3 m.

\*\*\* Rooting levels are 0.2 m.

TABLE 4. FRACTION OF THE TOTAL ROOT LENGTH IN DIFFERENT SOIL DEPTHS AND SIZE CLASSES. The mean total root length for four *Satureja* plants 49.2 m and for two *Colliguaya* plants 8.3 m.

Soil depth (m)	Root diameter class (mm)							
	0-0.5	0.5-1.0	1-2	2-4	4-6	6-8	8-10	> 10
<i>Satureja</i>								
0-0.1	0.265	0.064	0.031	0.029	0.017	0.011	0.008	0.005
0.1-0.2	0.105	0.048	0.050	0.021	0.010	0.003	0	0
0.2-0.3	0.093	0.050	0.052	0.019	0.006	0	0	0
0.3-0.4	0.025	0.023	0.016	0.006	0.001	0	0	0
0.4-0.5	0.009	0.007	0.007	0.001	0	0	0	0
0.5-0.6	0.007	0.005	0.001	0	0	0	0	0
0.6-0.7	0.002	0.002	0.002	0	0	0	0	0
Total	0.506	0.199	0.159	0.076	0.034	0.014	0.008	0.005
<i>Colliguaya</i>								
0-0.1	0.203	0.122	0.087	0.052	0.023	0.006	0	0
0.1-0.2	0.151	0.110	0.070	0.046	0	0	0	0
0.2-0.3	0.035	0.041	0.036	0	0	0	0	0
0.3-0.4	0.006	0.006	0.006	0	0	0	0	0
Total	0.395	0.279	0.199	0.098	0.023	0.006		

summer, so soil systems can be expected to be organized for the efficient uptake of these minerals. To absorb phosphorus efficiently a root system should have roots or mycorrhizae about 0.5 cm apart because of low mobility of phosphorus in the soil (Bielecki, 1973). For efficient absorption of nitrate, roots should be about 4 cm apart (Van Keulen et al., 1975) and for water, about 8 cm apart (Lambert and Penning de Vries, 1975). If a biomass of fine roots adequate to exploit the soil nitrate is added to our measured values, root:shoot ratios from 0.26 to 0.93 are calculated; to exploit the soil phosphate, root:shoot ratios from 0.34 to 3.35 are obtained. Ratios above 1.0 are always associated with rooting systems deeper than 0.5 m and small calculated root biomass densities. It is unrealistic to add the full biomass density to these sparse root systems, because the larger roots are not present to support the development of the fine roots. Thus, we conclude that the root-shoot ratios of chaparral shrubs, even though some are considered deep-rooted, have root:shoot ratios between 0.3 and 1.0 and have root biomasses concentrated near the soil surface.

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A NEW SPECIES OF IVESIA (ROSACEAE)  
FROM SOUTHEASTERN OREGON

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The geology and relative isolation of southeastern Oregon make the area an excellent location for discovering new and unusual plant species. Leslie Gulch in Malheur County is one site in particular whose botanical treasures have only recently been discovered (Glad, 1975; Barkley, in press). Approximately ten percent of the species found there are rare or endangered (Packard, pers. comm.), and several are endemic to the barren ash and tuff slopes lining the canyons in the Succor Creek and Owyhee River drainage basin. In this paper we present a new species of *Ivesia* (Rosaceae: Potentilleae) from Leslie Gulch. This species was initially discovered by the senior author while a student at the College of Idaho, Caldwell.

*Ivesia rhypara* Ertter & Reveal, sp. nov. Species insignis stylo solitaria, petalis brevibus albis, ramis prostratis et inflorescentiis apertis cymis, a speciebus nobis notis bene distincta. Fig. 1.

Low spreading herbaceous perennial from a branched caudex atop an extensive, woody root system, this often clothed with old, reddish-pubescent leaf-bases; herbage grayish- or greenish-white, villous to canescent, eglandular; stems erect before anthesis, becoming prostrate and trailing as the inflorescence develops and lengthens, 5-15 cm long; leaves essentially basal, canescent, 3-8 cm long, with 5-15 pairs of closely overlapping leaflets; leaflets divided to near the base into 3-5 segment, these ovate to rounded, 1.8-3 (-4) mm long; inflorescence a more or less open cyme, 3-20 cm long; bracts leafy below and often appearing near the middle of the stem due to the reduction and loss of the first branch of the inflorescence, 3-7 mm long, 1.5-4 mm long above in the inflorescence, mostly ovate; hypanthium shallowly cupulate, 2-2.3 (-2.5) mm wide, yellowish to golden within, the receptacle densely covered with long, white, silky-villous hairs; bractlets ovate, about two-thirds the length and one-half the width of the sepals; sepals 5, triangular, 1.8-2.5 mm long; petals 5, white, 0.8-1.5 mm long, 0.2-0.5 mm wide, narrowly spatulate to oblanceolate, inconspicuous; stamens 5, inserted well away from the margin of the receptacle, the filaments linear, 1.5-1.8 mm long, glabrous, the anthers yellow except for the magenta-colored marginal sutures, 0.4-0.5 mm long; pistil solitary, 1-2 mm long, glabrous; achenes smooth, brown, 1-1.3 mm long. Flowering from May to October.

<sup>1</sup> This paper has been submitted to the Department of Botany, University of Maryland, as partial fulfillment of two credits of Special Problems given during the Fall Semester of 1976.

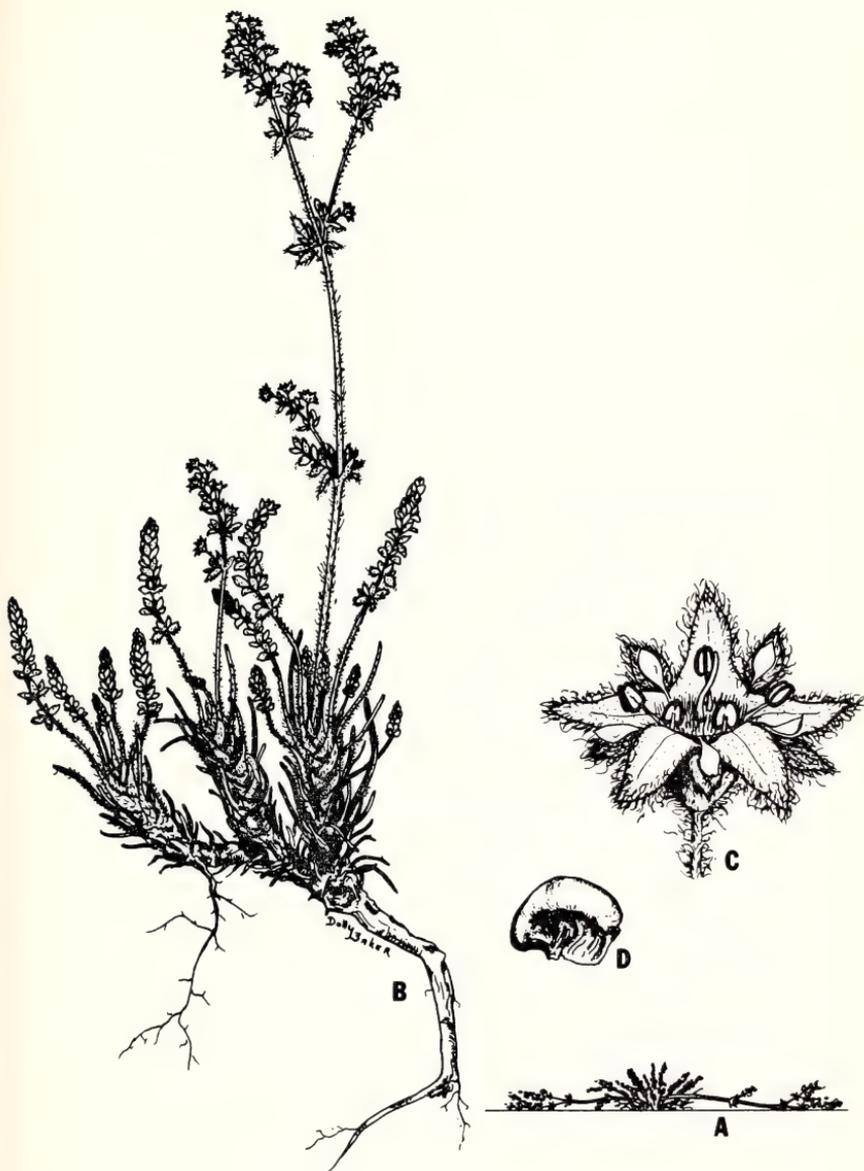


FIG. 1. Illustration of *Ivesia rhypara*. A, habit (x 1/5); B, details of the leaves and inflorescence, the latter shown in an upright position for convenience; see A for actual location (x 1); C, detail of flower (x 6); D, mature achene (x 10).

TYPE: OREGON, Malheur Co., along the rim above Leslie Gulch E of Owyhee Reservoir, 0.2 km down Leslie Gulch road from the entrance to the canyon, on red to yellow volcanic ash in sparse vegetation, at ca 1430 m, sec. 9, T.26S., R.45E., 13 Jul 1975, *Reveal & Ertter 3894* (Holotype: US, isotypes: BRY, CAS, CIC, GH, ID, K, MARY, MO, NY, OSC, RM, RSA, TEX, UC, UTC, WTU, and elsewhere).

ADDITIONAL SPECIMENS EXAMINED: OREGON, Malheur Co., Leslie Gulch, 30 Sep 1973, *Packard 73-293* (CIC); Leslie Gulch, 26 May 1974, *Ertter 47/4* (CIC).

*Ivesia rhypara* is not likely to be confused with any other species of the genus. In Keck's (1938) revision, *I. rhypara* would key out to *I. shockleyi* S. Wats., an alpine plant of the Sierra Nevada of California and west-central Nevada. Our new species may be quickly distinguished from that species by the denser, non-glandular pubescence, the consistently solitary style, and the small, white petals. In southeastern Oregon, only *I. baileyi* S. Wats. is regularly encountered, and then only in the higher mountains. It differs from *I. rhypara* in having an erect, glandular-pubescent stem, larger leaflets, and three to seven pistils. The intermountain species of *Ivesia* which are found in the desert all have more than five stamens, while those species in the region with five stamens all occur at higher elevations in more mesic sites. In addition, all these other species are glandular, less densely pubescent, and typically with yellow petals.

The new species is apparently confined to an area of less than one mile square on either side of the road entrance to Leslie Gulch, and has not been found in any adjacent areas in the Succor Creek drainage (Packard, pers. comm.). It has been found on soils ranging from a reddish tuff to a loose, yellowish volcanic ash. Near the road on the north side of the canyon, it is associated with *Poa sandbergii*, *Agropyron spicatum*, *Eriogonum strictum*, *Physaria chambersii*, *Astragalus sterilis*, *Linum perenne*, *Penstemon acuminatus*, *Eriophyllum lanatum*, and an unusual form of *Monardella odoratissima*. On the south side of the canyon, it grows on the bare ground among *Juniperus osteosperma* and *Purshia tridentata*. It is very local and relatively infrequent in all known locations, and should be considered an endangered species. Leslie Gulch is now open to recreational traffic, and off-road vehicle activities in the area could easily destroy the fragile slopes to which the species is restricted.

The species epithet is based on the Greek "rhyparos" meaning "dirty" or "grimy", not only in reference to the dirty or dusty appearance of the species, but also here applied to honor James W. Grimes, a fellow student and collector with the senior author of the Leslie Gulch flora. Grimes is currently attending Utah State University and working on the flora of the Leslie Gulch area as part of his Master's program.

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MISCELLANEOUS CHROMOSOME COUNTS OF  
WESTERN AMERICAN PLANTS—IV

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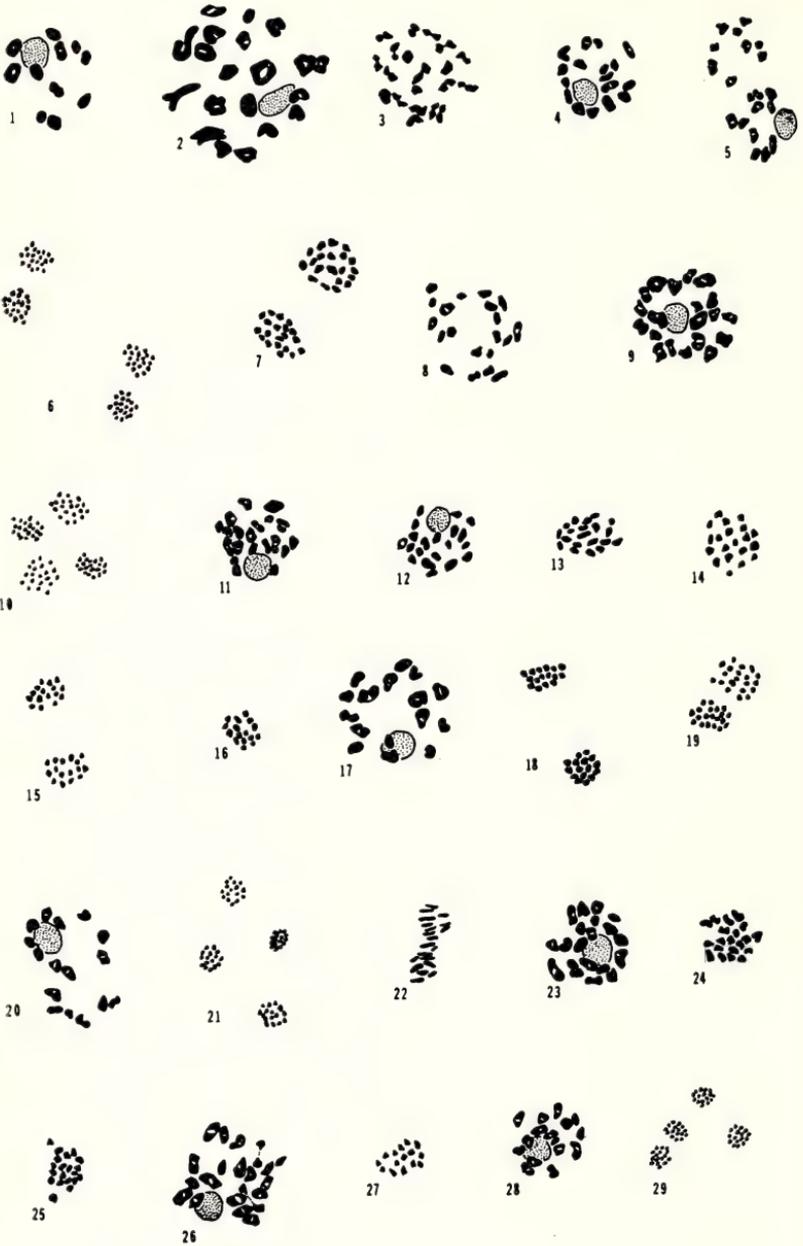
This series of papers, of which this is the fourth, reports chromosome counts of miscellaneous western American plants. Previous parts have dealt with plants collected of various floristic projects of the senior author (Reveal & Styer, 1973, 1974; Reveal & Spellenberg, 1976). The present contribution covers counts of plants collected in Baja California, Mexico, in February of 1973.

Flower buds were collected in developmental stages from plants growing in their native habitats, and were fixed in ethanol and glacial acetic acid (3:1). Anthers were squashed in acetocarmine and camera lucida drawings were prepared. The counts reported here were made by Reveal, but all of the species determinations except those of *Eriogonum*, or as indicated, were made by Moran. Voucher specimens are deposited at the San Diego Museum of Natural History (SD).

Chromosome numbers are reported for 31 taxa; for 26 of these we have seen no previous reports. Three counts represent first reports for the genus: *Chorizanthe* ( $n = 20$ ), *Wislizenia* ( $n = 20$ ), and *Errazurizia* ( $n = 14$ ).

*Garrya grisea* Wiggins.  $n = 11$ . Voucher: *M&R 20176* (Fig. 1), north slope of Cerro Azufre, ca 1600 m, B.Cfa.Sur (near 27°30'N, 112°36'W), 17 Feb 1973.

This first reported number for the species is common in the genus (Bolkhovskikh et al., 1969). The species has not been reported previously from south of Sierra San Pedro Mártir.



*Chorizanthe pulchella* Brandegee.  $n = 20$ . Voucher: *M&R 19625* (Figs. 2, 3), 2 mi S of El Crucero, ca 530 m, B.Cfa.Norte (near  $29^{\circ}14'N$ ,  $114^{\circ}11'W$ ), 1 Feb 1973.

This is the first published count for the genus *Chorizanthe*. Judging from Reveal's understanding of *Eriogonum*, the basic number of the genus would seem to be  $x = 10$ . On labels for the voucher, the chromosome number was given incorrectly as  $n = 15$ .

*Eriogonum elongatum* Benth. var. *areorivum* Reveal.  $n = 17$ . Vouchers: *M&R 19913* (Fig. 4), bed of Arroyo San José de Castro, ca 340 m, B.Cfa.Sur (near  $27^{\circ}33'N$ ,  $114^{\circ}32'W$ ), 7 Feb 1973; *M&R 19930* (Fig. 5), bed of Arroyo Largo, 4 mi E of the mouth, ca 110 m, B.Cfa.Sur (near  $27^{\circ}36'N$ ,  $114^{\circ}45'W$ ), 8 Feb 1973.

This count agrees with that given by Stokes and Stebbins (1955) for var. *elongatum*.

*Eriogonum encelioides* Reveal & Hanson.  $n = 20$ . Vouchers: *M&R 19813* (Fig. 6), Arroyo del Portezuelo, 9.5 mi S of San José de Castro, ca 275 m, B.Cfa.Sur (near  $27^{\circ}26'N$ ,  $114^{\circ}27'W$ ), 5 Feb 1973; *M&R 19967* (Fig. 7), Arroyo de las Casitas, 2.5 mi above the mouth, ca 100 m, B.Cfa.Sur (near  $27^{\circ}31'N$ ,  $114^{\circ}36'W$ ), 9 Feb 1973.

Reveal and Hanson (1967) associated this species with *Eriogonum elongatum*. However, examination of the plant in the field clearly shows it to be a member of section Fasciculata Benth. and most closely related to *E. molle* Brandegee, of Cedros Island.

*Eriogonum fasciculatum* Benth. var. *fasciculatum*.  $n = 20$ . Voucher: *M&R 20289* (Fig. 8), Colnett Mesa, 0.5 mi N of Colnett, ca 80 m, B.Cfa.Norte (near  $31^{\circ}05'N$ ,  $116^{\circ}13'W$ ), 25 Feb 1973.

This count agrees with previous reports for this variety (Stebbins, 1942; Stokes & Stebbins, 1955; Reveal, 1967).

*Eriogonum fasciculatum* Benth. var. *flavorirde* Munz & Johnston.  $n = 20$ . Vouchers: *M&R 19629* (Fig. 9), Arroyo León, 5 mi N of Punta Prieta, ca 250 m, B.Cfa.Norte (near  $29^{\circ}01'N$ ,  $114^{\circ}12'W$ ), 1 Feb 1973; *M&R 20163* (Figs. 12, 13), saddle on north side of Cerro Azufre, ca 1250 m, B.Cfa.Sur (near  $27^{\circ}30'N$ ,  $112^{\circ}36'W$ ), 17 Feb 1973.

FIGS. 1-29. 1. *Garrya grisea*,  $n = 11$ , diakinesis. 2. *Chorizanthe pulchella*,  $n = 20$ , diakinesis; 3, metaphase I. 4, 5. *Eriogonum elongatum* var. *areorivum*,  $n = 17$ , diakinesis. 6. *Eriogonum encelioides*,  $n = 20$ , telophase II; 7, anaphase I. 8. *Eriogonum fasciculatum* var. *fasciculatum*,  $n = 20$ , metaphase I. 9, 12. *Eriogonum fasciculatum* var. *flavorirde*,  $n = 20$ , diakinesis; 12, late diakinesis. 10. *Eriogonum fasciculatum* var. *emphereium*,  $n = 20$ , telophase II; 11, diakinesis. 14. *Eriogonum fastigiatum*,  $n = 20$ , metaphase I. 15. *Eriogonum inflatum* var. *deflatum*,  $n = 16$ , anaphase I; 16, metaphase I. 17. *Eriogonum intricatum*,  $n = 16$ , diakinesis; 18, telophase I. 19. *Eriogonum moranii*,  $n = 20$ , anaphase I. 20. *Eriogonum pilosum*,  $n = 16$ , diakinesis; 21, telophase II. 22, 24. *Eriogonum pondii*,  $n = 20$ , metaphase I; 23, diakinesis. 25. *Eriogonum preclarum*,  $n = 20$ , metaphase I; 26, diakinesis. 27. *Eriogonum repens*,  $n = 16$ , metaphase I; 28, diakinesis; 29, telophase II.

Shreve and Wiggins (1964) and Reveal and Munz (1968) considered this variety endemic to southern California, but on the basis of pubescence characters of leaves, involucre, and flowers, the plants from central Baja California can be referred only to var. *flavovirde*.

*Eriogonum fasciculatum* Benth. var. *emphereium* Reveal.  $n = 20$ . Vouchers: *M&R 19660* (Fig. 10), Picachos de Santa Clara, ca 350 m, B.Cfa.Sur (near  $27^{\circ}09'N$ ,  $113^{\circ}40'W$ ), 3 Feb 1973; *M&R 19690* (Fig. 11), north slope of SE peak, Picachos de Santa Clara, ca 475 m, B.Cfa. Sur (near  $27^{\circ}07'N$ ,  $113^{\circ}37'W$ ), 3 Feb 1973.

This recently proposed variety (Reveal, 1976) differs in its large flowers which may perhaps show past influence of gene flow by *Eriogonum pondii* Greene. No chromosomal abnormalities were noted in the several buds examined.

*Eriogonum fastigiatum* Parry.  $n = 20$ . Voucher: *M&R 20282* (Fig. 14), Colnett Mesa, 0.5 mi N of Colnett, ca 80 m, B.Cfa.Norte (near  $31^{\circ}05'N$ ,  $116^{\circ}13'W$ ), 25 Feb 1973.

*Eriogonum inflatum* Torr. & Frém. var. *deflatum* I. M. Johnston.  $n = 16$ . Vouchers: *M&R 19610* (Fig. 15), Arroyo San Francisquito, 4 mi NW of Las Arrastras, ca 350 m, B.Cfa.Norte (near  $29^{\circ}36'N$ ,  $114^{\circ}26'W$ ), 31 Jan 1973; *M&R 20037* (Fig. 16), grade near Lucifer, ca 110 m, B.Cfa.Sur (near  $27^{\circ}23'N$ ,  $112^{\circ}24'W$ ), 11 Feb 1973.

This count agrees with previously reported counts (Reveal, 1967).

*Eriogonum intricatum* Benth.  $n = 16$ . Vouchers: *M&R 19755* (Fig. 17), 8 mi NW of Asunción, ca 70 m, B.Cfa.Sur (near  $27^{\circ}13'N$ ,  $114^{\circ}21'W$ ), 4 Feb 1973; *M&R 19894* (Fig. 18), Arroyo Malarrimo, 11 mi S of the mouth, ca 75 m, B.Cfa.Sur (near  $27^{\circ}39'N$ ,  $114^{\circ}29'W$ ), 6 Feb 1973.

This Baja California endemic belongs to the *Eriogonum inflatum* complex and has the same chromosome number as *E. inflatum*.

*Eriogonum moranii* Reveal.  $n = 20$ . Voucher: *M&R 19611* (Fig. 19), Arroyo Calamajué, ca 330 m, B.Cfa.Norte (near  $29^{\circ}24'N$ ,  $114^{\circ}14'W$ ), 1 Feb 1973.

This count agrees with that published previously (Reveal, 1968).

*Eriogonum pilosum* S. Stokes.  $n = 16$ . Voucher: *M&R 20214* (Figs. 20, 21), Arroyo de la Purificación, ca 500 m, B.Cfa.Norte (near  $28^{\circ}10'N$ ,  $113^{\circ}15'W$ ), 19 Feb 1973.

Shreve and Wiggins (1964) included this species with *Eriogonum scalare* S. Wats., and their description of *E. scalare* applies in large part to *E. pilosum*, while the description of *E. pilosum* applies mainly to *E. repens* (S. Stokes) Reveal (Reveal, 1976). The leaves of *E. scalare* are elliptic, nearly glabrous, 5–15 mm long, and 2–6 mm wide, whereas those of *E. pilosum* are oblanceolate to oblong, wavy-margined, pilose 0.8–3 cm long, and 4–8 mm wide.

*Eriogonum pondii* Greene.  $n = 20$ . Vouchers: *M&R 19753* (Fig. 22), 8 mi NW of Asunción, ca 70 m, B.Cfa.Sur (near  $27^{\circ}13'N$ ,  $114^{\circ}21'W$ ),

4 Feb 1973; *M&R 19932* (Figs. 23, 24), bed of Arroyo Largo, 6.7 mi E of the mouth, ca 175 m, B.Cfa.Sur (near 27°36'N, 114°43'W), 8 Feb 1973.

In 1967, Reveal and Hanson proposed var. *gentryi* for the mainland plants of this species, except for the strictly coastal populations, with var. *pondii* restricted to Cedros and Natividad Islands and the Turtle Bay area. After further study, the apparent differences upon which var. *gentryi* were based now seem too trivial for varietal distinction, and therefore it should be considered a synonym of *E. pondii*.

*Eriogonum preclarum* Reveal.  $n = 20$ . Vouchers: *M&R 19814* (Fig. 25), Arroyo de Portezuelo, 9.5 mi S of San José de Castro, ca 275 m, B.Cfa.Sur (near 27°26'N, 114°27'W), 5 Feb 1973; *M&R 19955* (Fig. 26), bed of Arroyo de las Casitas, near the mouth, ca 10 m, B.Cfa.Sur (near 27°29'N, 114°38'W), 9 Feb 1973.

The type of this newly proposed species (Reveal, 1976), *M&R 19964*, was also counted and determined to be  $n = 20$ , but is not figured.

*Eriogonum repens* (S. Stokes) Reveal.  $n = 16$ . Vouchers: *M&R 19640* (Fig. 27), 1 mi N of San Angel, ca 50 m, B.Cfa.Sur (near 27°15'N, 113°10'W), 2 Feb 1973; *M&R 20135* (Figs. 28, 29), Valley de Tortuga, ca 80 m, B.Cfa.Sur (near 26°35'N, 113°50'W), 15 Feb 1973.

*Eriogonum thurberi* Torr.  $n = 20$ . Voucher: *M&R 20246* (Figs. 30–32), 2 mi NW of Desengaño, ca 580 m, B.Cfa.Norte (near 29°08'N, 114°05'W), 23 Feb 1973.

*Streptanthus arizonicus* S. Wats.  $n = 14$ . Voucher: *M&R 20159* (Figs. 33, 34), north slope of Cerro Azufre, ca 1250 m, B.Cfa.Sur (near 27°30'N, 112°36'W), 17 Feb 1973; identified by Reed Rollins.

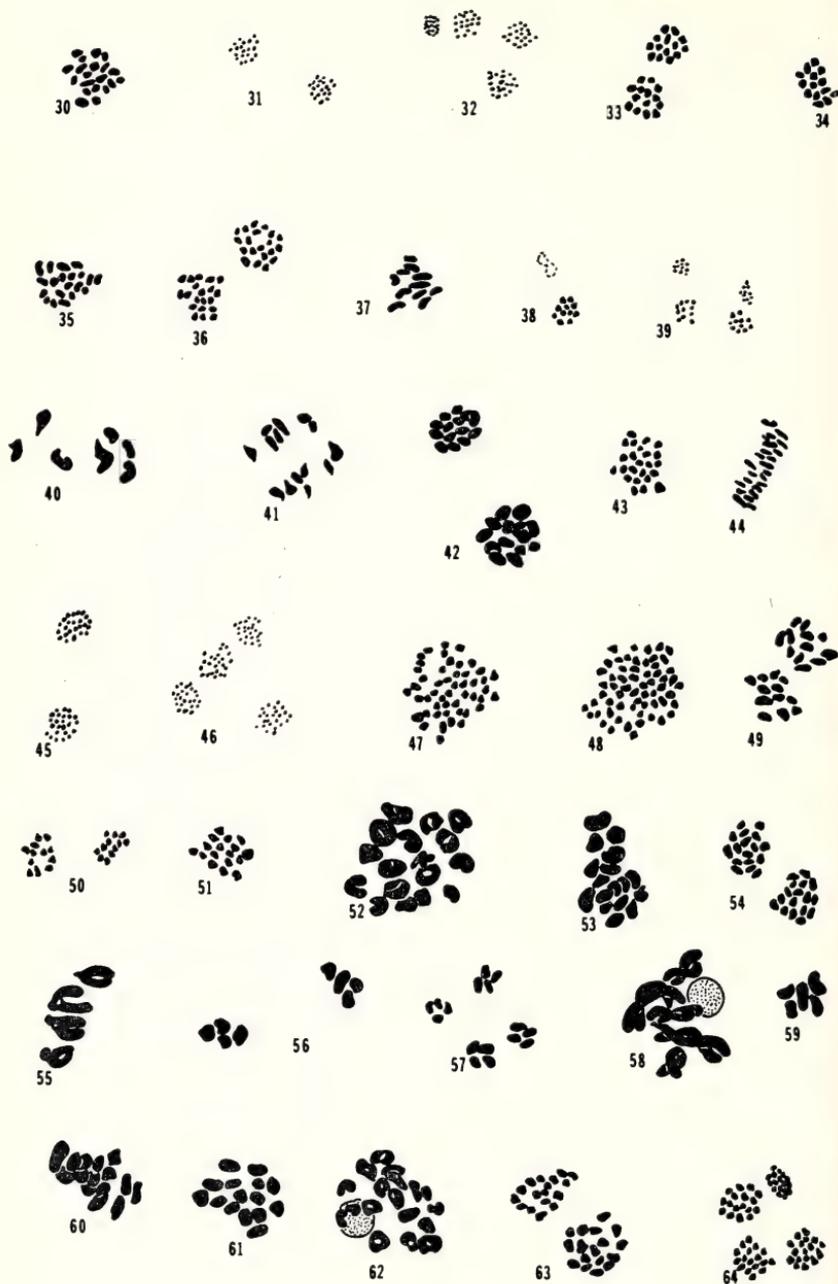
This collection represents a substantial southern range extension for the species, otherwise known from southern Arizona. *M&R 20192* ( $n = 14$ ) was also counted but is not illustrated.

*Wislizenia refracta* Engelm. in Wisliz.  $n = 20$ . Voucher: *M&R 20096* (Figs. 35, 36), Pozo de San Juanico, ca 25 m, B.Cfa.Sur (near 26°14'N, 112°28'W), 14 Feb 1973.

This seems to be the first count for the genus. The specimens are atypical of the species in being perennials, with woody stems to 1.5 cm thick at the base; but they seem not to differ otherwise from the more typical annual phase of the species. We collected the perennial form (*M&R 20153*) also at San Zacarías, where it is known as "Joaquito"; tea made from the leaves is said to be used internally and externally for scorpion stings.

*Astragalus magdalenae* Greene var. *magdalenae*.  $n = 11$ . Voucher: *M&R 19718* (Figs. 37–39), 4 mi NE of Abreojos, ca 5 m, B.Cfa.Sur (near 26°45'N, 113°34'W), 4 Feb 1973; identification confirmed by Rupert C. Barneby.

*Dalea bicolor* H.B.K. (unpublished new variety to be named by Barneby; pers. comm.).  $n = 7$ . Voucher: *M&R 20158* (Figs. 40, 41),



northeast ridge of Cerro Azufre, ca 850 m, B.Cfa.Sur (near 27°31'N, 113°34'W), 17 Feb 1973; identification confirmed by Rupert C. Barneby.

This new form of *Dalea bicolor* will be named in honor of C. R. Orcutt in the near future.

*Errazurizia benthamii* (Brandege) I. M. Johnston.  $n = 14$ . Voucher: *M&R 19865* (Fig. 42), Arroyo Malarrimo, 9 mi S of the mouth, ca 60 m, B.Cfa.Sur (near 27°41'N, 114°28'W), 6 Feb 1973.

This appears to be the first report for the genus.

*Lupinus arizonicus* (S. Wats.) S. Wats. var. *barbatulus* (Thornber) I. M. Johnston.  $n = 24$ . Voucher: *M&R 19845* (Figs. 43–46), Malarimo, ca 10 m, B.Cfa.Sur (near 27°48'N, 114°27'W), 6 Feb 1973; identification by David Dunn.

*Castilleja* aff. *lanata* A. Gray. Vouchers: *M&R 20249* ( $n = 48$ , Fig. 47), north slope of volcanic hill at top of Jaraguay Grade, ca 875 m, B.Cfa.Norte (near 29°37'N, 114°37'W), 24 Feb 1973; *M&R 20208* ( $n = 60$ , Fig. 48), north slope of Volcán las Tres Vírgenes, ca 1325 m, B.Cfa.Sur (near 27°29'N, 112°36'W), 18 Feb 1973; identifications by Noel H. Holmgren.

Holmgren reports that these two collections approach *Castilleja lanata* of southern Arizona eastward to Texas, but may be taxonomically distinct and deserve some formal recognition. In addition to the two ploidy levels reported here ( $n = 48, 60$ ), Lawrence R. Heckard has found an even lower ploidy level which he will report.

*Orobancha cooperi* (A. Gray) Heller.  $n = 12$ . Voucher: *M&R 19933* (Fig. 49), Arroyo Largo, 6.7 mi E of the mouth, ca 175 m, B.Cfa.Sur (near 27°36'N, 114°43'W), 8 Feb 1973.

Heckard and Chuang (1975) have reported *Orobancha cooperi* from Baja California, Mexico, and California, with counts of  $2n = 48, 72$ , and 96. Apparently, our count is the first diploid population reported for this species, and the first species of New World *Orobancha* with a haploid number of 12. Our plants differ from typical *O. cooperi* in having glabrous anthers.

FIGS. 30–64. 30. *Eriogonum thurberi*,  $n = 20$ , metaphase I; 31, telophase I; 32, telophase II. 33. *Streptanthus arizonicus*,  $n = 14$ , anaphase I; 34, metaphase I. 35. *Wislizenia refracta*,  $n = 20$ , metaphase I; 36, telophase I. 37. *Astragalus magdalenae* var. *magdalenae*,  $n = 11$ , metaphase I; 38, one complement of anaphase I; 39, telophase II. 40. *Dalea bicolor* var. *ined.*,  $n = 7$ , metaphase I; 41, anaphase I. 42. *Errazurizia benthamii*,  $n = 14$ , telophase I. 43, 44. *Lupinus arizonicus* var. *barbatulus*,  $n = 24$ , metaphase I; 45, telophase I; 46, telophase II. 47. *Castilleja* aff. *lanata*,  $n = 48$ , metaphase I; 48,  $n = 60$ , metaphase I. 49. *Orobancha cooperi*,  $n = 12$ , anaphase I. 50. *Salvia similis*,  $n = 12$ , telophase I. 51. *Encelia palmeri*,  $n = 17$ , metaphase I. 52. *Encelia stenophylla*,  $n = 17$ , diakinesis; 53, metaphase; 54, late anaphase I. 55. *Greenella ramulosa*,  $n = 4$ , diakinesis; 56, telophase I; 57, telophase II. 58. *Machaeranthera crispa*,  $n = 5$ , diakinesis; 59, metaphase I. 60, 61. *Porophyllum tridentatum*,  $n = 15$ , metaphase I. 62. *Viguiera lanata*,  $n = 17$ , diakinesis; 63, anaphase I; 64, telophase I.

*Salvia similis* Brandegee.  $n = 12$ . Voucher: *M&R 20108* (Fig. 50), in an arroyo 3 mi SW of Cadejé, ca 50 m, B.Cfa.Sur (near  $26^{\circ}20'N$ ,  $112^{\circ}24'W$ ), 14 Feb 1973.

*Encelia palmeri* Vasey & Rose.  $n = 17$ . Voucher: *M&R 20003* (Fig. 51), Arroyo Calvario, 6 mi N of San Andrés, ca 130 m, B.Cfa.Sur (near  $27^{\circ}20'N$ ,  $114^{\circ}26'W$ ), 10 Feb 1973.

*Encelia stenophylla* Greene.  $n = 17$ . Voucher: *M&R 19678* (Figs. 52–54), north slope of SE peak, Picachos de Santa Clara, ca 350 m, B.Cfa. Sur (near  $27^{\circ}07'N$ ,  $113^{\circ}37'W$ ), 3 Feb 1973.

Shreve and Wiggins (1964) reported this species for Cedros Island but not for peninsular Baja California. Our collections show it fairly common not only at Picachos de Santa Clara but also from Turtle Bay to Arroyo Malarrimo and to south of San José de Castro, from about 25 to 850 meters elevation.

*Greenella ramulosa* Greene.  $n = 4$ . Voucher: *M&R 19926* (Figs. 55–57), southeast side of Bahía Tortugas, ca 10 m, B.Cfa.Sur (near  $27^{\circ}39'N$ ,  $114^{\circ}51'W$ ), 8 Feb 1973.

This perennial species is restricted to the west coast of central Baja California. The only other species of the genus is an annual, found in Arizona, which likewise is  $n = 4$  (Solbrig et al., 1964). The proposal by Ruffin (1974) to reduce *Greenella* to *Xanthocephalum* is not adopted here.

*Machaeranthera crispa* (Brandegee) Turner & Horne.  $n = 5$ . Voucher: *M&R 20154* (Figs. 58, 59), San Zacarías, ca 170 m, B.Cfa.Sur (near  $27^{\circ}08'N$ ,  $112^{\circ}56'W$ ), 15 Feb 1973.

This count is consistent with the somatic number of  $2n = 10$  given by Turner and Horne (1964).

*Porophyllum tridentatum* Benth.  $n = 15$ . Voucher: *M&R 19965* (Figs. 60, 61), Arroyo de las Casitas, 1.5 mi above the mouth, ca 50 m, B.Cfa.Sur (near  $27^{\circ}30'N$ ,  $114^{\circ}36'W$ ), 9 Feb 1973; confirmed by John L. Strother.

Johnston (1965) published a count of  $2n = 30$  for what he called *Porophyllum tridentatum* var. *crassifolium*; but that is a valid species in the opinion of John L. Strother (pers. comm.). Shreve and Wiggins (1964) reported *P. tridentatum* only from the Magdalena Plain and adjacent islands, some 325 kilometers to the southeast.

*Viguiera lanata* (Kellogg) A. Gray.  $n = 17$ . Voucher: *M&R 19970* (Figs. 62–64), Arroyo de las Casitas, 8 mi above the mouth, ca 300 m, B.Cfa.Sur (near  $27^{\circ}33'N$ ,  $114^{\circ}35'W$ ), 9 Feb 1973.

Shreve and Wiggins (1964) reported this species as known only from Cedros and Natividad Islands, but they expressed the opinion that it should also occur on the mainland. Our collections confirm that expectation.

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FOUR NEW SPECIES OF CENTAURIUM (GENTIANACEAE)  
FROM MEXICO

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Work on a taxonomic revision of the New World members of *Centaurium* (Gentianaceae) has resulted in the recognition of four previously undescribed species from Mexico. Three are known to me only from herbarium specimens, but living material of a fourth has been collected and observed.

***Centaurium gentryi*** Broome, sp. nov. Herba annua parva caule simplici ramis paucis, rosula basali, foliis caulinis setaceis, et floribus paucis pentameris lobis corollae tubo longioribus. A *C. madrensi* foliis basalis multo majoribus persistentibus, nodis caulinis foliosis paucioribus, floribus majoribus differt. Fig. 1a, b.

TYPE: Mexico, Chihuahua, Rancho Byerly, Sierra Charuco (approx. 27°30'N, 108°40'W), on rocky igneous slopes in pine-oak forest, 1525–1770 m, 17–25 Apr 1948, *Gentry 8035* (Holotype: UC; isotypes: DS, MEXU, MICH, US).

Plants annual with erect simple stems 11–26 cm tall, branched mostly above the middle with only ca 3 elongate internodes, 10–55 mm long, beneath the first branch. Leaves strongly dimorphic, the basal 3–6 pairs in a rosette, these lance-ovate to broadly ovate, 5–12 mm long, 3–6 mm broad, the cauline leaves linear or subulate, 3–12 mm long and 0.5–1 mm broad, appressed to the stem. Inflorescence a simple paniculate or racemose cyme, sparingly branched, with the branches ascending at angles of 20–30° from the main axis, often uniflorous; pedicels of central flowers in a dichasium 46–56 mm long, but as short as 6 mm on lateral flowers. Flowers pentamerous, usually 1–6 per plant. Calyx 4.5–9.2 mm long, the lobes 4.2–8.7 mm long, subulate-attenuate and moderately keeled, without prominent hyaline margins, about equally the corolla-tube. Corolla vivid rose-pink without a prominent white eye, (11–) 18–22.5 mm long; corolla-tube (4–) 7–8.2 mm long, not constricted above ovary, the top slightly flared into a throat; corolla-lobes (7–) 12–15 mm long, (3.5–) 5.5–6.5 mm broad, lance-ovate, obtuse at tips. Stamens 4.5–7 mm long, inserted just below summit of ovary, shorter than or equalling style at anthesis; anthers linear before anthesis, 1.2–2 mm long when coiled; pollen grains 23.8–40.8  $\mu\text{m}$  in diameter. Ovary 4.2–7.5 mm long at anthesis; style exserted, 4.6–7 mm long, the stigma bilobed with lobes slightly broader than long. Capsule oblong, not resinous, ca 8 mm long and 3 mm broad; seeds reddish-brown, 0.3 mm long.

The Rio Mayo region of western Mexico has yielded a number of plant novelties, but the area has been little collected since Gentry's expeditions in the 1930s and 1940s. This very distinctive Rio Mayo *Centaurium* is accorded the rank of species, in spite of the fact that it is known only from a single collection. Its large, showy flowers with long exserted styles are reminiscent of those of *C. chironioides* (Griseb.) Druce, but in its habit, inflorescence, and leaf morphology it more resembles *C. madrense* (Hemsley) B. L. Robinson, a species of the Sierran region of Sinaloa, Durango, Nayarit, and Jalisco. It is probably more allied to those two Mexican species than to the *C. calycosum* (Buckley) Fern. complex of the United States and bordering states of Mexico. It differs from *C. madrense* by having much larger basal leaves, fewer leaf-bearing nodes beneath the inflorescence, broader and shorter calyx-lobes, and conspicuously larger corollas.



FIG. 1. *Centaurium gentryi*, a. habit (x0.5), b. flower (x1.2)—based on *Gentry 8035*; and *C. pterocaulle*, c. habit (x0.3), d. flower (x1.2)—based on *Smith M81*.

***Centaurium pterocaulle* Broome, sp. nov.** Herba annua, caule erecto alato, floribus paucis pentameris magnis, lobis corollae tubo longioribus. *Centaurio chironioide* affinis, caule et videtur simplici, alis usque ad 1 mm latis, undulatis, foliis inferioribus obovatis latoribus differt. Fig. 1c, d.

TYPE: Mexico, Hidalgo, Zimapan, *Coulter 941* (Holotype: K; isotype: GH).

Plants annual with erect, simple stems 23–39 cm tall, relatively stout and prominently 4-winged, the wings on the lower stem ca 1 mm wide and ruffled. Leaves cauline, 9–33 mm long, 6–13 mm wide, obovate, obscurely 3-nerved, obtuse-tipped at lower nodes, and becoming narrower and shorter upwards, narrowly obovate to oblanceolate with acute or acuminate tips, reduced to lanceolate bracts in the inflorescence. Stem-

wings and leaf margins blue-black upon drying. Inflorescence a simple determinate panicle with both dichasial and monochasial branching, the branches up to 20 cm long and leafy, only once or twice compound or uniflorous; pedicel of central flower of a dichasium 6–17 mm long, but as short as 2 mm on lateral flowers. Flowers pentamerous, showy, usually 4–10 per plant. Calyx 6–8 mm long, the lobes 4–5.5 mm long, narrowly triangular-attenuate to narrowly subulate-acuminate, about equally the corolla-tube, the hyaline margins narrow. Corolla apparently deep rose without white eye, 16–23 mm long; corolla-tube 6–9 mm long, slightly exceeding and constricted above the ovary; corolla-lobes 10–14 mm long, 4–7.5 mm wide, ovate or lance-ovate with acute or slightly acuminate tips. Stamens 4.5–5.5 mm long, inserted in corolla-tube just below the summit of the ovary and nearly equalling the style at anthesis; anthers linear-oblong before anthesis, 1.6–2.2 mm long when coiled; pollen grains 26.6–29.4  $\mu\text{m}$  (Carlson 3148) or 33.9–46.2  $\mu\text{m}$  (Smith M81) in diameter. Ovary oblong, thick-walled, ca 7–7.5 mm long; style exerted from corolla-tube, 5–7 mm long, the stigma bilobed with lobes slightly broader than long. Mature capsule not seen; partially mature one 7.6 mm long and 3.4 mm broad, oval with rounded apex; seeds not seen.

Mexico, in states of Morelos, Hidalgo, and San Luis Potosí, in montane pine forests at 1800–2500 m. Flowering specimens have been collected in January and April.

Additional Collections: MEXICO. MORELOS: in pine forest on Old Mexico City Highway, 16 Apr 1960, Smith M81 (TEX); between Cuernavaca and Mexico City on old road, km 62, 2070 m, 27 Jan 1955, Carlson 3148 (DUKE). SAN LUIS POTOSÍ: Cerro de la Silleta, near Xilitla, Paray 369 (MEXU).

Considerable variation exists among the four collections that I have included in this taxon. The Carlson specimen has strikingly large, broadly obovate leaves at the lower nodes reminiscent of *Schultesia lisianthoides* (Griseb.) Benth. & Hook. ex Hemsley or *Centaurium strictum* (Schiede) Druce. The broad lower leaves are absent in *Coulter 941* and *Smith M81*. The inflorescence is narrowest and shortest in *Carlson 3148*, but more open and divaricate with few branches in the other specimens. All specimens share the distinctive characters of the broad stem-wings, sharply keeled calyx-lobes, and large flowers. They also display a bluish color in the vegetative organs similar to that found in *C. chironioides* and *C. pauciflorum* (Mart. & Galeotti) B. L. Robinson, two other Mexican species probably closely related to *C. pterocaulis*.

The occurrence of these few specimens over so wide a geographic range within central Mexico suggests a species which at an earlier time has been more abundant. Undoubtedly the widespread destruction of forests in this most populated area of Mexico has drastically reduced the populations of this species. My several searches from 1969 to 1975 were unsuccessful.

***Centaurium wigginsii*** Broome, sp. nov. Herba annua caule simplici foliis caulinis obovatis oblongis decussatis, ramis divaricatis superne, floribus parvis pentameris roseis. *Centaurio stricto* ubique affinis, sed inflorescentia apertiore bracteis foliaceis, pedicellis longioribus, corollis majoribus roseis profundioribus, capsulis majoribus differt. Fig. 2.

TYPE: Mexico, Sinaloa, Highway 40 (Mazatlán-Durango highway), 34.3 mi E of Concordia, growing with *Centaurium nudicaule* and *C. quitense* on wet roadbank with oak and pine above, 1770 m, 17 Feb 1971, C. R. Broome 763 (Holotype: DUKE; isotypes: K, MEXU, NY, UC, US).

Plants annual with erect, simple stems (8.5–) 12–25 (–43) cm tall, branched from above middle or sometimes from base. Leaves cauline, markedly decussate, green, not in a definite basal rosette but clustered at lower nodes and longer than the contracted internodes, becoming more remote upward and shorter than the elongated upper internodes; leaf-blades obovate or oblong, the lower (5–) 12–22 mm long, (2–) 5–8 mm wide, the margins upturned and becoming narrower, (ob–) lanceolate above with flattened margins. Inflorescence open, branches rather divaricate, these branched again only once or twice, monochasially or dichasially; pedicels 0.5–1.0 (–1.9) mm long. Flowers pentamerous, (1–) 5–30 per plant. Calyx 3–5.3 mm long, the lobes lance-acuminate with well-developed hyaline margins, 2.5–5 mm long, about equally the corolla-tube. Corolla salverform, rose-pink with white eye, (6–) 8–10 mm long; corolla-tube (3–) 5–7 mm long, not constricted above ovary; corolla-lobes 3.4–4 mm long, 1.7–2.3 mm broad with rounded and slightly erose tips. Stamens 2.5–3.6 mm long, inserted just below summit of ovary and equalling or exceeding the style; anthers oblong to sagittate, 1.2–1.8 mm long before dehiscence; pollen grains 20.9–29.4  $\mu\text{m}$  in diameter. Ovary 4.2–5 mm long, bearing 2–3 rows of ovules on each carpel margin; style exerted from corolla-tube, 1.6–3 mm long, the stigma bilobed with the lobes flabellate. Capsule fusiform, 6.5–9 mm long, 1.8–3 mm broad; seeds ca 0.3 mm long, reddish-brown, ca 250 per capsule. Chromosome number:  $n = 22$ .

Known only from the Sierra Madre Occidental west of the summit of the high ridge of El Espinazo del Diablo along Mexico Highway 40, at ca 1600–2200 m, in Sinaloa and Durango, and one station in northern Nayarit. Moist, partly shaded steep clay banks of the oak-pine zone. Flowering specimens have been collected in February, March, and April.

Additional Collections: MEXICO. DURANGO: ca 2 mi SW of Revolcaderos enroute to Mazatlán on Hwy 40 on foot trail descending to rocky stream with oak-pine woods above, ca 2200 m, 26 Mar 1975, *Almeda 2529* (DUKE); along the Mazatlán-Durango highway 3–15 km toward El Salto from the Sinaloa boundary at El Palmito, 1950–2200 m, 13 Apr 1965, *McVaugh 23591* (MICH). SINALOA: Hwy 40 ca 4.7 mi N of El Carrizo in oak-pine forest zone at 1950 m, 26 Mar 1975, *Almeda 2526* (DUKE); dry hillside among pines and oak 49 mi E of Villa Union, 1630 m, 18 Mar 1955, *Wiggins 13179* (DS). NAYARIT: vicinity of Acaponeta, 9 Apr 1910, *Rose, Standley & Russell 14273* (F, GH, NY).

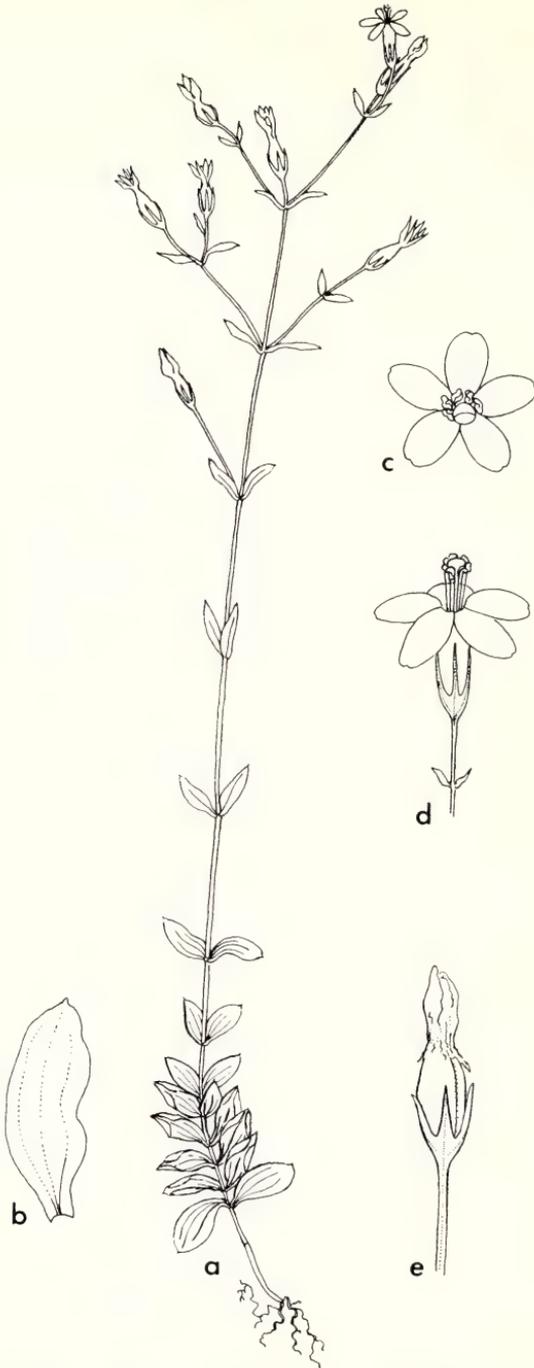


FIG. 2. *Centaurium wigginsii*. a. habit (x0.9), b. a lower leaf (x1.3), c. flower in top view (x2.5), d. flower in side view (x2.5), e. capsule with marcescent corolla (x2.5)—based on *Broome 763*.

The species is named for Professor Ira L. Wiggins, distinguished student of the Mexican flora, who made one of the earliest collections.

*Centaurium wigginsii* is related to *C. strictum*, a Mexican endemic found no farther north than Jalisco, in the Nueva Galicia region. The two species are quite similar in leaf morphology and habit, but differ significantly in the following characters:

	<i>C. wigginsii</i>	<i>C. strictum</i>
Branching angle	divaricate	strict
Inflorescence branches	with few inconspicuous bracts	conspicuously leafy
Pedice! of terminal flower	3.5-19 mm	1-6 mm
Corolla color	bright rose-pink	whitish to bluish or pale-pink
Corolla length	(6-) 8-10 mm	5-7.7 mm
Chromosome number	$n = 22$	$n = 21$

Experimental hybridization of several American species of *Centaurium* with *C. wigginsii* has confirmed that *C. strictum* is genetically similar as well (Broome, 1973). The  $F_1$  hybrids in crosses between the two had up to 70% pollen stainability and produced vigorous  $F_2$ 's. Significant (defined as greater than 1% pollen stainability in the  $F_1$  hybrid) affinities exist between *C. wigginsii* and only two other Mexican species as indicated by pollen stainability of the  $F_1$ 's: *C. quitense* (18-38%) and *C. nudicaule* (0.5-2.5%). It is my belief that *C. wigginsii* was derived directly from *C. strictum* by aneuploid increase, in the northernmost part of the range, followed by geographical isolation of the two species. *Centaurium wigginsii* is now sympatric with *C. nudicaule* in the same habitat, and is geographically but apparently not populationally sympatric with *C. setaceum* (Benth.) B. L. Robinson.

***Centaurium capense*** Broome, sp. nov. Herba annua caule simplici, ramosissimo e basi, foliis caulinis anguste ovatis, floribus numerosis parvis roseis, lobis corollae tubo brevioribus, stigmatibus bilobis. *Centaurio floribundo*, *C. tenuifloro*, *C. pulchello* floribus similis, a his speciebus pedicellis longis, rosulis basalibus nullis, et ramificatione divaricata saepe trichotoma differt. Fig. 3.

TYPE: Mexico, Baja California Sur, along stream below Santiago, between Santiago and Rivera, Cape Region, 6 May 1931, *Wiggins 5665* (Holotype: US; isotypes: DS, F, GH, MICH, UC).

Plants annual with erect, simple stems 7.5-47 cm tall, branched at most nodes. Basal rosette of leaves lacking, but the lower internodes often contracted and the lower leaves clustered, the upper 3-6 cauline internodes to 63 mm long and often much longer than the subtending leaves. Leaf-blades thin, (ob-) lance-ovate to lanceolate, 12-32 mm long, 1.5-12 mm wide, the largest ones borne at the middle nodes of the stem, much reduced on lateral branches, the larger leaves with 5 main nerves. Inflo-

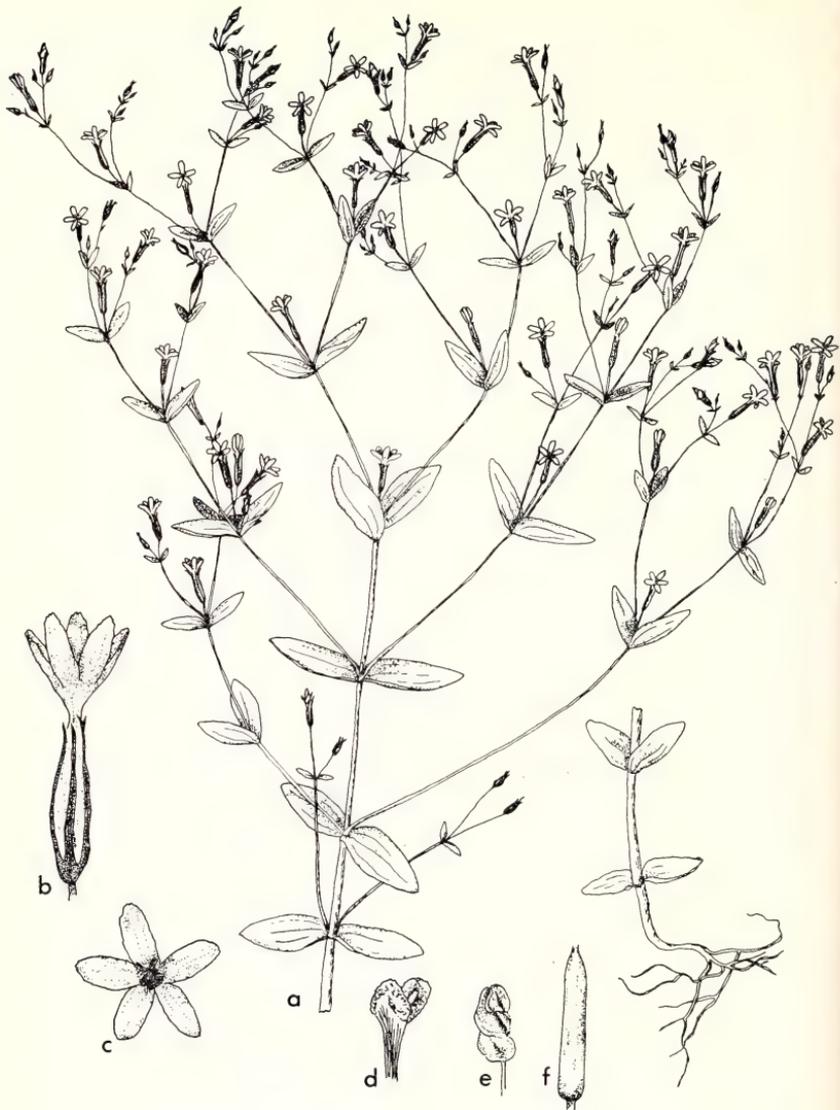


FIG. 3. *Centaureum capense*. a. habit (x0.5), b. flower in side view (x2), c. flower in top view (x2), d. style and stigma (x14.5), e. anther after dehiscence (x10.5), f. mature capsule, marcescent corolla removed (x2)—based on Wiggins 5608.

rescence a broad, divaricately branched compound cyme with the main branches arising from all but the lowermost one or two cauline nodes and diverging from the main axis at angles of 40–60°, these branched again 3–4 times, the branching mainly monochasial but with a high frequency of dichasial (trichotomous) branching at all levels; pedicels of central flowers in dichasia 5–20 mm long, usually shorter than the flowers but slightly longer on lateral flowers. Flowers pentamerous, 50 to several

hundred per plant. Calyx 5.5–10 mm long, the lobes 5–10 mm long, filiform, shorter than the corolla-tube, with inconspicuous hyaline margins. Corolla light to deep pink with small white eye, (9-) 10–16 mm long; corolla-tube (6-) 7–12.5 mm long, exceeding ovary by ca 2 mm and slightly constricted above it; corolla-lobes 3–4.7 mm long, 1–2 mm wide, lanceolate with blunt and minutely erose tips. Stamens inserted just above summit of ovary, exceeding style; anthers oblong, 0.7–1.5 mm long after anthesis, frequently bent over on filaments and shedding pollen directly onto stigma beneath; pollen grains 21.8–28.5  $\mu\text{m}$  in diameter. Ovary 5.2–8.5 mm long, ca 1 mm wide, bearing 2–3 rows of ovules on each carpel margin; style included or slightly exerted from corolla-tube, deeply divided with stigma-lobes ovoid, longer than broad. Capsule narrowly cylindrical, 9–11 (–12.5) mm long, 1.5–2 mm broad; seeds 0.15–0.2 mm long, deep reddish-brown.

Known from Baja California Sur only in the Cape Region in the Lagunan Woodland biome (Axelrod, 1958) of the mountains just southeast of La Paz and southward. In moist, sandy soil along streams and in washes. Flowering specimens have been collected from March through early May.

Additional Specimens: MEXICO. BAJA CALIFORNIA SUR: 22 mi S of La Paz, 8 May 1931, *Wiggins 5608* (DS); La Huerta, 19 May 1889, *Brandege s.n.* (UC); ca 6 mi SW from Santiago, Arroyo San Mateo, 30 Apr 1959, *Thomas 7722* (DS); along stream below Santiago between Rivera and Santiago, 6 May 1931, *Wiggins 5660B* (DS); Santiago, 31 Mar 1936, *Bailey 176* (F); El Reparito, S fork of Cañon San Pedro, ca 770 m, 23°20'N, 109°55'W, 8 May 1959, *Moran 7361* (DS); Arroyo Culebrado near junction of trails to Rancho la Frágua and Rancho Sauce (SE of Cerro Giganta), ca 400 m, 26°3.5'N, 111°28.5'W, 31 Mar 1960, *Carter & Ferris 4065* (UC); Arroyo del Salto, E of La Paz, in moist granitic sand under palms, 24°12'N, 110°7.5'W, 30 Mar 1949, *Carter 2576* (UC); San José del Cabo, 2 Apr 1892, *Brandege s.n.* (UC); San Lazaro Canyon, ca 100 m, 23°08'N, 109°48'W, 2 May 1959 *Moran 7329* (DS); Potrero de Almenta, Arroyo de Almenta, E slope of Sierra de la Victoria inland from Caduano, 1036 m, 9–11 May 1959, *Thomas 7825* (DS, GH, US).

This interesting species has been distributed as *Centaurium exaltatum* (Griseb) W. F. Wight or as *C. nudicaule*, two other small-flowered species which also occur on the Baja California peninsula. On closer inspection, the new species was found to differ from those taxa in several characters:

	<i>C. exaltatum</i>	<i>C. capense</i>	<i>C. nudicaule</i>
Stigma lobe shape	flabelliform or reniform	ovoid	flabelliform
Style division	shallow	deep	shallow
Corolla length	10–19 mm	10–16 mm	6.5–10 mm
Capsule length	10–15 mm	9–12.5 mm	6–9.5 mm
Capsule width	1.8–3.5 mm	1.5–2 mm	1.2–3 mm
Cauline leaf shape	lanceolate	lance-ovate to lanceolate	linear or subulate

Type of cyme	narrow, rather strict	broad divaricate	narrow, branches ascending
Central pedicel	longer than flower	shorter than flower	longer than flower

The origins of this species are obscure. My initial hypothesis that this endemic was derived from migrant populations of *Centaurium exaltatum* has been rejected on morphological grounds. The style is unusual as it is distinctly branched beneath the papillose surface of the stigma lobes. The lobes are devoid of papillae in the central portion of the inside surface. These are features found, to my knowledge, only in those species allied to *C. minus* Moench, including the California taxon, *C. floribundum* (Benth.) B. L. Robinson. Besides *C. floribundum* and *C. capense*, no other American species have been found to have this stylar morphology. The very narrowly cylindrical ovary and capsule of both species also ally them to *C. minus*. *Centaurium capense*, like *C. floribundum*, in all probability has its closest relatives in Europe or Asia.

#### ACKNOWLEDGMENTS

This paper is based on a portion of a dissertation submitted to the faculty of Duke University in partial fulfillment of the doctoral degree. I wish to acknowledge the support of National Science Foundation Systematics Training grants GB-6393 and GB-23200 during this research. The illustrations were prepared by Karen Teramura (Fig. 1), Susan Carlton Smith (Fig. 2), and Lyn Loveless (Fig. 3). My thanks to the curators of the following herbaria for allowing me to study their material: DS, DUKE, F, GH, K, MEXU, MICH, NY, TEX, UC, US.

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BARBARA D. WEBSTER, *Editor*

September 1, 1977

**PSILOACEAE SYMPOSIUM REPRINTS AVAILABLE.**—The recent symposium entitled "Taxonomic and Morphological Relationships of the Psilotaceae," which was presented during the 1976 AIBS meetings at Tulane University, will be published in the January-March 1977 issue of *BRITTONIA*. This symposium, under the chairmanship of Richard A. White (Duke University) and sponsored by the American Fern Society, the American Society of Plant Taxonomists, and the Pteridological, Paleobotanical, Structural and Systematic Sections of the Botanical Society of America, summarizes the major points of the current controversy surrounding this enigmatic plant group.

Contributors are: David W. Bierhorst (University of Massachusetts), The systematic position of *Psilotum* and *Tmesipteris*; Patricia G. Gensel (University of North Carolina), Morphologic and taxonomic relationships of the Psilotaceae relative to evolutionary lines in early land vascular plants; Donald R. Kaplan (University of California—Berkeley), Morphopological status of the shoot systems of Psilotaceae; and Warren H. Wagner, Jr. (University of Michigan), Systematic implications of the Psilotaceae. The set of papers, together with introduction and discussion, will be printed as a unit and become available in April as a separate through the New York Botanical Garden. Copies can be obtained by sending your order, along with \$3.00 per copy (\$2.50 each in quantities of 30 or more), to: *BRITTONIA*, New York Botanical Garden, Bronx, NY 10458. No orders will be filled unless accompanied by payment.





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David Leech, 1972

Volume 25 of *Madroño* is dedicated to Professor G. Ledyard Stebbins, Jr., in recognition of the exceptional scope and importance of his contributions to evolutionary botany that have extended from his dissertation work with *Antennaria* through the revolutionary 1938 study of *Crepis* with E. B. Babcock and to the present time; in recognition of his extensive contributions to the taxonomy, reproductive biology, ecology, and floristics of California plants; and in recognition of his service to the California Botanical Society, particularly as its President in 1964.

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SYSTEMATICS AND REPRODUCTIVE BIOLOGY OF  
LOMATIUM FARINOSUM (GEYER EX HOOKER)  
COULTER & ROSE (UMBELLIFERAE)

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The large western North American genus *Lomatium* is replete with systematic problems. Because many of the approximately seventy species currently recognized are poorly represented in herbaria, their taxonomic limits are vague. Almost nothing is known about reproductive biology in the genus.

*Lomatium farinosum* is a member of the diminutive, "tuberous" group of species designated by Marcus E. Jones (1908) as section *Cous*. It is native to the sagebrush-bunchgrass steppe of the Columbia River Basin and flowers from late March to early May. The species consists of two geographically significant varieties which are morphologically distinguishable only by differences in floral color (Schlessman, 1976). Variety *farinosum*, which occurs throughout most of the range of the species, has white petals and reddish-purple anthers and stylopodia. Variety *hambleniae*, found only in the extreme western portion of the range, has yellow petals, anthers and stylopodia (Fig. 1). Previous investigators have noted the morphological similarity of the two taxa but have maintained them as separate species, presumably on the basis of their apparent geographical isolation (Mathias & Constance, 1942, 1945; Hitchcock, Cronquist, Ownbey & Thompson, 1961).

MATERIALS AND METHODS

Field studies in 1976 and 1977 included collection of living and dried specimens, cytological materials and floral visitors, as well as observations of floral phenology and behavior of pollinators. Chromosome counts were obtained using standard acetocarmine squash techniques. Pollen viability was estimated by determining the stainability of pollen from dried specimens in a solution of aniline blue and lactophenol. My collections, which include vouchers for chromosome number and pollen viability determinations, are kept at WTU. Specimens from the following herbaria were also utilized: ID, K, NY, OSC, ORE, Reed College, UC, Walla Walla College, WS and WTU.

Experimental tests of the breeding system and artificial hybridizations were carried out in an insect-free cage in the greenhouse. To test for apomixis, flowers were emasculated in bud and plants left undisturbed until the development of fruit could be determined. Seed set due to selfing in the absence of floral visitors was determined by placing three

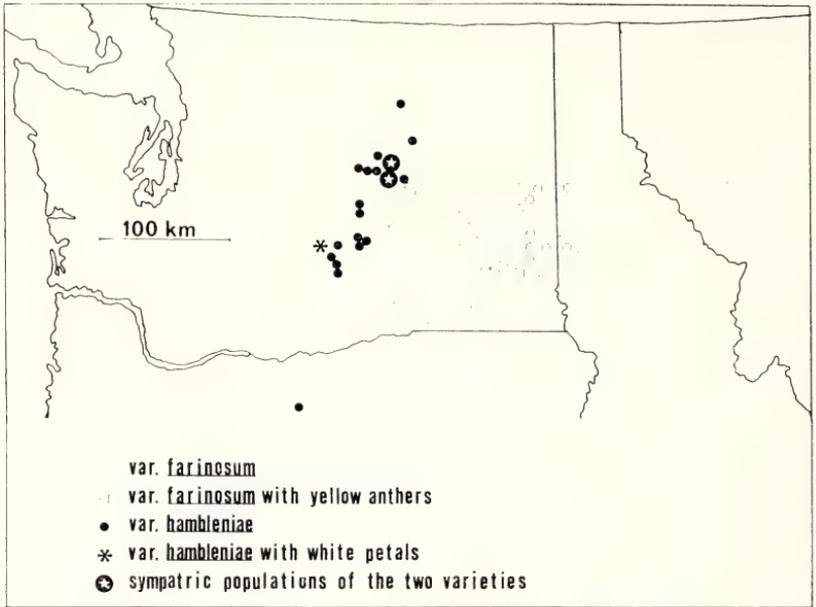


FIG. 1. Distribution of *Lomatium farinosum*.

individuals of var. *farinosum* and three of var. *hambleniae* in the cage while the flowers were in bud and leaving them undisturbed for the course of the experiment. For hybridization studies, flowers of the pistillate parent were emasculated in bud and the remaining flowers removed from the inflorescence. Pollen was transferred once or twice a day for two to four consecutive days.

#### RESULTS

The distributions of the two varieties of *Lomatium farinosum* overlap in Douglas, Grant, Kittitas and Yakima counties, Washington. Data from herbarium labels indicated that sympatric populations of the two varieties would be found at Grand Coulee, Steamboat Rock, Dry Falls and Sun Lakes in Grant County, Washington. Searches revealed such populations only at Steamboat Rock and Sun Lakes (Fig. 1).

Although floral color provides the only clear distinction between the two varieties (Table 1), variation is found in both. Individuals with yellow, rather than purple, anthers have been collected in three populations of var. *farinosum*; and plants with white, rather than yellow, petals occur in one population of var. *hambleniae*. Several intermediate forms are present at both sites where populations of the two varieties are known to be sympatric (Fig. 1). These intermediates may have the following combinations of characters: yellow petals, purple anthers and

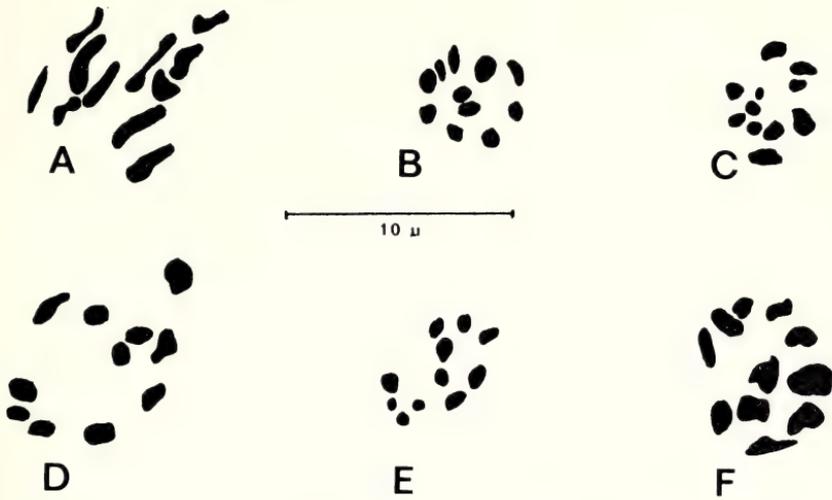


FIG. 2. Camera lucida drawings of the chromosomes of *Lomatium farinosum*.  $n = 11$ . A-D, var. *farinosum*, Schlessman 54, 56, 58, 60; E-F, var. *hambleniae*, Schlessman 73, 94. All figures represent prophase I except A, which is metaphase II.

purple stylopodia; or white petals, purple anthers and yellow stylopodia; or white petals, yellow anthers and yellow stylopodia.

Chromosome counts were obtained from four populations of var. *farinosum* and from two of var. *hambleniae*. All counts are  $n = 11$  (Fig. 2). No significant differences among the pollen viabilities of the two varieties and the intermediates were found (Table 2).

*Lomatium farinosum* is andromonoecious, each plant bearing both functionally staminate and hermaphroditic flowers. The staminate flowers have well-developed stylopodia but lack styles. They do not produce functional ovaries or set seed (Hardin, 1929; Schlessman, 1976). The hermaphroditic flowers are strongly protogynous, the styles withering before pollen is shed. Each plant produces one to several compound umbels, which are borne singly on scapose peduncles (see illustration in vol. 3, p. 553, Hitchcock, Cronquist, Ownbey & Thompson, 1961). The period of anthesis of each umbel overlaps with that of the preceding one.

The ratio of staminate to hermaphroditic flowers in an umbel varies according to the sequence in which the umbels are produced. The first umbel is composed completely or predominantly of staminate flowers. In each sequential umbel the proportion of staminate flowers decreases so that the flowers of the last umbels are predominantly hermaphroditic (Fig. 3). These bisexual flowers tend to be clustered in the outermost umbellets and are usually the outermost flowers within an umbellet. Flowering occurs centripetally in each umbel and umbellet. Within um-

TABLE 1. COMPARISON OF THE VARIETIES OF *LOMATIUM FARINOSUM* AND NATURALLY OCCURRING INTERMEDIATE FORMS. For the first five characters, mean values are followed by standard deviations in parentheses. Data were obtained from over 120 specimens.

Character	var. <i>farinosum</i>	var. <i>hambleniae</i>	Intermediates
1. Height in cm	17 (6)	20 (4)	17.5 (9.5)
2. Ray length in fruit (cm)	3.5 (2)	4 (1)	4 (1)
3. Pedicel length in fruit (mm)	14 (6)	17 (6)	17 (6)
4. Maximum fruit length (mm)	5.5 (1)	6.4 (1)	5.5 (1)
5. Maximum fruit width (mm)	2.5 (0.5)	2.5 (0.5)	2.5 (0)
6. Longest leaf segments	1 cm or more	1 cm or more	1 cm or more
7. Oil tubes on commissure	4-6	4-6	4-7
8. Fruit surface	glabrous	glabrous	glabrous
9. Habit	acaulescent	acaulescent	acaulescent
10. Bractlet shape	linear to lanceolate	linear to lanceolate	linear to lanceolate
11. Petal color	white	yellow	white or yellow
12. Anther color	purple	yellow	purple or yellow
13. Stylopodium color	purple	yellow	purple or yellow

TABLE 2. POLLEN VIABILITY OF *LOMATIUM FARINOSUM*.

	Number of determinations	Mean (%)	Range	Standard deviation
var. <i>farinosum</i>	25	92	58-100	10
var. <i>hambleniae</i>	17	88	59-100	12
intermediates	13	86	51-100	13

bellets the flowers are tightly clustered so that geitonogamous pollination can occur without transfer of pollen by insects.

Floral visitors to *Lomatium farinosum* include leaf-cutting bees (Megachilidae), halictid bees (Halictidae), cuckoo bees (Anthophoridae), sphecid wasps (Sphecidae), mason wasps (Vespinidae), tachinid flies (Tachinidae), bee flies (Bombyliidae) and midges (Chironomidae). Typically, an insect will land on one of the outer umbellets and wander over that

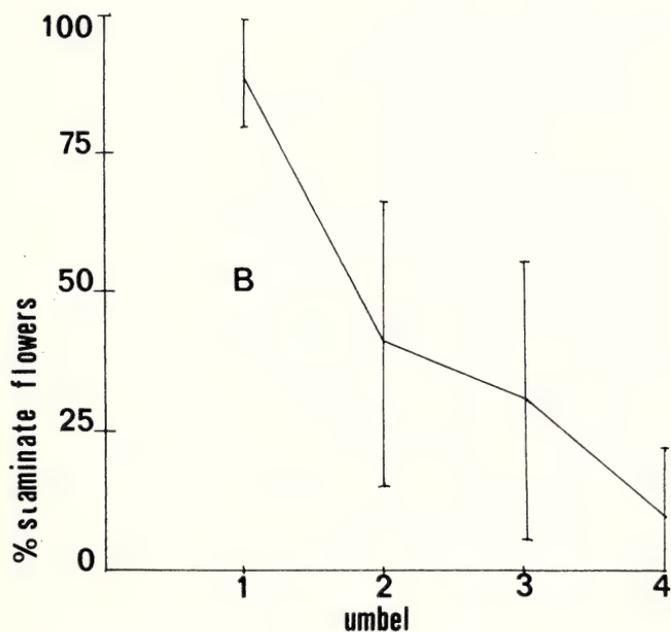
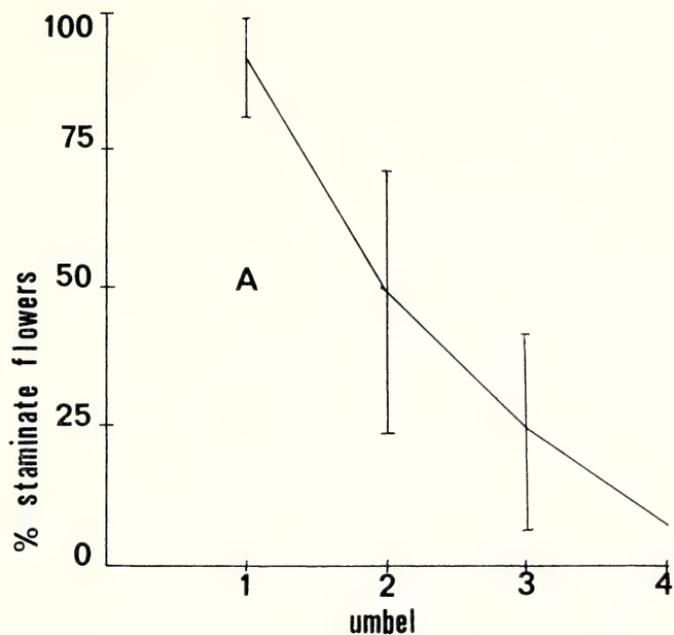


FIG. 3. Percentages of staminate flowers in the umbels of *Lomatium farinosum*. Umbels are numbered in the sequence in which anthesis occurs. Lines connect the mean percentages and vertical bars indicate standard deviations. A, var. *farinosum*, data from 30 specimens; B, var. *hambleniae*, data from 30 specimens.

TABLE 3. RESULTS OF ARTIFICIAL HYBRIDIZATIONS. Collection numbers are my own. The letters after collection numbers indicate colors of the petals, anthers and stylopodia, respectively (e.g., WPY denotes an intermediate form with white petals, purple anthers and yellow stylopodia).

Taxa	♀	Cross	♂	Number of flowers	Flowers producing seed	%
var. <i>farinosum</i> x var. <i>hambleniae</i>		379 x 282		20	18	90
var. <i>hambleniae</i> x var. <i>farinosum</i>		474 x 158		3	2	67
		179 x 174		10	10	100
		474 x 174		10	10	100
		480 x 158		<u>15</u>	<u>15</u>	100
				total 38	total 37	$\bar{x}$ 96
intermediate x var. <i>farinosum</i>	200 (WYY) x 158			11	3	27
	200 (YPP) x 174			10	4	40
	200 (WYY) x 174			<u>10</u>	<u>10</u>	100
				total 31	total 17	$\bar{x}$ 55
intermediate x var. <i>hambleniae</i>	200 (YPP) x 474			10	0	0
	200 (WPY) x 474			<u>8</u>	<u>8</u>	100
				total 18	total 8	$\bar{x}$ 44

umbellet from several seconds to three or four minutes before flying to another umbellet. If any anthers have dehisced, the entire underside of the insect may be exposed to pollen. Floral visitors may spread pollen from flower to flower within inflorescences as well as between inflorescences. No differences between var. *farinosum* and var. *hambleniae* in the kinds of floral visitors or pollinator behavior were observed. In populations consisting of both varieties and intermediate forms, floral visitors did not exhibit constancy for any floral type.

None of the 30 flowers emasculated to test for apomixis (10 for var. *farinosum*, 20 for var. *hambleniae*) set seed. The six plants used to test for selfing in the absence of insects produced a total of 261 flowers, only 10 of which (4%) yielded fruit. Seed production from crosses between the two varieties ranged from 67–100%, and that from crosses between intermediates and typical forms ranged from 27–100% (Table 3.) All flowers which bore fruit produced two morphologically normal seeds.

#### DISCUSSION

It is clear from their almost identical morphologies, chromosomal numbers, sympatry and naturally occurring intermediates that the white-

and yellow-petaled plants examined are conspecific. My crossing studies strongly suggest that the naturally occurring intermediates arose through hybridization between the two typical forms, and that some gene flow still exists between them. In my opinion the significant geographical trend in distribution of the two color forms warrants taxonomic recognition of two varieties. This treatment is consistent with that of other investigators dealing with infraspecific variation in floral color in *Lomatium* (Mathias & Constance, 1945; Hitchcock, Cronquist, Ownbey & Thompson, 1961). Although the data are insufficient to establish a pattern, intervarietal crosses appear to be more successful than those between either variety and the intermediate forms. Cytological abnormalities undetectable by determinations of pollen viability may reduce the fertility of intermediates. The two crosses between intermediates and typical forms that resulted in full seed set may have involved progeny of backcrosses to one of the typical forms.

Dichogamy is a common adaptation for outcrossing in self-compatible plants (Baker, 1960). Although protogyny apparently prevents autogamy in *Lomatium farinosum*, the compact umbellets and the centripetal sequence of anthesis increase the likelihood of geitonogamy with or without the aid of insect vectors. The seed set in my selfing experiments, which were conducted in the absence of any floral visitors, was probably due to geitonogamous selfing. Studies to determine the extent to which insect-mediated geitonogamy may occur in *L. farinosum* and other "tuberous" species of *Lomatium* have been initiated. The position of the hermaphroditic flowers is also an adaptation for outcrossing in *L. farinosum*. Since hermaphroditic flowers are often the first of an umbellet or umbel to reach anthesis, pollinations occurring soon after the flowers open are likely to be xenogamous.

Regular patterns of change in proportions of staminate and hermaphroditic flowers have been reported for many andromonoecious Umbelliferae (Müller, 1883; Hardin, 1929; Bell, 1971; Schlessman, 1976). The widespread occurrence and general constancy of these patterns indicate that they are genetically controlled. Experiments utilizing altered environmental conditions or growth hormones have produced minor variations in the ratio of staminate to hermaphroditic flowers, but no change in overall pattern (Braak & Kho, 1958; Quagliotti, 1967). These patterns may have evolved under selection brought about by dichogamy (Bell, 1971; Schlessman, 1976). In the case of a protogynous species such as *Lomatium farinosum*, little or no pollen would be available to hermaphroditic flowers in the first umbels to reach anthesis and few of these flowers would set seed. Selection for the conservation of reproductive effort would result in elimination of hermaphroditic flowers from the first umbels and a preponderance of them in later-flowering umbels. Cruden (1976) has reported preliminary evidence of ecotypic variation in proportions of staminate and hermaphroditic flowers in *Heracleum lanatum*

Michx. Since my data represent several populations, such variation may contribute to the large standard deviations in percentages of staminate flowers in *L. farinosum*.

Bell (1971) has proposed that uniformity of floral structure in Umbelliferae represents an ancient adaptive peak for utilization of unspecialized pollinators. He has suggested that studies of the comparatively minor changes in breeding systems superposed since this adaptive peak was reached may have wide applications to evolutionary studies within the family. Investigations of reproductive biology have clarified the infraspecific relationships of *Lomatium farinosum*. Comparative studies of floral biology and breeding systems should elucidate phylogenetic relationships among the species of this taxonomically "difficult" genus.

#### TAXONOMY

##### Key to the varieties of *Lomatium farinosum*

Petals white; anthers purple; stylopodia purple . . . . var. *farinosum*  
 Petals, anthers and stylopodia yellow . . . . . var. *hambleniae*

Recognition of var. *hambleniae* as an infraspecific taxon requires the following new combination. The correct citation and synonymy of these taxa are as follows.

*Lomatium farinosum* (Geyer ex Hooker) Coulter & Rose var. *farinosum*,  
 Contr. U.S. Natl. Herb. 7:210. 1900.

Basionym: *Peucedanum farinosum* Geyer ex Hooker, Lond. Jour. Bot. 6:235. 1847. TYPE: USA, Idaho, "On an isolated rock in the Coer [sic] d'Alene Mountains, on wet clay, with *Sedum stenopetalon* [sic] and *Platyspermum*," April, 1844, Geyer 325 (Holotype: K!).—*Cogswellia farinosa* (Geyer ex Hooker) M. E. Jones, Contr. West. Bot. 12:33. 1908.

*Lomatium farinosum* (Geyer ex Hooker) Coulter & Rose var. **hambleniae**  
 (Mathias & Constance) Schlessman, comb. nov.

Basionym: *Lomatium hambleniae* Mathias & Constance, Bull. Torrey Bot. Club 69(3):153. 1952. TYPE: USA, Washington, Grant County, "on a level scabrock bench at Dry Falls, Grand Coulee," 22 April 1941, Frances G. Hamblen s.n. (Holotype: UC! Isotype: WS!).

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## JEFFREY PINE AND VEGETATION OF THE SOUTHERN MODOC NATIONAL FOREST

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Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) ranges the length of California in forested areas and extends into southern Oregon and northern Baja California (Griffin and Critchfield, 1972). It occurs in several forest and woodland communities but also forms a fairly distinctive Jeffrey pine forest type east of the Sierra Nevada-Cascade ranges (Society of American Foresters, 1954). Jeffrey pine forests reach widespread development near the Owens River headwaters and Mono Lake and in eastern Plumas and Lassen counties. Elsewhere, Jeffrey pine occurs as an element of the mixed conifer forest (Griffin and Critchfield, 1972), a vegetation type roughly equivalent to the yellow pine forest of Munz and Keck (1949) and to several forest types recognized by the Society of American Foresters (1954). In some of the latter, Jeffrey pine and ponderosa pine (*Pinus ponderosa* Laws.) mingle freely. Such forests are classed as ponderosa pine forest types without particular analysis, even though Jeffrey pine sometimes predominates.

As an element of mixed conifer forests, Jeffrey pine reaches its northern limit in the Siskiyou Mountains of southern Oregon (Whittaker, 1960; Franklin and Dyrness, 1973). To the south, it has generally been included in forest communities dominated by ponderosa pine (Munz and Keck, 1949; Griffin and Critchfield, 1972; Horton, 1960; Minnich, 1976; Thorne, 1976). However, Jeffrey pine increases in importance toward higher elevations and toward the interior (Haller, 1962; Griffin and Critchfield, 1972), and forested areas dominated by Jeffrey pine to the virtual exclusion of ponderosa pine have been noted in the Sierra Nevada of Kern County (Twisselman, 1967) and Fresno County (Klyver, 1931), on Mt. Pinos (Vogl and Miller, 1968), in the San Gabriel Mountains (Thorne, pers. comm.), and in the San Bernardino Mountains (Vasek, 1966). Furthermore, *P. jeffreyi* dominates forests in the peninsular ranges (Santa Rosa Mountains, Laguna Mountains) of southern California. Whereas, *P. ponderosa* reaches a southern limit near Cuyamaca Lake in San Diego County, California (Haller, 1959), *P. jeffreyi* continues south to the Sierra Juarez and the Sierra San Pedro Martir of Baja California where it is a dominant in forested areas (Haller, pers. comm.).

Several questions arise concerning the community definition, composition, and ecology and the phytogeographic history of Jeffrey pine forests in the south relative to those in the north and of such forests relative to mixed conifer forests. Accordingly, a long-range program of vegetation sampling was initiated in the northern Jeffrey pine forests to provide a data base from which north-south comparisons and interpretations might be made. That project is a long way from fruition. However, shortly after sampling several plots in the Modoc National Forest, several vegetation-soil maps (U.S. Forest Service, 1953a) for the sampled area came to my attention. These maps are part of a series prepared by the State Cooperative Soil-vegetation Survey (U.S.D.A. Forest Service, 1958). Most of the available vegetation-soil map coverage applies to the coast range forests and coverage is sparse for the region east of the Sierra Nevada-Cascade ranges. Consequently, the coincidence in sampling areas is fortuitous.

My few ground samples could be correlated with broad scale coverage of more than 200 sections (520 km<sup>2</sup>) and an opportunity was presented to address several general questions regarding species composition and species associations, and the environmental and distributional relations of northern Jeffrey pine forests. Consideration of these parameters may lead to a better understanding of the northern Jeffrey pine forests and provide a focal reference for investigation of those to the south.

This paper characterizes a Jeffrey pine forest near the northern limit of that forest type and draws relationships to comparable forests farther south.

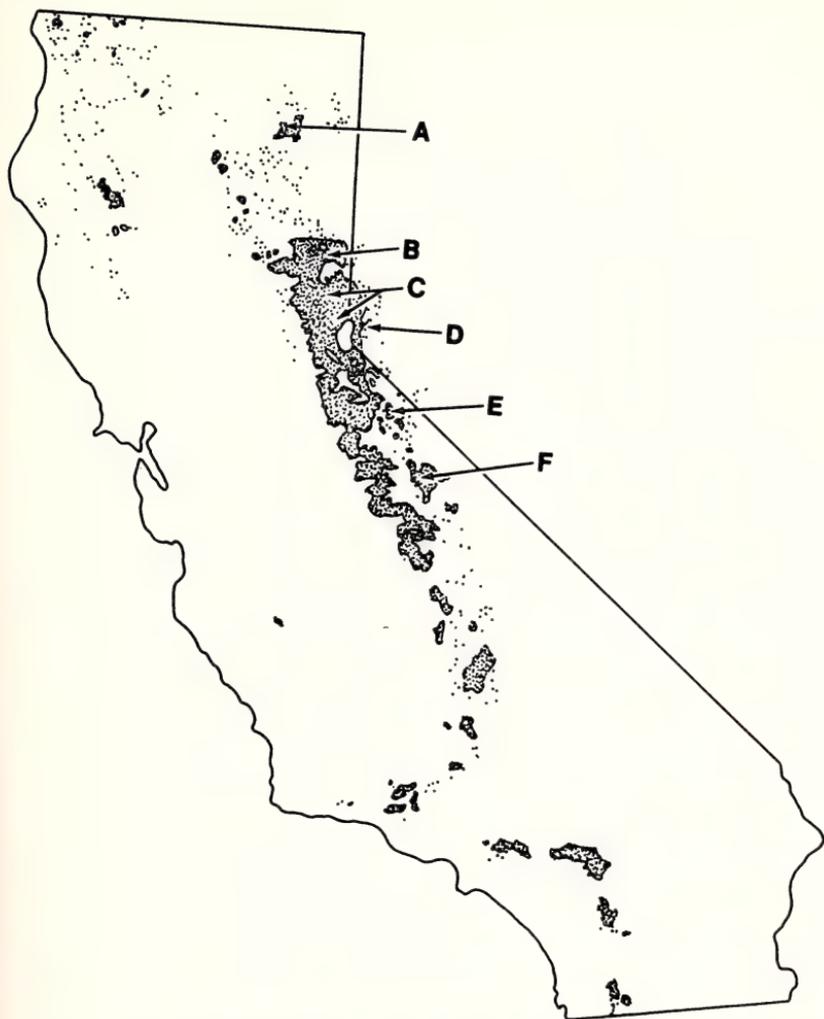


FIG. 1. Map showing the distribution of *Pinus jeffreyi* and the locations of sampling areas in California: A, southern Modoc National Forest; B, Plumas N.F.; C, Tahoe N.F.; D, Toiyabe N.F. (Nevada); E, Devils Gate Pass; F, Deadman Summit. Adapted from Griffin and Critchfield, 1972.

#### METHODS

This study employed two approaches: a simulated aerial point sampling based on vegetation-soil maps and direct ground sampling.

Vegetation-soil maps were compiled by the U.S. Forest Service (1953a) from aerial photographs plus direct ground observations and supplemental soil samples. Vegetation-soil maps resemble a jig-saw puzzle in which units of irregular shape and variable size are each coded for characteristics of the constituent vegetation and soil types (Colwell, 1974). Each cover element comprising more than 20% of the total cover, and

the included species, each comprising at least 20% of the cover in that element, is listed in order of decreasing cover value (U.S. Forest Service, 1953b). Soil series, depth, texture and exposure are coded for each unit. Thus a large body of semi-quantitative descriptive information is available for a significant segment of forest.

Vegetation-soil map coverage for the Modoc National Forest and for all northeast California includes only that portion of the Big Valley District, Modoc National Forest (Fig. 1), located in Lassen County, south of the Modoc County town of Adin. The National Forest Boundary is irregular and encloses a mapped area of 208 full sections and parts of 27 other sections. Vegetation of this forest segment was sampled as follows:

- 1) A series of 10 transects was made from west to east across alternate tiers of sections. The first transect started southeast of Adin, and south of the county line, with section 36, R9E T39N, and included 10 consecutive sections. The last transect, 29 km to the south, started with sections 31 to 34, R8E T36N, skipped 11 private, unmapped sections, and ended at sections 34 and 35, R10E T36N, for an interrupted transect of 6 sections.

- 2) Each transect consisted of 2 tracks parallel to the north section line and located respectively  $\frac{1}{4}$  and  $\frac{3}{4}$  of the way to the south section line.

- 3) Five sample points were equally spaced along each track, starting at the west edge of each section, providing 10 sample points per section.

- 4) The vegetation-soil unit at each sample point was recorded.

- 5) The accumulated data for 105 full sections (1050 sample points) were tabulated to yield frequency data for each major species and several non-specific cover elements (e.g. bare ground).

Direct ground samples were taken from the Modoc, Plumas, Tahoe and Toiyabe National Forests (Fig. 1) during Sept. and Oct. 1974. Sampling areas potentially dominated by Jeffrey pine were selected using a published range map (Griffin and Critchfield, 1972) before going into the field. In each area sample points were located at 100-pace intervals (about 160 m) along a line-of-sight transect established on a diagonal to the general slope. Sample points were used to center temporary circular sample plots of 100 m<sup>2</sup>. In each plot dbh was recorded by species for each tree taller than 2 m; height was recorded by species for each tree shorter than 2 m; and 2 diameters were recorded by species for each shrub. Basal area for trees and crown cover for shrubs were calculated from half-diameters by assuming circular shapes. For non-circular shrubs, the longest diameter (a) and a perpendicular short diameter (b) were measured and the crown cover area calculated from  $A = \pi (a/2 \cdot b/2)$ . For prostrate or sprawling shrubs such as *Ceanothus prostratus* and *Symphoricarpos acutus*, density was arbitrarily assumed to be one plant per plot and ground cover was estimated visually for each plot.

Crown cover for Jeffrey pine was estimated from basal area. The crown cover/basal area for 10 trees on which both parameters were measured

ranged from 30 to 165; 100 was selected as representative. The same conversion factor was applied to other tree species but possible error was not estimated.

Five to 8 plots were scored in each sampling area. Data include density, cover, and frequency for each species. Relative density, relative cover, and relative frequency for each species were calculated and summed to obtain an Importance Value (Mueller-Dombois and Ellenberg 1974), a convenient statistic for comparing forest stands in different areas. In addition, exploratory data, gathered during preliminary method evaluations in 1972, were included to characterize forests in Mono County (Fig. 1).

Individual pine trees sometimes posed problems in identification by manifesting several traits from two species. These were listed as hybrid derivatives under the species most closely resembled.

In the Modoc Forest, *P. ponderosa* includes 7 putative hybrid derivatives, and *P. jeffreyi* includes 6 putative hybrid derivatives. In the Plumas Forest, 6 hybrid derivatives are included in *P. ponderosa* and 2 in *P. jeffreyi*. In the Tahoe region, all trees observed were typical Jeffrey pine. However, *Pinus washoensis* occurs nearby (Haller, 1961), and it is possible that some Washoe pine data is included under Jeffrey pine in that area.

Identity of the juniper subspecies posed another problem. The southern Modoc Forest is at the transition between the usually dioecious, forest-dwelling *Juniperus occidentalis* ssp. *australis* and the slightly smaller, commonly monocious, woodland forming *J. occidentalis* ssp. *occidentalis* (Vasek 1966, Vasek and Thorne 1977). This paper deals primarily with *J. o. australis* but some influence of *J. o. occidentalis* in the open woodland areas cannot be ruled out.

#### RESULTS AND DISCUSSION

*Vegetation structure based on vegetation map data.* Vegetation of the southern Modoc National Forest consists of a mixture of tree, shrub, and herbaceous species arranged on and around a series of small volcanic mountains. Topographic relief of the region ranges from elevations of about 1280 m at Adin to about 1950 m at the top of Hayden Hill. The 3 vegetational phases (forest, woodland and scrub) are identified on the basis of whether trees or shrubby elements dominate, or whether only shrubby species occur. The 3 phases are arbitrarily defined for descriptive convenience since forests grade into woodlands and woodlands into scrub.

Forests occupy about 39% of the area (Table 1) based on frequency of sample points in forest areas. Woodland occupies about 43%, and scrub or brush vegetation about 17%. In general, then, the mapped vegetation within the National Forest boundary is relatively open, more than 60% having no or rather sparse tree cover.

TABLE 1. FREQUENCY OF SPECIES AND COVER ELEMENTS IN THREE SUB-GROUPS BASED ON VEGETATION STRUCTURE. I, shrubs only; II, shrubs dominant; III, trees dominant. % = percent occurrence in total sample; N = number of sample points.

For *Abies concolor*, the symbol W is used for convenience, rather than  $\hat{W}$ .

Species or element	Symbol	Observed Frequency				
		I	II	III	Total	%
<b>Trees</b>						
<i>Abies concolor</i>	W	—	8	82	90	8.6
<i>Calocedrus decurrens</i>	I	—	11	78	89	8.5
<i>Pinus ponderosa</i>	Y	—	140	325	465	44.3
<i>Pinus jeffreyi</i>	J	—	269	342	611	58.2
<i>Quercus kelloggii</i>	B	—	17	10	27	2.6
<i>Juniperus occidentalis</i>	Jo	—	292	71	363	34.6
<b>Woody shrubs</b>						
<i>Ceanothus velutinus</i>	Cv	5	3	5	13	1.2
<i>Ceanothus prostratus</i>	Cpo	1	43	72	116	11.0
<i>Arctostaphylos patula</i>	Ap	50	105	43	198	18.9
<i>Cercocarpus ledifolius</i>	Cl	62	215	115	392	37.3
<i>Amelanchier pallida</i>	Aa	26	9	1	36	3.4
<i>Prunus emarginata</i> , <i>P. demissa</i>	Pe,Pd	3	1	—	4	0.4
<i>Symphoricarpos</i> <i>vaccinoides</i>	Sar	—	3	2	5	0.5
<b>Brush</b>						
<i>Artemisia tridentata</i>	Atr	82	254	61	397	37.8
<i>Purshia tridentata</i>	Pt	59	183	51	293	27.9
<i>Chrysothamnus</i> <i>nauseosus</i>	Chn	15	57	13	85	8.1
<i>Chrysothamnus</i> <i>viscidiflorus</i>	Chv	8	12	—	20	1.9
<i>Artemisia arbuscula</i>	Aar	49	82	11	142	13.5
<i>Artemisia cana</i>	Arc	3	—	—	3	0.3
<b>Herbs and other</b>						
<i>Wyethia mollis</i>	Wm	4	32	51	87	8.3
Grasses and herbs	Gr	130	303	164	597	56.9
Bare ground	Ba	115	222	232	569	54.2
	N	183	454	413	1050/4602	
	%	17.4	43.2	39.3		

Areas of dense forest grade into less dense forest patches, some with a shrubby understory or intermittent open or shrubby areas. Open forests grade into woodlands. Vegetation structure appears to be influenced by, or correlated with, soil characteristics. Forests preferentially occur on north slopes with deep soil and low surface rock cover (Table 2). Woodland tends to occur on south slopes with greater surface rock cover and soil of intermediate depth. Scrub vegetation occupies shallow soils (Table 2).

TABLE 2. FREQUENCY OF SEVERAL SOIL CHARACTERISTICS IN THREE VEGETATION STRUCTURAL SUBGROUPS (as in Table 1). N = number of sample points; NC = number of sample points with unclassified soil. Surface rock categories R0, R4, R3, R2 and R1 respectively indicate 0-5, 5-20, 20-50, 50-80 and 80-100% imbedded large rocks or bed rock; average surface rock cover is calculated from class mid-point values. Soil depth is indicated in feet, the letter s indicating stones equal to about 1 ft of soil; soil series with arbitrary numbers.

	I	II	III	Total	%
N	183	454	413	1050	
NC	18	4	1	23	
Aspect					
North	67	130	256	453	44.1
South	98	320	156	574	55.9
Surface rock (Ave. = 14.9% surface rock cover)					
R0 (0-5%)	64	129	249	442	43.0
R4 (5-20%)	48	176	109	333	32.4
R3 (20-50%)	45	114	42	201	19.6
R2 (50-80%)	8	31	10	49	4.8
R1 (80-100%)	—	—	2	2	0.2
Soil depth (average = 2.43)					
5	—	—	17	17	1.7
5s	—	—	31	31	3.0
4	7	22	26	55	5.4
4s	10	25	188	223	21.7
3	8	20	10	38	3.7
3s	7	148	93	248	24.1
2	11	19	1	31	3.0
2s	86	154	35	275	26.8
1	2	4	—	6	0.6
1s	34	58	11	103	10.0
Soil series					
714	28	129	107	264	25.7
720	45	147	197	389	37.9
722	11	54	80	145	14.1
761	3	10	—	13	1.3
763	6	5	—	11	1.1
765	28	44	9	81	7.9
776	39	38	10	87	8.5
777	1	16	1	18	1.8
Misc.	4	7	8	19	1.9

The several soil series are arbitrarily numbered (Colwell, 1974) and several of the major soils and their frequency distribution are listed in Table 2. Soil 720, a loam with good permeability, good drainage and slight acidity is most frequent. Other soils differ as follows: loam 722 is neutral with excessive drainage; gravelly-sandy loam 714 drains excessively as does loam 765; stony loam 766 and stony-sandy loam 777 drain poorly and have slow permeability; sandy loam 763 has imperfect drainage; and clay loam 761 is alkaline with slow permeability.

TABLE 3. AVERAGE FREQUENCY OF SOUTH-FACING ASPECT, SURFACE ROCK COVER, AND DEPTH OF SOILS ON WHICH THE INDICATED SPECIES OR COVER ELEMENTS OCCUR. Notations as in Tables 1 and 2.

	South aspect	Surface rock	Soil depth
	Av. %	Av. %	Av. ft.
Trees			
W	22.2	4.7	3.6
I	24.7	8.9	3.2
Y	38.4	7.6	2.9
J	47.7	9.7	2.9
B	40.7	14.1	2.1
Jo	77.7	25.9	1.7
Woody shrubs			
Cv	7.7	7.3	3.5
Cpo	47.8	10.5	3.0
Ap	55.3	11.8	2.4
Cl	52.8	13.5	2.4
Aa	44.4	10.8	1.7
Brush			
Atr	51.0	12.7	2.2
Pt	51.5	14.1	2.1
Chn	76.2	15.7	2.2
Chv	62.1	9.3	1.8
Aar	83.2	41.7	1.0
Herbs and other			
Wm	57.5	9.7	2.6
Gr	62.5	17.3	2.2
Ba	59.7	20.8	2.2

*Vegetational composition based on vegetation maps.* The 21 species observed, plus grasses (including associated herbs and bare ground), are grouped according to growth form in Table 1.

*Pinus jeffreyi* has the highest frequency followed by *P. ponderosa*, *Artemisia tridentata*, *Cercocarpus ledifolius*, *Juniperus occidentalis*, and *Purshia tridentata*. The non-specific cover elements, grasses and bare ground, also have high frequencies which total about 25% of all the frequency occurrences (= relative frequency), and emphasize the open nature of the vegetation. The high frequency of bare ground in forested areas doubtless reflects the nature of the geology with its exposed volcanic ridges, peaks, and abrupt slopes.

Tree species array along a gradient initially identified on the basis of soil depth (Table 3). *Abies concolor* occurs on soils averaging 110 cm in depth whereas *Juniperus occidentalis* occurs on soils averaging 52 cm. Other tree species fill in the gradient in the sequence listed in Table 3.

The same species follow a similar gradient in surface rock cover from about 5% average surface rock for soils of *A. concolor* to 26% for *J. occidentalis* (Table 3). However, the internal gradient sequence differs

TABLE 4. RELATIVE FREQUENCY OF PLANT SPECIES AND COVER ELEMENTS ON SEVERAL COMMON SOILS.

	Soil series								
	720	722	714	765	776	777	763	761	Other
Trees									
W	67	30		1					2
I	85	8	3	1					2
Y	47	20	30	1					2
J	46	20	31	1	1				1
B	63	15	4	11					7
Jo	28	11	21	15	13	5	4		3
Woody shrubs									
Cv	69	8	23						
Cpo	90	1	8	1					
Ap	79	14	6						1
Cl	47	20	27	4					2
Aa	67	8	8	6					11
Brush									
Atr	38	13	29	18	1				1
Pt	43	9	23	20	3				2
Chn	17	28	26	27	1				1
Chv	50	3	43						3
Aar	3		2	3	59	13	8	7	5
Herbs and others									
Wm	86	3	1	9					
Gr	19	13	35	13	13	3	2	2	1
Ba	42	10	16	8	15	3	2	2	1

slightly from the soil depth sequence in that soils of *Calocedrus* have a little more surface rock, on average, than do soils on which *P. ponderosa* occurs.

A pattern of nearly parallel soil gradients is extended to the parameter of slope aspect. This gradient ranges from a 22% occurrence of *A. concolor* on south facing soil formations (= 78% preference for north aspects) to 78% preference for south aspects for *J. occidentalis*. On slope aspect, however, *Quercus kelloggii* assumes a gradient sequence position close to *P. ponderosa* rather than between *P. jeffreyi* and *J. occidentalis* as observed in the 2 other gradients.

All tree species grow on soil 720 and usually one or more other soils. *Calocedrus* is most frequent on soil 720, followed by *Abies* and then *Q. kelloggii*. Most notably, *J. occidentalis* occurs on a wide range of soil types, with significant occurrence on heavy-textured soils such as 776 and 777 (Table 4).

Woody shrub species assort along a soil depth gradient (Table 3) closely parallel to that for tree species. Along a gradient from deep to shallow soils, *Ceanothus velutinus* is followed by *C. prostratus*, *Arctostaphylos patula*, *Cercocarpus ledifolius*, and *Amelanchier pallida*.

TABLE 5. SOIL CHARACTERISTICS ALONG AN ASSOCIATION GRADIENT IDENTIFIED ON THE BASIS OF RELATIVE DOMINANCE OF JEFFREY PINE VS. PONDEROSA PINE AT ONE EXTREME AND MOUNTAIN JUNIPER AT THE OTHER. Relative dominance is indicated by the sequence of species symbols.

Associa- tion	N	South Surface Soil				Soil series					
		Rel. Freq.	aspect %	rock Av. %	depth Av. ft.	720	714	722	765	776	777
Y	39	4.2	33.3	6.7	3.2	92	5	—	—	—	—
YJ	308	33.3	33.8	5.6	3.4	41	33	24	—	—	—
JY	118	12.8	52.1	10.7	2.7	50	28	17	—	—	—
J	97	10.5	52.6	8.1	2.6	47	38	14	—	—	—
JoJy	59	6.4	48.3	12.6	2.4	43	28	22	—	—	—
JoJ	88	9.5	85.2	21.7	1.9	57	23	15	—	—	—
Jo	216	23.3	82.6	31.5	1.4	12	19	—	23	21	8

The surface rock cover gradient for woody shrubs is less regular and less extensive than for trees. *Ceanothus velutinus* grows on soils with about 7% surface rock. Other shrub species form a group with soil surface rock cover averages ranging from 10.5–13.5%

A stepped gradient in slope aspect is apparent for soils on which shrubs occur (Table 3). A strong preference (92%) for north aspects places *C. velutinus* in a class by itself. The other shrub species array near neutral values (i.e. 50%) with *A. pallida* and *C. prostratus* showing slight preference for north aspects and *Arctostaphylos* and *Cercocarpus* showing slight preference for south.

Shrubs closely parallel the pattern described for trees with regard to soil type. Generally a decreasing occurrence on soil 720 follows a slightly different species sequence than was observed in the soil depth gradient (Table 4). *Ceanothus prostratus* is most frequent on soil 720 whereas *Cercocarpus ledifolius* is least frequent.

Soft shrub or "brush" species occupy similar gradients, but in contrast to trees and woody shrubs, the soil depth gradient range is lower, the range of surface rock cover higher, and the range of preference for soils with south aspect greater (Table 3). Generally, *Artemisia tridentata* and *Purshia tridentata* occur on the most favorable of the "brush soils". *Artemisia arbuscula* characteristically occupies heavy soils and is essentially excluded from soil 720 (Table 4).

The cover elements conferring an open character to the vegetation, i.e., *Wyethia mollis*, grasses and bare ground, usually occupy soils that generally face south (Table 3). Those are somewhat shallow but deeper than most of the "brush" soils. Surface rock cover is moderate for soils of *W. mollis* and rather extensive for grasses and bare ground.

TABLE 6. CROWN COVER AND VEGETATION CHARACTERISTICS OF PERENNIAL SPECIES IN 5 SAMPLE AREAS IN MODOC NATIONAL FOREST HAVING JEFFREY PINE AS A DOMINANT ELEMENT. Locations listed in Table 8. D = density; F = frequency; C = crown cover in m<sup>2</sup>; I.V. = importance value derived from summation of relative D, F and C; \* = cover estimate (or partly). \*\* = *Ribes viscosissimum* at area III.

Species	Sample area					Total			
	I	II	III	IV	V	D	F	C	I.V.
<i>Abies concolor</i>	19.18					13	1	19.18	3.7
<i>Calocedrus decurrens</i>	14.22					3	1	14.22	2.0
<i>Pinus ponderosa</i>	30.59	312.48	0.64	48.62		62	15	392.33	40.2
<i>Pinus jeffreyi</i>	77.58	202.74	185.50	285.34	118.20	114	25	869.36	79.2
<i>Juniperus occidentalis</i>	15.36		32.73	102.40	176.54	44	17	327.03	35.7
<i>Amelanchier pallida</i>	0.68		0.62	0.30		13	9	1.60	8.9
<i>Arctostaphylos patula</i>			0.13			2	1	0.13	1.1
<i>Artemisia tridentata</i>	10.87		..15.93			155	7	26.80	29.9
<i>Cercocarpus ledifolius</i>	76.84	2.37	34.57	81.49	73.39	100	24	268.66	46.6
<i>Ceanothus prostratus*</i>	4.00	44.00	14.00	0.50		8	8	62.50	10.4
<i>Ceanothus velutinus</i>				0.20		1	1	0.02	1.0
<i>Chrysothamnus nauseosus</i>			0.84			5	2	0.84	2.3
<i>Penstemon dentatus</i>				0.03		1	1	0.03	1.0
<i>Purshia tridentata</i>		2.77	15.12	0.61	2.53	107	13	21.03	26.9
<i>Ribes velutinum**</i>			0.89	1.91		8	5	2.80	5.1
<i>Rosa californica</i>			8.81			13	1	8.81	3.2
<i>Symphoricarpos vaccinoideus</i>			0.27			15	1	0.27	3.1
Total	249.32	564.36	310.05	521.22	370.66	664	132	2015.61	300.3
Number of plots	6	6	8	7	6		33		
Average cover	41.6	94.1	38.8	74.5	61.8		61.08		
Average tree cover	26.2	85.9	27.4	62.3	49.1		49.16		

*Jeffrey pine gradient segment.* Since Jeffrey pine comprises a major focus in this study, its position in a gradient relative to other species was examined in detail. Seven association categories were identified (Table 5) based on relative dominance of *P. jeffreyi*. *Pinus ponderosa* and *Juniperus occidentalis* occur at either end of this gradient segment. *Pinus jeffreyi* occurs in the 5 intervening categories according to its increasing dominance relative to *P. ponderosa* (steps 1-4) and its decreasing dominance relative to *J. occidentalis* (steps 4-7).

In this analysis, mixed forests dominated by *P. ponderosa* are most frequent (Table 5), followed by *Juniperus* woodlands. Unmixed stands of Jeffrey and ponderosa pines are much less frequent than those of western juniper, reinforcing other indications concerning the general dry, open nature of the southern Modoc forest. Even though selection of study area was based on Jeffrey pine dominance, unmixed Jeffrey pine forests occupy only a narrow band along the available gradient (Table 5).

On this gradient, *P. ponderosa* occupies deep soils with little surface rock and shows definite north aspect preference. *Juniperus occidentalis* occupies shallow soils with much surface rock and shows strong south aspect preference. Unmixed stands of ponderosa pine strongly correlate with soil 720. Jeffrey pine and ponderosa-Jeffrey stands occur on soil 720 but more often on soils with excessive drainage. Jeffrey pine dominance relative to ponderosa pine correlates with south slope preference, greater surface rock cover, and shallow soils. *Juniperus occidentalis* occupies a variety of soil types especially, where it occurs alone, the heavy soils (Table 5). Its dominance relative to Jeffrey pine correlates with greater south slope preference, greater surface rock cover, and shallower soils. Soil preferences are clear but broad overlapping ranges of tolerance permit cohabitation over considerable area.

*Vegetation of the southern Modoc Forest based on ground samples.* This study also involved comparison of the southern Modoc Forest with other northern California forests having Jeffrey pine as a dominant element. Ground-level vegetation samples from 5 forest areas of the southern Modoc Forest indicate an average cover of 61% and an average tree cover of 49% (Table 6). The 5 tree species and 12 shrub, brush and suffrutescent species observed suggest low species diversity. The most important species, on the basis of Importance Values, include 3 trees and 4 shrubs in the sequence *Pinus jeffreyi*, *Cercocarpus ledifolius*, *Pinus ponderosa*, *Juniperus occidentalis*, *Artemisia tridentata*, *Purshia tridentata* and *Ceanothus prostratus* (Table 6). Considerable variation in importance values suggests that few species are dominant in the region.

The occurrence of several vegetational phases is apparent from the variation among sample areas (Table 6). Few species were observed in samples areas II and V; each was dominated by 2 tree and one shrub species. However, a mesic forest of ponderosa and Jeffrey pine occurs in

TABLE 7. LOCATION OF GROUND SAMPLES IN A SEGMENT OF THE SOUTHERN MODOC NATIONAL FOREST AND CORRELATION WITH MAP VEGETATION UNITS. Species codes are listed in Table 1 \* = probable hybrid derivative. ( ) indicates present, but low in cover.

Sample Area	1	2	3	4	5
Section	Ash Creek	Foster Spring	Hayden Hill	Johnson Mill	Willow Ridge
Range	10E	10E	31, 30	1, 2	17
Township	38N	37N	10E	10E	10E
Map	Cl Ba J Y	Y J Ba	Gr Ba Atr Y J	Cl Ba Jo J	Cl Gr Jo J
Vegetation Codes	W J Ba	Gr Ba Cl J	Gr Ba Cl J	Y J Ba Gr	Cl Gr Jo JY
Ground	Ba Y J Gr Chn Atr	J Y	J	J	Jo
Sample	I J Y Cl	Y Cpo	J Atr	Cl	Cl (JY)*
Vegetation	Cl J Y	Y Cpo	J	Jo	Jo Cl
Vegetation	Cl J (Jo)	Y	J (Atr)	Cl J	J Cl
Codes	Cl J (Y)	Y	Jo J	Cl J	J Cl Jo
	W Y	J (Y)	Pt (JoJ)	J Y	Jo
			Cl (Pt)		
			J Cl Cpo		
Summation					
Map code	J Cl Y W Chn	Y J Ba	J Cl Atr Y	J Cl Jo Y	Cl Jo JY
Ground code	Atr Ba Gr	Ba Gr	Ba Gr	Ba Ba	Gr Gr
	J Cl Y W I Atr	Y J Ba	J Cl Jo Atr Pt	J Jo Cl Y	JoJ Cl
	Ba Ba		Ba Ba	Ba Ba	Ba Ba

area II whereas a drier more open forest-woodland of *J. occidentalis*, *P. jeffreyi* and *C. ledifolius* occurs in area V.

Greater diversity of species in areas I, IV, and especially III apparently correlates with considerable local topographic diversity and vegetational mosaics. A mesic Jeffrey pine forest in area I includes *Abies concolor* and *Calocedrus decurrens* but also more xeric open patches of *Artemisia tridentata*, *Cercocarpus ledifolius* and *Juniperus occidentalis*. Areas III and IV are drier, including open slopes, ridges and spurs, with a variety of shrub-woodland elements and slopes forested with Jeffrey pine.

*Comparison of methods.* Comparison of ground observations (Table 6) and the vegetation map discussed above suggests that different forests may have been under consideration. However, the 2 sets of information are based on methodologies differing in scale of observation, qualifications for inclusion, and extent of coverage.

To reconcile these differences, ground samples were correlated with vegetation map units by determining their location on topographic maps and soil vegetation maps, listing the map vegetation codes at those locations, and applying similar codes to ground vegetation samples (Table 7). The 2 sets of vegetation codes still look somewhat different. However, if the apparent greater heterogeneity of the ground samples, due to the scale of observation, is ameliorated by summing the codes for several samples in each sample area, and if bare ground symbols are added to ground vegetation codes to allow for the different method of recording ground cover, the 2 sets of summation codes (Table 7) are quite similar.

A few differences remain. At Ash Creek, *Calocedrus* is recorded in ground but not in map samples, with a low cover value in one plot (Table 7). This difference is doubtless due to low density sampling variation and perhaps to a sampling location at the edge of mapped vegetation. At Foster Spring, ground samples indicate *P. ponderosa* on benches and gentle slopes and *P. jeffreyi* in cold air drainage ways. However, ground samples code exactly the same as vegetation map samples. Generalizing to the scale of the map, therefore, does result in a slight loss of resolution.

At Hayden Hill, the vegetation map omitted *J. occidentalis* (probably by error) and ground samples included only minimum *P. ponderosa* cover. Observational notes between ground sample plots record occasional cones of *P. ponderosa* on the ground and old stumps of large ponderosa trees. Therefore, there is some *P. ponderosa* in the area even though significant occurrence was not recorded in sample plots. Depending on the time of lumbering operations, considerable *P. ponderosa* timber could have been standing at the time of original mapping.

At Johnson Mill, practically identical codes prevail for both ground and map samples.

At Willow Ridge, map codes list *P. ponderosa* and grass cover but ground samples record *P. jeffreyi* and low total cover but not *P. ponderosa* (Table 7). Perhaps *P. ponderosa* was prevalent at the time of map-

TABLE 8. CROWN COVER AND VEGETATION CHARACTERISTICS OF 3 SAMPLE AREAS IN PLUMAS NATIONAL FOREST. I, Forest road S27, 10 mi. N of Beckwourth; II, 0.2 mi. E of Lake Davis, N of Portola; III, Frenchman Lake, 2 mi. W of dam. Headings and notations as in Table 7.

Species	Sample area			Total			
	I	II	III	D	F	C	I.V.
<i>Abies concolor</i>	1.66	125.35	3.57	26	8	158.58	20.4
<i>Calocedrus decurrens</i>	9.50	189.86		27	7	199.36	22.4
<i>Pinus ponderosa</i>	102.49	154.95		55	6	257.44	28.4
<i>Pinus jeffreyi</i>	90.23	53.68	132.64	85	13	276.55	39.5
<i>Juniperus occidentalis</i>	166.18	0.16		5	4	166.34	15.0
<i>Amelanchier pallida</i>	0.08	0.06	5.89	8	5	6.03	5.6
<i>Arctostaphylos patula</i>	32.00	5.66	18.01	62	12	55.67	21.3
<i>Artemisia tridentata</i>	0.39	0.80	35.28	222	7	36.47	35.3
<i>Cercocarpus ledifolius</i>	4.53			16	2	4.53	3.9
<i>Ceanothus velutinus</i>	6.83	5.34	104.96	36	8	117.13	18.9
<i>Ceanothus prostratus*</i>	80.00	63.00	53.00	14	14	196.00	26.5
<i>Eriogonum marifolium</i>	0.42			35	2	0.42	6.0
<i>Eriogonum ovalifolium</i>	0.12			21	1	0.12	3.4
<i>Haplopappus acaulis</i>	0.07			3	1	0.07	1.2
<i>Haplopappus bloomeri</i>			4.42	80	5	4.42	14.2
<i>Penstemon deustus</i>	0.06		0.01	11	2	0.07	3.0
<i>Phlox</i> sp.	1.89			64	2	1.89	9.6
<i>Purshia tridentata</i>	2.43	0.12	3.21	44	12	5.76	15.9
<i>Symphoricarpos acutus*</i>	18.00	3.00	0.90	8	8	21.90	9.2
Total	516.88	601.98	389.89	822	119	1508.75	300.1
Number of plots	5	5	5			15	
Average cover	103.38	120.40	77.98			100.58	
Average tree cover	74.01	104.80	32.84			63.88	

ping and was subsequently lumbered out. The presence of *P. ponderosa* on favorable soils about  $\frac{1}{4}$  mi distant might account for the discrepancy between map and ground vegetation codes.

Grass cover values were not recorded at Willow Ridge. Grass patches were noted but bare ground was more prevalent. For practical purposes, in this comparison grass cover and bare ground are equivalent. Correspondence between ground samples and map samples is rather close and lends confidence to their complementary use in regional comparisons.

*The Jeffrey Pine Forests of Plumas and Tahoe National Forests.* Ground level vegetation samples from 3 forest areas in Plumas National Forest (Table 8) indicate an average cover of 100% and an average tree cover of 64%. Both values are higher than comparable values in the Modoc Forest suggesting a denser vegetation and more mesic conditions. The most important species, on the basis of importance values, include 5 trees and 6 shrubs in the sequence *Pinus jeffreyi*, *Artemisia tridentata*, *Pinus ponderosa*, *Ceanothus prostratus*, *Calocedrus decurrens*, *Arctostaphylos patula*, *Abies concolor*, *Ceanothus velutinus*, *Purshia tridentata*, *Juniperus occidentalis* and *Haplopappus bloomeri*.

Fairly uniform importance values suggest that more than a few species assume dominant roles in the region. The 5 tree species are the same as those in the Modoc Forest. The 14 species of shrubs and suffrutescent plants represent a net increase of 2 species in 15 sample plots as compared with 12 species observed in 33 sample plots in the Modoc Forest.

Greater variety of species and increased dominance of more species, especially shrubs, probably derives from greater gross environmental and topographic variation and greater disturbance in the Plumas Forest.

Topographic variation ranges from the west slope position (high precipitation) of Davis Lake, and the high elevation (2000 m) and near sub-alpine ridges of the mountains north of Beckwourth, to the low broad ridges and volcanic tablelands at Frenchman Lake in a local rain shadow. The general topographic diversity provides several different habitat systems in which different species assume roles of major importance. The compositional differences among the 3 sample areas (Table 8) produce an overall effect of fairly uniform average importance values for the region.

The relative amount of disturbance follows the same sequence: slight disturbance at Davis Lake derives from the management practice of cutting understory white fir; greater disturbance north of Beckwourth derives from current logging, especially construction of logging roads; much greater general disturbance from logging and burning over many years is evident at Frenchman Lake. The variety of successional stages apparent at Frenchman Lake contribute to marked diversity and general openness of the vegetation despite a relatively mesic appearance (compared to the Modoc Forest). Consequently, successional species like *Ceanothus velutinus*, *Arctostaphylos patula*, and *Ceanothus prostratus*, as well as generalists like *Artesmisia tridentata*, assume greater importance values than they do in the Modoc Forest. The more mesic conditions in the Plumas Forest probably account for the lower importance values of *Cercocarpus ledifolius*, *Amelanchier pallida*, and perhaps *Purshia tridentata*.

The longevity of disturbance at Frenchman Lake is indicated by the large size of *Ceanothus velutinus* clones (Zavitkovski and Newton 1968), some of which reach 20 m in diameter. An instructive appraisal of the rate of secondary succession might be derived from collation of clone size and age distributions.

Vegetation samples from 5 forest areas in the Tahoe National Forest (including one in Toiyabe N.F.) indicate an average cover of 76% and an average tree cover of 66% (Table 9). This forest is fairly open but considerable heterogeneity among sample areas is evident in cover and composition (Table 9). Relatively mesic conditions are indicated south of Truckee at high elevations by the dominance of *Abies concolor* and the presence of *Pinus lambertiana*. Relatively xeric conditions are indicated south of Carson City at low elevations by the absence of all trees except

TABLE 9. CROWN COVER AREA AND VEGETATION CHARACTERISTICS OF 5 SAMPLE AREAS IN TAHOE AND TOYOBE NATIONAL FORESTS, I, II, III—Hennes Pass Road, about 15 mi. N of Truckee and respectively 1.5 mi. W, 1.1 mi. E and 5.7 mi. E of State Highway 89; IV—Pole Creek Road, 6 mi. S of Truckee; V—Old Highway U.S. 50, S of Carson City and 2.6 mi. W of U.S. 395. Headings as in Table 7.

Species	Sample area					Total			
	I	II	III	IV	V	D	F	C	I.V.
<i>Pinus lambertiana</i>				9.13		1	1	9.13	1.2
<i>Abies concolor</i>	35.60	1.94	8.30	501.81		59	12	547.65	38.1
<i>Calocedrus decurrens</i>	19.36					7	1	19.36	2.3
<i>Pinus jeffreyi</i>	253.60	292.15	162.51	169.03	300.42	297	30	1177.71	100.9
<i>Juniperus occidentalis</i>		11.04	200.24			15	8	211.28	16.1
<i>Amelanchier pallida</i>			0.06	0.05		7	6	0.11	4.8
<i>Arctostaphylos nevadensis</i>				7.03		5	5	7.03	4.2
<i>Arctostaphylos patula</i>	105.90	2.67	0.01			66	7	108.58	16.0
<i>Artemisia tridentata</i>		2.25	6.09		14.18	203	13	22.52	29.4
<i>Ceanothus cordulatus</i>	4.93			0.02		9	4	4.95	3.9
<i>Ceanothus prostratus*</i>	57.00	2.25	6.00	4.01		12	12	69.26	12.5
<i>Chrysothamnus nauseosus</i>					0.02	2	3	0.02	2.2
<i>Haplopappus bloomeri</i>	0.75	0.02				26	3	0.77	4.5
<i>Penstemon deustus</i>	0.10					4	1	0.10	1.1
<i>Phlox</i> sp.			1.30	0.01		28	3	1.31	4.8
<i>Purshia tridentata</i>	19.98	3.80	29.29		23.90	277	18	76.97	42.3
<i>Quercus vaccinifolia</i>				0.01		2	2	0.01	1.6
<i>Ribes roezlii</i>			0.63	0.03		4	4	0.66	3.1
<i>Rosa californica</i>	1.00					2	2	1.00	1.6
<i>Symphoricarpos acutus</i>	0.30		1.90	7.05		12	12	9.25	9.8
Total	498.52	316.12	416.33	698.17	338.53	1038	147	2267.67	300.4
Number of plots	6	6	7	6	5	30			
Average cover	83.09	52.69	59.48	116.36	67.83				75.59
Average tree cover	51.40	50.86	53.01	113.32	60.08				65.50

TABLE 10. VEGETATION AT DEVIL'S GATE PASS, MONO COUNTY, CALIFORNIA, AUG 1, 1972. Importance values are based on 2 belt transects (A, B), each 50 x 2 m; crown diameters of all shrubs, and trunk diameters of all trees over 2 m high, rooted within the transect area, were measured; small trees were included in determining frequency; otherwise, methods are as in Table 7 to 9; *Ceanothus velutinus* is also common in the area but did not occur on the observed transects.

Species	I.V. A	I.V. B
<i>Pinus jeffreyi</i>	131.8	70.3
<i>Cercocarpus ledifolius</i>	30.4	72.5
<i>Artemisia tridentata</i>	104.2	70.6
<i>Ribes viscosissimum</i>	24.7	9.3
<i>Leptodactylon pungens</i>	8.8	37.6
<i>Symphoricarpos vaccinoides</i>		16.1
<i>Purshia tridentata</i>		15.5
<i>Juniperus occidentalis</i>		8.0
Total plants	47	150

TABLE 11. IMPORTANCE VALUES FOR 3 AREAS NEAR DEADMAN SUMMIT, MONO COUNTY, CALIF. AUG. 1 AND 2 1972. Based on 7 belt transects, 50 x 2 m. I, Lower mountain slopes; II, flat at base of mountain slopes; III, pumic flat, 4 mi. E of summit; *Pinus murrayana* also was common in areas I and III but did not occur on sample plots.

Species	I		II			III	
<i>Abies magnifica</i>	55.8	197.6					
<i>Pinus monticola</i>	39.5	—					
<i>Pinus jeffreyi</i>	204.7	102.4	86.6	150.8	142.9	112.2	97.8
<i>Purshia tridentata</i>			213.4	122.3	103.0	132.4	50.8
<i>Leptodactylon pungens</i>				26.9	54.3	—	7.0
<i>Artemisia tridentata</i>						42.8	88.7
<i>Chrysothamnus parryi</i>						12.7	41.4
<i>Lupinus breweri</i>							14.2

*P. jeffreyi*. Cold conditions are indicated for the general east Sierra region south of Truckee by the absence of *P. ponderosa* (Haller, 1959). However, north of Truckee the east side ponderosa pines are morphologically and physiologically like those of the interior Pacific Northwest (Haller, pers. comm.). Primarily they are highly cold tolerant and compete well with Jeffery pine. South of Truckee, where ponderosa pine is absent or sparse (for reasons not apparent), *P. jeffreyi* assumes a role of strong dominance, even more exaggerated than in the Modoc Forest. The cold conditions and strong Sierra Nevada rain shadow probably combine to eliminate other species selectively.

The most important species in the Tahoe Forest, based on importance values are, in sequence *Pinus jeffreyi*, *Purshia tridentata*, *Abies concolor*, *Artemisia tridentata*, *Juniperus occidentalis*, *Arctostaphylo patula* and *Ceanothus prostratus*.

An increase in the number of shrub and suffrutescent species, as compared to the Modoc and Plumas forests, may be accounted for by the wide elevational range and pronounced rain shadow. Disturbance by fire was evident only in sample area I (Table 9) where *Arctostaphylos patula*, *Ceanothus cordulatus* and *Ceanothus prostratus* are most prominent (Skau et al., 1970).

*Arctostaphylos nevadensis* and *Quercus vaccinifolia* in sample plots south of Truckee but not in sampled areas to the north indicate a high elevation forest transitional to the Sierra Nevada red fir forest (Oosting and Billings, 1943). Furthermore, I observed a few red fir (*Abies magnifica*) in the area but not on the sample plots.

*Jeffrey pine forests in Mono County.* An open stand of Jeffrey pine at Devil's Gate Pass (Table 10) consists of a few large trees with a multiple understory of *Cercocarpus ledifolius*, *Artemisia*, and *Ribes*. Still farther south in Mono County, an extensive open forest of Jeffrey pine occurs on the high elevation pumice plateau near Deadman Summit where open ground and a shrub understory of *Purshia* and *Artemisia* are significant (Table 11). Toward the base of the Sierra Nevada, Jeffrey pine and *Purshia* increase (Table 11) to positions of strong dominance similar to the sample from Toiyabe National Forest (Table 9, area V). On the steep slopes, Jeffrey pine forests grade into dense forests of red fir with an admixture of western white pine but with virtually no shrub understory (Table 12). Lodgepole pine (*Pinus murrayana*) is common in the region but not in the few transects observed.

#### SUMMARY AND CONCLUSIONS

The southern Modoc National Forest was analyzed from vegetation-soil map data that expanded ground observational coverage to over 500 km<sup>2</sup>. Information from the vegetation map agreed satisfactorily with ground observations when scale of observation was accounted for. Thus, vegetation map data provide a viable base for quantitative interpretation of vegetation over large areas. The vegetation pattern is one in which forests occur on favorable, deep soils, brush vegetation occurs on poor soils in the basins, and intermediate soils are occupied by open forests and woodlands. The observed gradient places *Abies concolor* and *Calocedrus decurrens* in deep soils at the most mesic end of the vegetation gradient. *Pinus ponderosa*, *P. jeffreyi* and *Juniperus occidentalis* occur respectively along the gradient of decreasing soil depth and quality until only brush species, *Artemisia tridentata*, and finally *A. arbuscula*, occur on the shallowest, poorest soils.

*Pinus jeffreyi* occurs in pure stands, i.e., without other tree species, with a frequency of only 16%, and *P. ponderosa* occurs in pure stands with a frequency of only 8%. More often they occur in mixed forests and Jeffrey pine also occurs with *Juniperus occidentalis* in open forests or woodlands.

The pattern of vegetational distribution is mediated by soil characteristics but complicated by other factors such as successional status and management practices. Woody shrubs may have roles in secondary succession and their fairly low frequencies except on volcanic ridges suggests that the Modoc Forest is generally stable and relatively undisturbed. Logging over the years may have influenced some compositional changes in the forest. Primarily, *Pinus ponderosa* seems less prominent now than indicated on the vegetation map compiled in 1953, at least in 2 specific localities. Such compositional changes, mediated by lumbering, render difficult the interpretation of the forest in terms of natural plant communities. Nevertheless, those forests are the *de facto* communities and bear considerable resemblance to pristine vegetation.

The southern Modoc Forest was compared to forests with Jeffrey pine in the Plumas and Tahoe Forests to the south. Each forest has its range of characteristics with respect to cover, important species, diversity of species and successional status.

In broad terms, Jeffrey pine forests range along at least 2 general gradients, both modified by altitudinal variation. One gradient proceeds essentially west-east and is influenced by decreasing moisture associated with the Sierran rain shadow. Depending on elevation, the more mesic forest to the west is either a red fir or Sierra Nevada ponderosa pine forest. The more xeric vegetation to the east is either a western juniper woodland or Great Basin sagebrush.

The second gradient runs north-south and is probably primarily influenced by temperature. The major range for Jeffrey pine occurs to the south where it occupies a broader elevational range (Haller, 1959). Jeffrey pine as a forest type stops north of the southern Modoc Forest study region. Still further north Jeffrey pine occurs mainly as an element of ponderosa pine forests. However, patches of Jeffrey pine occur in the Warner Mountains (Milligan, 1969) in forests considered to be depauperate Sierran forests by Critchfield and Allenbaugh (1969). Vegetation of the Warner Mountains is considered to be transitional to the Great Basin (Milligan, 1969) and cold dry conditions appear limiting to the northeast. To the northwest, however, excessive moisture may be limiting. Haller (1959) indicates more rapid growth by ponderosa than by Jeffrey pine in areas of ample moisture. The southern Oregon limit for Jeffrey pine on serpentine (Whittaker, 1960) may be instructive in this regard. Thus, the northern range of Jeffrey pine seems limited where conflicting moisture-temperature gradients meet and are superceded by other factors.

The *narrow* occurrence of unmixed Jeffrey pine on a broad gradient in the Modoc Forest may be a consequence of its position near the northern limits of its range. Therefore, relative breadth of occurrence on a gradient toward the center of the range of distribution should be determined in addressing the question of whether Jeffrey pine forests merit widespread

recognition as a separate community or whether they represent merely a phase of the mixed conifer forest.

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### THREE NEW SPECIES OF *JATROPHA* (EUPHORBIACEAE) FROM WESTERN MEXICO

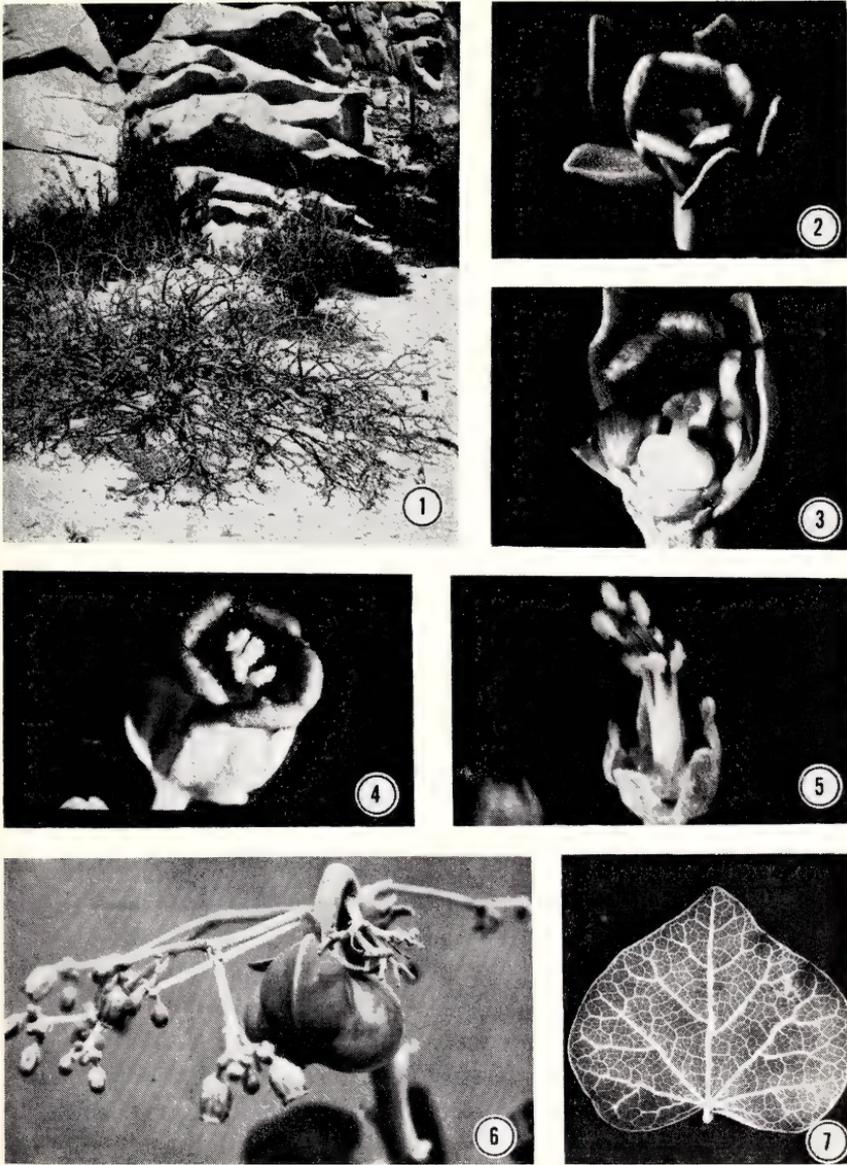
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In the course of field studies for an infrageneric revision of the genus *Jatropha* (Dehgan, 1976), three Mexican collections—two from Baja California and one from Jalisco—were found to differ from all species previously described from these areas (Mueller, 1866; Pax, 1910; Standley, 1923; McVaugh, 1945a, 1945b; Wilbur, 1954; Shreve and Wiggins, 1964). Following are descriptions of these taxa and comparisons with related species. Since all three species were either dormant or at least not flowering at the time of collection, cuttings and/or seedlings were grown to maturity in the greenhouse. The descriptions that follow are therefore based primarily on these greenhouse plants.

1. *Jatropha giffordiana* Dehgan and Webster, sp. nov. sect. *Loureira* subsect. *Canescentes*; a *J. canescenti* et *J. cinerea* differt foliis glabriusculis exstipulatis, inflorescentia ♂ florem ♀ solitarium efferenti, petalis rubris, pistillo 3-loculato, stylis 2 stigmatibus multifidis (Figs. 1-7).

*Shrub* ca 1-1.5 m high; caudex thickened, stem and branches succulent, branches spreading and decumbent; bark fissured and peeling on older branches; short shoots numerous and distinct on older branches, 2-5 cm long, pubescent, with small leaves crowded near the apex. *Leaf*-with-petiole 3.5-8.5 cm long, 3-7 cm wide; stipules not evident; blade broadly ovate, unlobed, entire (completely devoid of glands), pubescent on the veins abaxially but otherwise glabrous, palmatinerved with five prominent and two weaker lateral veins, cordate at base, acute at apex. *Inflorescences* gynodioecious, terminal on branches or more often on short shoots, the plants pistillate and staminate; in the staminate racemose-paniculate, with many ♂ flowers and one central ♀ flower; pistillate inflorescence racemose, of 2-5 flowers; axis villose, ca 5-12 cm long in the male and 1.5-2.5 cm in the female; paracladia mostly 2-4 cm long in



FIGS. 1-7. *Jatropha giffordiana*. 1. Growth habit. 2. Pistillate flower, X2. 3. Detail of the pistillate flower, X3. 4. Staminate flower, X4. 5. Detail of the staminate flower, X4. 6. Staminate inflorescence with a 3-locular fruit from the single pistillate flower at the center, X1. 7. Cleared leaf, X1.

the male; lower bracts entire (not glandular), narrowly lanceolate, villose, ca 1–2 mm long in the male and 3–7 mm long in the female. *Staminate flower* urceolate, ca 8–10 mm long and 5–7 mm wide, with densely villose pedicel ca 3–4 mm long; calyx lobes 5, elliptic, somewhat pointed, entire (not glandular), ca 2–3 mm long and 1–1.5 mm wide, not imbricate; petals connate to more than  $\frac{2}{3}$  their length, bright red, pubescent adaxially; disc segments 5, spherical, massive, ca 1 mm high and wide; stamens 10, monadelphous-biseriate, filaments connate to more than  $\frac{2}{3}$  their length, ca 5–8 mm long, anthers elliptic, ca 1.3–1.5 mm long. *Pistillate flower* campanulate, ca 10–12 mm wide (somewhat wider in the staminate inflorescence), with densely villose, large and more or less foliaceous calyx lobes ca 15–20 mm long, 10–13 mm wide, not imbricate; petals connate to about the middle, bright red, villose adaxially; disc dissected, of (8) 10 glands, somewhat taller than broad, ca 0.7–1.0 mm wide and 0.8–1.1 mm high; ovary glabrous, of (2–) 3 carpels (always three in the terminal pistillate flower of an otherwise staminate inflorescence); stylar column thick, connate to above the middle, dilated to 2 multifid stigmata. *Capsules* distinctly (2–) 3-lobed, ca 2–2.5 cm long and wide, somewhat dry, tardily dehiscent; seeds grayish-brown, more or less spherical, 1–1.5 cm long and wide, caruncle vestigial.

TYPE: Baja California, Cabo San Lucas, on dunes near the beach and facing the rocky hill, 17 Mar 1974, *Dehgan B74.019*. The population consisted of 20–25 plants. Type specimens from greenhouse-grown plants are deposited at DAV.

This species is named in honor of Professor Ernest M. Gifford for his contributions to the morphology of vascular plants in general and of shoot apices in particular.

*Jatropha giffordiana* is closely related to *J. canescens* and *J. cinerea* (*sensu lato*) as shown by several common characters in their vegetative morphology. McVaugh (1945b), with some justification, relegated *J. canescens* to synonymy under *J. cinerea* and in fact referred to it as a "race" of the latter. Taxonomic evidence presented elsewhere (Dehgan, 1976), however, shows the two species to be closely related but distinct. The intermediacy of certain populations ("races" *fide* McVaugh) in Baja California and western Mexico probably results from introgressive hybridization between the two taxa. *Jatropha canescens* (*sensu stricto*) is a disjunct relictual species otherwise occurring as isolated populations in northern parts of the Sonora Desert and in Magdalena Island (see Dehgan, 1976 for discussion). The extremely variable *Jatropha cinerea* (*sensu lato*), on the other hand, is widespread in western Mexico, particularly in coastal areas and from San Felipe southward in Baja California, but not on Magdalena Island.

*Jatropha giffordiana* differs from both *J. canescens* and *J. cinerea* in its decumbent growth habit, gynodioecious inflorescence, absence of stipules, bright red petals, and mainly 3-carpellate gynoeceia with multifid

stigmata. In fact, the multifid stigma is unique for the entire genus. The occurrence of *J. giffordiana* as a small population apparently endemic to the tip of Baja California, a more tropical and moister region below the Tropic of Cancer, is also of some significance, since it may be an ancestral relict.

The following key describes extremes of *J. canescens-cinerea* complex and disregards intermediate individuals or populations as discussed by McVaugh (1945b). Further clarification of this species complex, including *J. giffordiana*, requires detailed biosystematic studies of various populations. No populations intermediate between *J. giffordiana* and the other two species have been observed. The descriptions of the two species as given by Pax (1910), particularly that of *J. canescens*, are quite inaccurate; and those of McVaugh (1945b) and Shreve and Wiggins (1964), for the reasons given above, are somewhat confusing. And finally, it should be emphasized that similarity of the vegetative characters, especially of the herbarium material, can be quite deceiving. The following somewhat deliberately detailed diagnostic key should, we hope, clear up the long-standing confusion with regard to the distinctiveness of the taxa under consideration.

- a. Gynodioecious shrubs with decumbent branches and distinct short shoots; stipules absent; leaves sparsely pubescent on the veins, otherwise glabrous; staminate inflorescence racemose-paniculate with a single pistillate flower at the center; pistillate flowers campanulate, the staminate urceolate; ♀ calyx lobes 15–20 mm long, 10–13 mm wide; petals bright red; stylar column thick, dilated to 2 multifid stigmata . . . . . *J. giffordiana*.
- a. Dioecious erect shrubs with or without distinct short shoots; stipules early deciduous or persistent; leaves pubescent on one or both surfaces; staminate inflorescence paniculate and lax or nearly sessile and compact without the central pistillate flower; flowers subglobose or tubular in one or both sexes; ♀ calyx lobes 8–12 mm long, 6–10 mm wide; petals greenish-yellow or pink-rose; stylar column narrow, dilated to 2 (rarely 3) bifid stigmata . . . . . b.
- b. Nodes swollen and with very short arrested shoots; stipules linear-lanceolate and persistent; leaves orbicular, unlobed, entire and densely pubescent on both surfaces; male inflorescence subsessile, compact and many flowered; flowers of both sexes ± tubular; petals greenish-yellow . . . . . *J. canescens*.
- b. Nodes not swollen and without arrested shoots; stipules lanceolate, early deciduous; leaves ovate-orbicular, often 3–5 lobed, with glandular margin when young, pubescent only on the adaxial surface; male inflorescence pedicellate, paniculate and lax; staminate flowers tubular but pistillate flowers subglobose; petals pink-rose . . . . . *J. cinerea*.

Specimens of *Jatropha canescens* examined: SONORA: thorn scrub on lava, flat at base of slope, 15 mi SE of Guaymas, 21 Jun 1972, *Webster & Lynch 17002* (DAV). SINALOA: cactus thorn scrub on silty soil, plains ca 8 mi NW of Guamuchil, alt 20 ft, *Webster & Lynch 17038* (DAV). BAJA CAL. SUR: Magdalena Island, cactus thorn scrub on silty soil, foothills, alt ca 100 ft, 20 Mar 1974, *Dehgan & Webster 874.038* (DAV).

2. *Jatropha moranii* Dehgan and Webster, sp. nov. sect. *Platyphyllae*; a *J. purpurea* differt foliis exstipulatis 5-lobatis, bracteis eglandulosis, sepalis integris foliaceis, petalis chloroleucis recurvatis (Figs. 8–13).

*Small shrub* less than 1 m high with succulent stem and branches and a distinct woody caudex; bark fissured but not peeling, brown with white epidermal markings; short shoots not evident. *Leaf*—with—petiole ca 2.5–5.5 cm long and 1.5–3 cm wide; stipules not evident; blades ovate, distinctly 5-lobed, the margin ciliate with knob-shaped stipitate glands 2–4 mm long, papillose abaxially but papillose and hirsute adaxially particularly near the margins; palmately netted with 5 prominent veins, cordate at the base, cuspidate at the apex. *Inflorescence* monoecious, subterminal (occasionally appearing terminal or lateral); dichasia compound, paracladia of 1–2 dichasia each terminating in a pistillate flower; coflorescence present and often distinct; inflorescence axis downy, ca 2–4.5 cm long, axes of paracladia ca 1–1.5 cm long; lower bracts entire (rarely with 1 or 2 glands), hirsute, lanceolate, ca 3–7 mm long. *Staminate flowers* subglobose, ca 8–12 mm long and 6–9 mm wide, with downy short pedicel 4–6 mm long; calyx lobes 5, elliptic, pointed, entire (not glandular), downy, ca 5–9 mm long and 2–5 mm wide, imbricate at base; petals recurved, connate to about  $\frac{1}{2}$  their length, white, glabrous on both surfaces; disc segments 5, spherical, massive, ca 1–1.5 mm high and wide; stamens 10, monadelphous-biseriate, connate for most of their length; filaments ca 5–8 mm long; anthers elliptic, 1–1.3 mm long. *Pistillate flowers* campanulate, ca 10–14 mm long and 12–18 mm wide, with downy pedicel 8–11 mm long; calyx lobes 5, broadly elliptic, pointed, entire (not glandular), papillose on both surfaces, large and more or less foliaceous, ca 10–25 mm long and 10–15 mm wide, not imbricate; petals recurved, connate below the middle, white, glabrous on both surfaces; disc segments 5, broader than tall, ca 1.5–2.5 mm wide and 0.8–1 mm high; stylar column thick, connate to above the middle, dilated into 3 bifid stigmata. *Capsules* trilocular and distinctly trilobed, ca 1.5–2 mm long and wide, somewhat dry, tardily dehiscent; seeds grayish brown, more or less spherical, ca 1–1.5 cm long and slightly less wide, the caruncle lacerate.

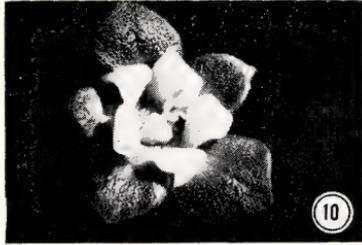
TYPE: Baja California Sur, Cabo San Lucas, 6 Aug 1932, *John Thomas Howell 10606* (CAS, holotype).



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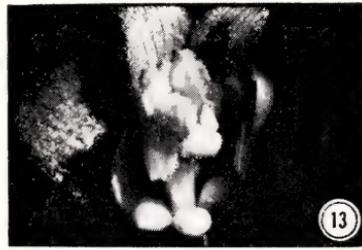
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FIGS. 8-13. *Jatropha moranii*. 8. Growth habit (greenhouse grown plant). 9. Inflorescence and leaves, ca. X1. 10. Pistillate flower, X3. 11. Detail of pistillate flower, X6. 12. Staminate flower, X5. 13. Detail of staminate flower, X5.

Additional collection: Cabo San Lucas, above the air strip, alt. ca 10 m, on alluvial rocky areas, Jul 1968, *John E. Bleck & Charles Glass 680—Dehgan B74.052* from greenhouse grown plants (DAV).

This species is named after Dr. Reid Moran of the San Diego Natural History Museum for his contributions toward the understanding of the flora of Baja California.

*Jatropha moranii* resembles *J. purpurea* in growth habit and in structure of the inflorescence. However, several characters suggest that the

two may not even be closely related. *Jatropha moranii* is quite distinct in its lack of stipitate glands on bracts and calyx lobes and its lack of stipules and its recurved white petals. Since we have seen no specimens of *J. purpurea* in Baja California and no herbarium specimens from Baja California, we suggest that references to *J. purpurea* in Baja California (e.g., by Standley, 1923; Shreve and Wiggins, 1964) may be based on *J. moranii*. These two species can be distinguished by the following synoptic key:

Stipules dissected into gland-tipped segments; petiole slender, 20–40 mm long; leaf blade 3–4 cm wide, shallowly 3-lobed, the median lobe narrowly triangular and much longer than the lower lobes, upper margins of lobes dentate but less conspicuously glandular than the basal margin. Bracts glandular-ciliate; sepals glandular-ciliate, linear-lanceolate in the pistillate flower; petals red, not recurved . . . . . *J. purpurea*.

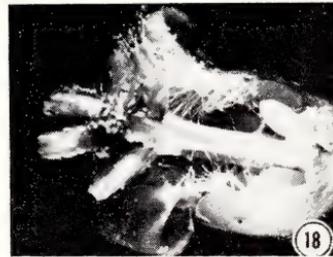
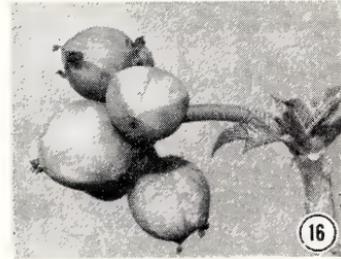
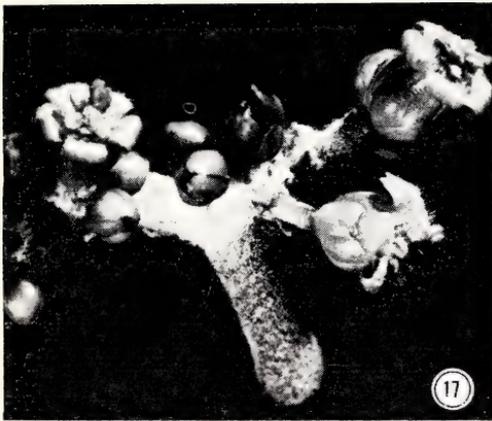
Stipules absent; petiole stout, 5–18 mm long; leaf blade 1.5–3 cm wide, shallowly 5-lobed, the median lobe widely triangular and nearly like the other lobes, margins evenly glandular throughout. Bracts mostly without glands; sepals entire (not glandular), broadly elliptic and more or less foliaceous in the pistillate flower; petals greenish-white, recurved . . . *J. moranii*.

Specimen of *J. purpurea* examined: SINALOA: Cerro Llano Redondo, west of Caymanero, 8 Oct 1944, *Howard Scott Gentry 7088* (DS).

3. ***Jatropha mcvaughii*** Dehgan and Webster, sp. nov. sect. *Curcas*; a *J. curcas* differt ramis cortice fissurato, foliis pubescentibus, inflorescentiis dioeciis, petalis in dimidio inferiore connatis, styliis crassis, seminibus 10–12 mm longis non incrustatis (Figs. 14–18).

Syn. *Jatropha curcas* var. *rufus* McVaugh, Bull. Torrey Bot Club 72: 284. 1945.

*Shrub* or small tree, 1.5–3.5 m high; branches and foliage pubescent; bark fissured or cracked, but not peeling. *Leaf*-with-petiole 25–35 cm long when mature; stipules narrowly lanceolate, early deciduous; blades ovate, 5–7 (9) lobed with the upper lobes extending to near the midrib and lower lobes shallow, mostly 15–25 cm long and nearly as wide, palmatinerved, with 7(9) primary nerves, broadly cordate at the base, cuspidate at the apex, pubescent on both surfaces; margins entire (completely devoid of glands). *Inflorescence* dioecious, terminal on branches, with typical jatrophioid compound dischasia in both sexes but with much smaller number of flowers in the pistillate inflorescence; axis tomentose, ca 7–12 cm long in the staminate and 3–6 cm in the pistillate; paracladia terminating in a single flower; those of the pistillate inflorescence ca 1–2.5 cm long, but those of the staminate inflorescence 1–1.5 cm long; lower bracts entire, lanceolate, pubescent, 4–9 mm long in the male,



FIGS. 14-18. *Jatropha mcvaughii*. 14. Pistillate inflorescence, X3. 15. Detail of pistillate flower, X4. 16. Fruit, ca X1. 17. Staminate inflorescence, X4. 18. Detail of staminate flower, X8.

somewhat longer in the female. *Staminate flowers*  $\pm$  tubular with corolla tube longer than the lobes, 8-12 mm long and 5-8 mm wide; pedicel tomentose, ca 4-8 mm long; calyx lobes 5, elliptic, pointed, entire (not glandular), smaller than in the female, ca 4-7 mm long and 2-3 mm wide, imbricate; petals obovate, connate to about  $\frac{1}{2}$  or more of their length, greenish-yellow, hirsute adaxially, villose abaxially; disc segments 5, massive, ellipsoid, ca 2-3.5 mm long and 1-1.5 mm wide; stamens 10, monadelphous, scarcely bi-seriate, the filaments connate to about  $\frac{1}{2}$  their length, ca 3-5 mm long; anthers oblong elliptic, somewhat flattened at the apex, ca 1.5-2 mm long. *Pistillate flowers* ca 5-11 mm long, with tomentose pedicel,  $\pm$  campanulate, corolla tube shorter than or nearly equalling lobes, ca 8-11 mm long and 10-14 mm wide; calyx lobes 5, elliptic, pointed, entire (not glandular), ca 7-10 mm long and 3.5-5 mm wide, imbricate; petals obovate, connate to about  $\frac{1}{3}$  their length, greenish-yellow, hirsute adaxially, villose abaxially; disc segments

5, massive, broader than long, ca 1–1.3 mm long and 2.5–4 mm wide; ovary glabrous, of 3 carpels; stylar column thickened, connate to about middle, not dilated but with 3 bifurcate, massive, dark green stigmata. *Capsules* ellipsoidal, ca 2 cm long and 1.5 cm broad,  $\pm$  fleshy, at length drying and tardily dehiscent; seeds light brown, 10–12 mm long and 8–10 mm wide, the caruncle appressed to the beak and nearly vestigial, ca 1 mm or less long and 1.5–2 mm wide.

TYPE: Mexico, Jalisco, Playa Scandida, Dec 1974, *Dehgan B74206* (DAV). The species has been observed from Mazatlán to an elevation of ca 350 m on the road to Durango.

Additional specimens examined: SINALOA: Ymala, Aug 1891, *Palmer 1413* (US, holotype); Mazatlán, *Ortega 7299* (CAS); Culiacán and vicinity, *Howard Gentry 7046* (CAS). NAYARIT: thorn woodland 11–12 mi NE of Singayta, alt ca 200 ft, 25 Jun 1972, *Webster & Lynch 17070* (♀), *17073* (♂) (DAV).

This species is named in honor of Professor Rogers McVaugh, in recognition of his contributions toward understanding of the genus *Jatropha* in particular (1944, 1945a, 1945b) and to the systematics of neotropical flowering plants in general.

*Jatropha mcvaughii* was earlier described as *J. curcas* var. *rufus* by McVaugh (1945b). Although originally distinguished by McVaugh solely on the basis of pubescence, it actually differs from *J. curcas* in a number of characters: fissured bark, dioecious inflorescences, longer corolla tube, thick stylar column with undilated stigmata, and smaller smoother seeds. Although the color and quantity of pubescence does furnish a convenient recognition feature for *J. mcvaughii*, the dioecious flower production seems systematically more important. We thus conclude that while *J. mcvaughii* clearly belongs to sect. *Curcas* and is closely related to *J. curcas*, it differs sufficiently from the latter to be considered a distinct species, as is evident in the following synoptic key:

- Bark smooth, branches and mature foliage glabrous; leaf blades unlobed or with (3)5–7 very shallow lobes; monoecious, bisexual or often unisexual; petals greenish or yellowish-white, connate at the base; styles slender, dilated into massive stigmata; capsule ca 3 cm long and 1.5 cm broad; seeds 15–32 mm long, blackish-encrustate-striate . . . . . *J. curcas*.  
 Bark fissured or cracked, branches and mature foliage pubescent; leaf blade with 5–7(–9) deeper lobes; dioecious; petals greenish-yellow, connate to about half their length; styles thick, undilated, with fleshy stigmata; capsule ca 2 cm long and 1 cm broad; seeds 10–12 mm long, light brown and without striations . . . . . *J. mcvaughii*.

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CHEMOTAXONOMIC STUDIES  
IN THE SAXIFRAGACEAE S.L.  
9. FLAVONOIDS OF JEPSONIA

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*Jepsonia* is a small genus of the Saxifragaceae restricted to California and northern Baja California. Ornduff (1961) described the distylous nature of the flowers and, more recently, presented a detailed account of the ecology, morphology and systematics of the genus (Ornduff, 1969). No chemical study of the genus appears to have been done. An investigation of the polyphenolic constituents of *Jepsonia* was thus undertaken as part of a general chemotaxonomic survey of the family. It was hoped that flavonoid data might yield additional characters useful for characterizing the species and offer insights into the enigmatic relationships between *Jepsonia* and other genera in the family.

MATERIAL AND METHODS

The plant collections used in this study are: *J. heterandra* Eastw., Bagby, Mariposa Co., Cal., 20 Mar 1970, G. D. Cromwell 101, RSA; *J. malvifolia* (Greene) Small, Santa Catalina Island, Los Angeles Co., Cal., 8 Mar 1970, R. F. Thorne 39392, RSA; *J. parryi* (Torr.) Small,

Old Mission Dam, San Diego Co., Cal., 12 Apr 1970, Cromwell 107, RSA; Old Mission Dam, San Diego Co., Cal., 2 Nov 1970, Cromwell 109, RSA; Los Alamos Canyon, Riverside Co., Cal., 15 Feb 1972, Cromwell 709, RSA; Jatay, Baja Cal., 21 Mar 1970, Thorne 39421 RSA; Baja Cal., Spring 1973, Tom Mulroy (Pomona College) (s.n.) RSA.

Flavonoid constituents were isolated and purified by the procedures described by Wilkins and Bohm (1976a). The compounds were identified by chromatography against standards, partial and total hydrolyses, and ultraviolet spectral methods (Mabry et al., 1970). These procedures were used on the pooled extracts of *J. parryi* and the extract from *J. heterandra*. Compounds present in *J. malvifolia* were determined solely on the basis of chromatography against standards because of the small amount of plant material which was available.

### RESULTS

The flavonoids of *Jepsonia* are based upon the common flavonols kaempferol, quercetin, and myricetin (Table 1). All compounds are 3-O-glycosylated derivatives. The compounds indicated as "K-acyl" and "Q-acyl" are gallic acid esters of the corresponding kaempferol-3-O-glucoside and quercetin-3-O-glucoside. The quantities available were too small to allow detailed study but the derivatives have chromatographic characteristics and color test behavior identical to those of the flavonol-3-O-glucoside-6"-gallyl derivatives identified in *Tellima* (Collins et al., 1975) and *Heuchera* (Wilkins and Bohm, 1976a, and unpubl.). Gallotannins were shown to be present by chromatography and characteristic color reaction using ferricyanide reagent but very limited material precluded further study.

One population of *Jepsonia parryi* was sampled in the autumn and in the spring and both collections were chemically identical. The flavonoid profiles of these samples were identical although there were differences in the relative concentrations of the compounds. No significance can be attributed to this quantitative variation without extensive additional sampling of this species.

### DISCUSSION

Taxonomic opinion has been divided on the number of species of *Jepsonia*. The genus was considered to be monotypic by Jepson (1925, 1936) and Munz (1959) although its "polymorphous" nature was recognized by Munz (1959). At the other extreme Small and Rydberg (1905), Bacigalupi (1944) and Ornduff (1969) recognized three species. Ornduff (1969) based his taxonomic conclusions primarily on an array of morphological traits that separate the three species and on hybridizations among the species. He pointed out the importance of studying living material in the identification of species of *Jepsonia*.

We undertook study of the flavonoids of *Jepsonia* with the hope that

TABLE 1. FLAVONOIDS AND A GALLIC ACID DERIVATIVE OF JEPSONIA.

	<i>J.</i> <i>parryi</i>	<i>J.</i> <i>malvifolia</i> <sup>a</sup>	<i>J.</i> <i>heterandra</i>
Kaempferol-3-0-rhamnoside	+	+	-
Kaempferol-3-0-glucoside	+	+	+
Kaempferol-3-0-galactoside	trace	ND <sup>b</sup>	-
Quercetin-3-0-glucoside	+	+	+
Myricetin-3-0-glucoside	+	+	+
Kaempferol-3-0-rutinoside	+	+	+
Kaempferol-3-0-xylosylxyloside	+	+	+
Quercetin-3-0-rutinoside	+	+	+
Quercetin-3-0-xylosylxyloside	+	+	+
Kaempferol-acyl <sup>c</sup>	+	+	-
Quercetin-acyl <sup>c</sup>	+	+	-
Gallotannin test <sup>d</sup>	+	+	+

<sup>a</sup>) determined by comparative chromatography only.

<sup>b</sup>) ND = not determined.

<sup>c</sup>) kaempferol- and quercetin-3-0-glucoside-7"-gallate.

<sup>d</sup>) blue coloration with ferricyanide reagent.

additional characters of systematic value would be found that might shed light on the relationships among the species and of the genus (cf. Wilkins and Bohm, 1976a; Bohm and Wilkins, 1976). This study showed that there are very few differences among the species of *Jepsonia* in their flavonoid biochemistry. *Jepsonia parryi* and *J. malvifolia*, both occurring in southern California and Baja California, have an identical array of flavonoids. *Jepsonia heterandra* from the foothills of the central Sierra Nevada differs from these two species in that it lacks kaempferol-3-0-rhamnoside, kaempferol-3-0-galactoside and the 6"-0-gallyl derivative of the flavonol glucosides. Kaempferol-3-0-galactoside occurs only as a trace constituent of *J. parryi*; it was not sought in *J. malvifolia* due to lack of plant material.

Two types of gallic acid derivatives occur: the 6"-0-gallylated flavonol glucosides and an unidentified compound indicated only as positive "gallotannin test". The capacity to make gallic acid derivatives characterizes the genus; the nature of the derivatives appears to be useful in assessing relationships.

Despite the limited taxonomic value of the flavonoid differences within *Jepsonia* it is of interest that *J. parryi* and *J. malvifolia*, which have adjacent geographical ranges and show the largest degree of crossability (Ornduff, 1969), should exhibit identical pigment profiles.

Ornduff (1969) stated that, while *Jepsonia* has no close relatives in

the family, it may be allied with such genera as *Bolandra*, *Boykinia*, *Heuchera*, *Darmera* (*Peltiphyllum*), *Suksdorfia* and *Tellima*. Since detailed flavonoid data are available on all of these except *Bolandra*, some intergeneric comparisons are possible.

*Heuchera micrantha* Dougl. var. *diversifolia* (Ryd.) R. B. & L. and *H. cylindrica* Dougl. var. *glabella* (T. & G.) Wheelock possess exceedingly complex flavonoid mixtures; at least 60 compounds occur in the former and about 40 are known in the latter (Wilkins and Bohm, 1976a; and unpubl.). The major compounds are flavonols which exist in a wide variety of mono-, di-, and triglycosylated forms. The flavonols are kaempferol, quercetin, and myricetin but small quantities of the O-methylated flavonols isorhamnetin, larycitrin, and syringetin also occur. Both *Heuchera* species possess 6''-O-gallyl derivatives of kaempferol and quercetin glucosides, accumulate a small amount of the flavone luteolin, and have a variety of tannins.

*Tellima grandiflora* (Pursh) Dougl. has a simpler array of compounds but shares with *Heuchera* the ability to make gallylated flavonol derivatives. It does not have flavone derivatives. *Tellima* is the only genus of Saxifragaceae so far studied that produces 4'-O-glucosides (Collins and Bohm, 1974). It also has a complex array of tannins (Wilkins and Bohm, 1976b, c).

*Damera peltata* (Torr.) Voss also has fewer compounds than *Heuchera* although they share some flavonol mono- and diglycosides. Tannins are also present in *Darmera* but they appear to be simpler than those in *Heuchera* or *Tellima* (Bohm and Wilkins, 1976).

Preliminary study of *Suksdorfia ranunculifolia* (Hook.) Engl. (Bohm, unpubl.) showed a very simple array of flavonol mono-, di-, and triglycosides. Gallylated flavonol glycosides were not observed in *Darmera* or the one *Suksdorfia* species examined.

Finally, studies of *Boykinia* (Gornall and Bohm, unpubl.) show the presence of flavonols and flavones in roughly equal amounts. A moderately simple pattern of monoglycosides is present but the complex array of diglycosides is reminiscent of *Heuchera*. Gallylated flavonol glycosides do not appear to be present, but 6-hydroxylation and 3-O-methylation occur, which characters have been seen in the family so far only in *Chrysosplenium* (Bohm et al, 1977, and ref. cited therein).

As in all of the genera of Saxifragaceae whose flavonoid profiles have been studied to date, *Jepsonia* has a unique combination of compounds. However, the flavonols present and their glycosylated derivatives are clearly related to those found in other members of the family. *Jepsonia* most closely resembles *Darmera* in its flavonol glycosides *per se*. The presence of gallylated flavonol glycosides and other simple gallic acid derivatives in *Jepsonia* suggests possible relationships with the two tannin-producing genera studied to date: *Heuchera* and *Tellima*.

## ACKNOWLEDGMENTS

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STEPHANOMERIA MALHEURENSIS (COMPOSITAE),  
A NEW SPECIES FROM OREGON

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Evidence has been amassed that supports the hypothesis that the diploid annual plant informally referred to as "Malheurensis" in a series of publications (Gottlieb, 1973, 1974, 1977, 1978) has evolved from the population of *Stephanomeria exigua* ssp. *coronaria* (Greene) Gottlieb with which it is still biotically sympatric. The two taxa are morphologically extremely similar; however, they can be reliably distinguished by differences in achene length and weight. Reproductive isolation between them in nature appears complete and is maintained by three factors: (1) pollen movement is restricted by differences in breeding system; (2) there is a crossability factor(s) that reduces seed set from interspecific cross-pollinations compared to conspecific ones by about 50%; and (3) several differences in chromosomal structural arrangement exist, including a reciprocal translocation, which reduce fertility of  $F_1$  hybrids to 25% (Gottlieb, 1973). Consequently, it is appropriate to validate the new taxon as a species. It appears to be one of the very few examples of the recent natural origin of a diploid plant species.

***Stephanomeria malheurensis*** Gottlieb, sp. nov. Differt a *S. exigua* ssp. *coronaria* acheniis longioribus (plerumque 3.3–3.8 mm longis) et gravioribus (medie  $87.3 \pm 0.44$  mg per 100 achenia) pappi setis longioribus (plerumque 5–6 mm longis) et numerosioribus (9–12 vel –15).

TYPE: Oregon, Harney County, 27 mi S of Burns, between Mile Posts 25 and 26 on Highway 205, in parts of sections 11 and 12, T 27 S, R 30 E, Willamette Meridian, elevation 1524 m, 2 Jul 1975, *Gottlieb 750*, (Holotype, OSC; isotype, NY).

Distribution: Known only from the type locality, the top of a broad hill with soil derived from volcanic tuff in an area surrounded by basaltic soils. The locality has been designated a Scientific Study Site by the Bureau of Land Management, which has jurisdiction over the land, in order to preserve the species and to permit additional scientific research on it. The site, including approximately 160 acres, has been enclosed within a barbed-wire fence.

Plants annual; taproot with lateral branches often  $> 30$  cm long; the basal leaf rosette generally  $< 15$  cm in diameter at bolting; herbage glabrous; rosette leaves generally entire to pinnatifid, oblanceolate to spatulate; stem single, generally  $< 60$  cm long; branches averaging 23 in number; length of branch between adjacent heads averaging 1.9 cm; heads on short peduncles 5–15 mm long, often having shorter secondary peduncles also bearing heads; involucre cylindrical or oblong with a

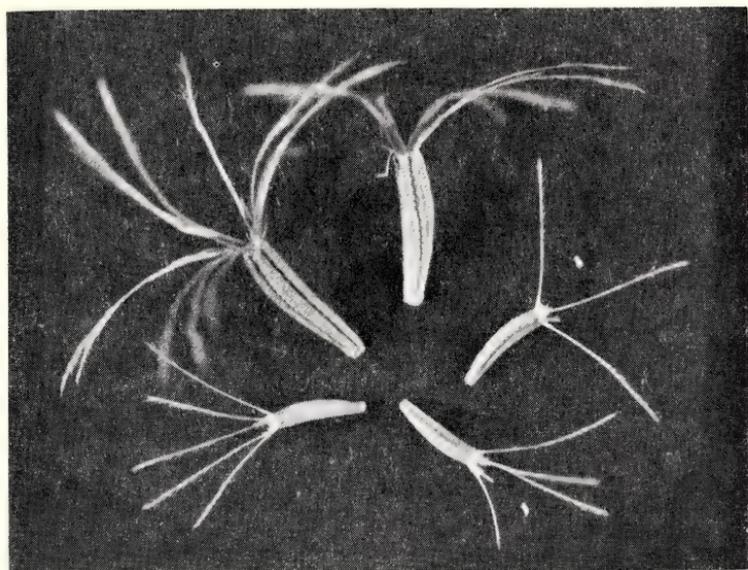


FIG. 1. Representative achenes of *Stephanomeria malheurensis* (large achenes) and *S. exigua* ssp. *coronaria* (small achenes).

series of equal-sized phyllaries averaging 8.0–9.5 mm long, equivalent in number to the number of florets, subtended by fewer appressed calyculate bractlets; florets 5–6 per head; ligules averaging 8.2–9.4 mm long and 3.2–3.6 mm wide, dark pink, pink, very light pink, white, or rarely orange-yellow; styles white or pink; anther apex most often dark pink, occasionally white; achenes tan or light brown, averaging 3.3–3.8 mm long, five-sided with a narrow longitudinal groove on each side, the surface generally rugose-tuberculate; pappus bristles generally 9–12 (–15) in number, thickened and often connate in groups of 2–4 at their bases, averaging 5–6 mm long, plumose on their distal 50–60%. Chromosome number,  $n = 8$ .

In addition to the differences in their achene sizes, *S. malheurensis* can be distinguished from *S. exigua* ssp. *coronaria* in the uniform garden in a number of quantitative characters including cotyledon length, number of branches per stem, length of internodes along the branches between adjacent heads, number of florets per head, and ligule length/width ratio (Gottlieb, 1973, 1977). They also differ in breeding system: *S. exigua* ssp. *coronaria* has a sporophytic self-incompatibility system that prevents self-pollen from germinating on stigmas of the same plant, making it an obligate outcrosser. *Stephanomeria malheurensis* is predominantly self-pollinating. Comparative information regarding variation in the electrophoretic mobilities of a sample of their enzymes, cytogenetic behavior

and fertility of interspecific hybrids, growth rates under different experimental conditions, phenotypic variability, phenotypic plasticity, and requirements for seed germination have been described in the previously cited publications.

#### ACKNOWLEDGMENTS

I thank Prof. Kenton L. Chambers for translating the species description into Latin and for reviewing the manuscript.

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## TAXONOMY OF AXINIPHYLLUM (ASTERACEAE-HELIANTHEAE)

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*Axiniphyllum* is a small herbaceous genus of four poorly known species of south-central Mexico (states of Guerrero and Oaxaca). It was erected by Bentham in 1872 to accommodate two rayless species, *A. corymbosum* and *A. tomentosum*, the former serving as the type for the genus. The latter species, however, had been described earlier under the name *Polymnia scabrum*; hence *Axiniphyllum scabrum* is the correct binomial for this taxon, as noted by Blake (1930).

I became interested in the genus through my efforts to position what appeared to be an unidentified *Rumfordia*. While it seemed close to *Axiniphyllum*, it possessed well-developed rays. *Rumfordia*, with well-defined ray florets, appeared more remote, except for the relatively recently proposed *R. pinnatisecta* (Wilson, 1958). The latter, however, seemed exceptional in *Rumfordia*, and careful comparisons of the 10 or more species of the latter genus and the two original species proposed by Bentham for *Axiniphyllum* have convinced me that Wilson erred in placing *R. pinnatisecta* in *Rumfordia*. *Rumfordia pinnatisecta* is much closer to *Axiniphyllum* and I have therefore transferred it to what I believe is its correct phyletic position, alongside the newly proposed *A. sagittalobum*.

As to the generic relationship of *Axiniphyllum*, Bentham (1872) noted that it was "in many respects allied to *Zaluzania* and *Sabazia*." The latter genus is readily distinguished by its white rays, more delicate habit, non-clasping leaves, style branches, etc.; in short, the similarity is presumably superficial. The same may be said for the alternate-leaved *Zaluzania* (Olsen, 1977); Bentham, presumably, was unduly influenced by the epappose achenes of both genera.

I would relate *Axiniphyllum* to *Rumfordia* as would Sanders (1977), primarily through the two radiate species proposed here and the herbaceous *R. alcortae* Rzedowski. The latter, in most of its major characters (involucre, achenes, and style branches), is like *Rumfordia* but approaches *Axiniphyllum* in its habit, leaf shape and inflorescence. The following key serves to distinguish the two genera:

- 1. Style branches narrowly linear, prominently pubescent on the abaxial surfaces; apical appendage elongate, conical, as long as or longer than the style branch width; ray achenes 4-sided, not conspicuously radially flattened; outermost (5-6) involucre bracts densely stipitate-glandular, similar in shape and texture to those which they subtend . . . . . *Axiniphyllum*.
- 1. Style branches linear, glabrous or merely papillose on the abaxial surface; apical appendage short, half or less as long as the style branch width; ray achenes radially flattened, usually prominently so; outermost bracts 5, sharply relexed, not densely stipitate-glandular, markedly different in texture and shape from those within . . . *Rumfordia*.

AXINIPHYLLUM Benth.

Perennial herbs up to 1 m tall. Leaves opposite, connate, the blades coarsely pubescent and variously lobed. Heads 1- several in loose corymbose panicles. Involucre bracts imbricate in 2-3 series, the outer coarsely pubescent or glandular. Receptacle nearly flat to short-conical, with well-developed, acute, scarious, 2-4 nerved paleae. Ray florets present or absent; when present, pistillate and fertile. Disk florets fertile with elongate, cylindrical, 5-lobed limbs. Anther sacs obtuse at the base, the apical appendages narrowly ovate to ovate-cuspidate. Style branches linear-subulate, markedly short, pubescent on the exterior surfaces, the appendages elongate-conical, pubescent. Achenes black, glabrous, epappose. Chromosome number unknown.

Type species: *Axiniphyllum corymbosum* Benth.

Key to Species

- 1. Heads without ray florets (2)
  - 2. Heads small, 8-10 mm high; outermost involucre bracts 5-7 mm long . . . . . 1. *A. corymbosum*
  - 2. Heads large, 15-20 mm high; outermost involucre bracts 15-25 mm long . . . . . 2. *A. scabrum*

## 1. Heads with ray florets (3)

3. Terminal lobe of leaf blade closely serrate, sagittate in outline; flowering heads 2–5, on ultimate peduncles 4–8 cm long  
 . . . . . 3. *A. sagittalobum*

3. Terminal lobe of leaf blade crenulate, variously shaped; flowering heads 6–30, on ultimate peduncles 2–3 cm long  
 . . . . . 4. *A. pinnatisectum*

## 1. AXINIPHYLLUM CORYMBOSUM Benth., Hook Icon. Pl. 12:17. 1872.

TYPE: MEXICO. OAXACA: "woods in the province of Oaxaca, at an elevation of 7500 feet", Sep 1840, *H. Galeotti 2089* (Holotype: K!).

Sparsely branched, perennial herbs up to 70 cm tall. Leaves sagittate, irregularly dentate or lobed to nearly entire, the petioles winged, auriculate, connate. Heads 8–10 mm high, arranged in a very loose corymbose panicle, the ultimate peduncles 2–5 cm long. Involucres 6–8 mm long, the bracts imbricate in 2–3 series, scabrous-pubescent to variously stipitate-glandular, often intermixed. Ray florets absent. Disk florets ca 40, fertile; corolla sparsely pubescent, ca 5 mm long; achenes epappose, glabrous, black, 4-sided, 2–3 mm long, ca 1 mm wide, the upper, broadest, portion quadroid in cross section.

DISTRIBUTION. Montane forests of south-central Mexico (Guerrero and Oaxaca) from 1800–2500 m, reportedly growing in the shade of

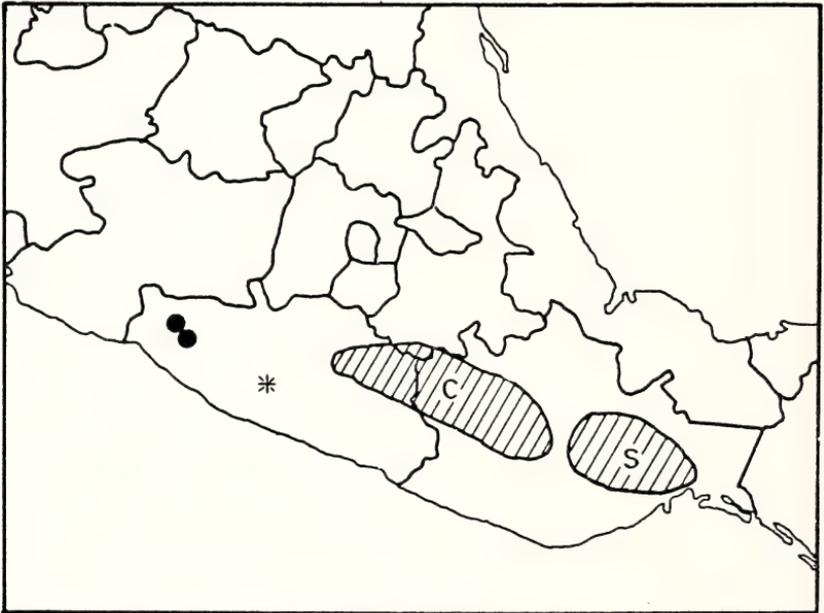


FIG. 1. Distribution of *Axiniphyllum* species: *A. corymbosum* (area surrounding C; *A. scabrum* (area surrounding S); *A. sagittalobum* (asterisk); *A. pinnatisectum* (dots).

oaks and pines as a "subherbacea anual geofita" (*Kruse 2666*), although the specimens concerned appear to have arisen from lignescent, perennial rootstocks. Sept.-Nov. (Fig. 1).

Additional specimens examined: MEXICO. GUERRERO: Mazatlán, cerro Alquitran, 7 Nov 1969, *Kruse 2666* (FM, US); without locality, *Sesse & Mociño "1490"* (fragment) also numbered "2825" (FM).

Bentham's description of the species was accompanied by a good drawing showing a somewhat more overly-pubescent corolla and a more congested inflorescence (because of the immature nature of the specimen) than is typical of the taxon. Mature achenes, as he noted, were lacking. However, in most other details, the few collections available to me match the holotype and drawings quite nicely, except for its reported annual habit, which is presumably an observational error to be attributed to the collector since this is so noted by appropriate symbol on his collection label. Galeotti also describes the corollas as "yellow & rosy" but recent collections by *Kruse (2666, FM, US)* describe the flowers as white, although in the dried state they appear to be somewhat on the yellow side.

2. *AXINIPHYLLUM SCABRUM* (Zucc.) Blake, *Contrib. U.S. Nat. Herb.* 26:248. 1930. *Polymnia scabra* Zucc., *Abh. Akad. Wiss. München* 1:313. 1832. TYPE: Grown in the Botanical Garden at Munich from seeds collected in Mexico by *Karwinsky s.n.*, 1829 (Holotype, M; isotypes, BM!, P; phototype US!).

*Polymnia aspera* Mart. ex DC., *Prodr.* 5:515. 1836 (Holotype, P). According to Blake, this name is based in part on portions of the above type, the specific epithet itself being a "slip of memory" on Martius' part, Zuccarini's earlier name having been intended.

*Axiniphyllum tomentosum* Benth., *Hook. Icon. Pl.* 12:17. 1872. TYPE: MEXICO: Without locality, 1846, *Bates s.n.* (Holotype, K; phototype US!).

Robust perennial herb up to 1 m tall. Leaves broadly sagittate, those at mid-stem as broad as or broader than long, scaberrimous above, densely canescent or tomentose beneath, irregularly dentate or lobed to nearly entire, the petioles winged, auriculate, connate. Heads 15–20 mm high, arranged in broad open corymbose panicles, the ultimate peduncles 1–7 cm long. Involucral bracts 2–3 seriate, densely stipitate-glandular, the 5 or 6 outermost bracts (15–25 mm long) equalling or exceeding the head proper, spreading or reflexed at maturity in the manner of *Rumfordia*. Ray florets absent. Disk florets numerous (50–80), fertile; corolla pubescent, 6–7 mm long, the limb abrupt, about twice as long as the tube; achenes epappose, 3–4 mm long, 1–2 mm wide, black, glabrous, 4-sided in cross section near the apex.

DISTRIBUTION. Known only from montane regions in the state of Oaxaca, Mexico, where it reportedly occurs in "weedy fields" and "shrubby slopes" in oak forest zones at about 2000 m. Aug-Nov. (Fig. 1).

Additional selected specimens examined: OAXACA: 11.5 mi N of Telixtlahuaca, 6 Nov 1966, *Anderson & Laskowski 4138* (FM, GH); 5 mi NE of Mexican Highway 190, near Oaxaca, 26 Aug 1965, *Breedlove 12202* (US); hills near Oaxaca, Aug 1894, *Pringle 4826* (FM); Sierra de San Felipe, 8 Sep 1894, *Smith 284* (FM, US).

This is a very distinct taxon, easily recognized by its large heads with prominent, often reflexed, outer involucre bracts. It is apparently relatively common in spite of its restricted distribution, being known by at least 10 separate collections from among the herbaria from which I borrowed.

3. *Axiniphyllum sagittalobum* Turner, sp. nov.

TYPE: MEXICO. GUERRERO: Districta Mina, Toro Muerte, 2800 m, 30 Oct 1939, *G. B. Hinton et al. 14761* (Holotype, LL; isotypes, MICH, NY, US).

Herbae perennae (?) ad 1 m altae caulibus saepe rigide erectibus unusquisque 2–5 capitata. Folia irregulariter lyrata vel repanda parte terminali sagittata irregulariter serrata utrinque pubescentia pilis brevibus crispatis. Pedunculi 5–8 cm longi stipitato-glandulares. Flores radiati 8, pistillati fructiferi ligulis "luteolis" ca 8 cm longis, 5–6 mm latis apice trilobatis. Flores disci ca 40 hermaphroditi fructiferi. Styli rami complanati linearis-lanceolati subtus pubescentes lineis stigmaticis infine bene evolutis sed apicem versus gradatim cum appendice terminali confluentibus. Achaenia uniformia nigra glabra pappis nullis.

Perennial (?) herb up to 1 m high, the stems mostly stiffly erect, glabrate and unbranched. Leaves opposite, connate, irregularly lyrate to repand, the terminal portion sagittate, irregularly serrate, pubescent on both sides with short, crisp, hairs, especially along the veins. Heads 2–5 to a stem, borne upon elongate stipitate-glandular peduncles, 5–8 cm long; involucre 2–3 seriate, the outermost whorls linear-lanceolate, densely stipitate-glandular, variously reflexed with age. Receptacle chaffy, puberulent, short-conical, knobby (with age). Ray florets 8, pistillate, fertile, "pale yellow", the ligules ca 8 mm long, 5–6 mm wide, 3-lobed at the apex; tube ca 2 mm long, densely pubescent with both glandular and nonglandular, uniseriate trichomes. Disk florets ca 40, perfect, fertile; corolla 5–6 mm long; tube ca 1.5 mm long, the limb abruptly ampliate, 5-lobed, sparsely pubescent. Style branches flat, linear lanceolate, pubescent beneath, the stigmatic lines well developed below but gradually merging into the acuminate appendage. Ray and disk achenes similar, falcate (the outermost) to clavate, black, glabrous, epappose.

DISTRIBUTION: Known only from the type collection.

The species is undoubtedly closely related to *Axiniphyllum pinnatisectum* but can be readily distinguished by its sagittate, markedly ser-



FIG. 2. Habit sketch of *Axiniphyllum pinnatisectum* ( $\times \frac{1}{2}$ ). Hinton 9756 (MICH).

rate, terminal leaf lobes, somewhat larger heads and more conspicuous outer involucre bracts. However, both of these taxa are too poorly represented in herbaria to speculate upon the constancy of these characters and additional collections showing populational intergradation might mark these as no more than varietally distinct. A wide range of pinnatifid leaf forms is found among the isotypes of this taxon but none approaches that found in *A. sagittalobum*.

4. ***Axiniphyllum pinnatisectum*** (P. G. Wilson) Turner, comb. nov. (Fig. 2). *Rumfordia pinnatisecta* P. G. Wilson, Kew Bull. 1958:164, 1958. TYPE: MEXICO. GUERRERO: Mina Dist., Aguazarca-File, pine forest, 30 Nov 1937, *Hinton et al.* 11289 (Holotype, K!; isotypes NY!, US!).

Perennial herb up to 1.5 m in height. Similar to *Axiniphyllum sagittalobum* but readily distinguished by the characters listed in the key to species.

DISTRIBUTION: Known only from the state of Guerrero where it reportedly occurs in pine forests at ca 2300 m elevation. Oct-Nov. (Fig. 1).

Additional specimens examined: GUERRERO: Dist. Mina, Armenia, pine forests, 2340 m, 23 Oct 1936, *Hinton et al.* 9756 (GH, NY, TEX, US).

Wilson presumably relegated this species to the genus *Rumfordia* largely because of its radiate heads. In most other characters, however, it is much closer to *Axiniphyllum corymbosum* and I find no hesitation in making the necessary transfer.

#### ACKNOWLEDGMENTS

This study is based upon material from the following herbaria: British Museum (BM), Field Museum (FM), Gray (GH), Kew Gardens (K), Lundell (LL), Univ. of Michigan (MICH), New York Botanical Garden (NY), Univ. of Texas (TEX) and the United States National Museum (US). My thanks to the directors for the loan of material. Dr. M. C. Johnston provided the Latin description, for which I am grateful. Supported in part by N.S.F. Grant 1013950.

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## NOTES AND NEWS

REDUCTION OF *GUNNERA KILIPIANA* TO SYNONYMY WITH *G. MEXICANA*.—The taxonomy of many plants has been obscured by poorly collected and poorly preserved material. The literature is replete with synonyms reflecting the tendency to multiply taxa needlessly when treating fragmentary or incomplete data. Those taxa inhabiting remote areas or possessing large, cumbersome organs are especially prone to such treatment. *Gunnera* L., a gigantic herb of the tropical montane cloud forest, usually placed in the Haloragaceae, has suffered much in this manner.

In the summer of 1912, J. A. Purpus collected *Gunnera* (Purpus 8568) in the Sierra Chiconquiaco above Misantla in Veracruz, Mexico. T. S. Brandegee named it a new species, *G. mexicana* Bdg., in 1922 (Brandegee, Univ. Cal. Publ. Bot. 12:181–188. 1922). C. L. Lundell studied material of *Gunnera* which Eizi Matuda (no. 2763) had collected from Volcán Tacaná in Chiapas in 1939 and found noticeable differences between it and Brandegee's published description. In 1940 he named the Matuda specimen *G. kilipiana* Lundell (Lundell, Phytologia 1:449–453. 1940).

After examining the collections of D. S. Barrington from the type locality of *G. mexicana* above Misantla where he collected in December, 1971, I was struck by the great similarity between his material and Lundell's type of *G. kilipiana* from Chiapas. I have since examined the 2 sheets of *G. mexicana* from the Gray Herbarium (both labeled "isotype") and the holotype from the University of California, Berkeley, and have examined living material of both in the field. I am convinced that Brandegee erred in his description and misled Lundell, who subsequently named a new species needlessly. *Gunnera kilipiana* is synonymous with *G. mexicana*.

The holotype of *G. mexicana* (UCB 206237) consists of a habit photograph, an inflorescence and a piece of a leaf folded like a fan into a rough triangle with a short stub of petiole at the narrowest end. The Gray Herbarium isotypes consist of similarly folded, but smaller pieces. Careful examination reveals that, by carefully matching cut edges, impressions of veins and decayed spots, all three pieces were once part of the same leaf (minus its petiole). Brandegee based his description on only the middle section of this single leaf.

Brandegee's error was never discovered. Inasmuch as the material Lundell had from Chiapas differed from Brandegee's description, he distinguished it from *G. mexicana*, noting that this, the only other Mexican species, was known to him from the brief original description only. He explained that his new species "apparently differs from *G. kilipiana* amply in its leaf form being *attenuate at the base* rather than deeply cordate" (my emphasis). The photograph was not mentioned.

Brandegee's published description states: "foliis . . . latitudine valde variabilibus, prope apicem usque ad 14 cm latis, ca. 32 cm longis in petiolum brevissimum gradatim angustatis . . .," and "This extralimital species differs from the generic description in the shape of the leaves. The leaves in circumscription are rounded at the top and *attenuate into a very short petiole*" (my emphasis).

This description could not apply to the *Gunnera* which Purpus collected if Brandegee had described whole leaves. Most *Gunnera* have cordate leaves; a few have peltate ones. Purpus easily recognized *Gunnera* in the field; this would have been unlikely if it had differed greatly from known species. From his journal of that trip he states: "Otra vez llegó el aguacero, tremendo; subiendo, al pasar encontramos totonacas que se protegían del agua con las hojas de la *Gunnera* y de un *Caladium*. Con tal motivo, tuve que acostarme para que mi ropa se secara . . ." (in Sousa Sanchez, Univ. Cal. Publ. Bot. 51:1–36. 1969).

If he had used it as an umbrella, as he says, it must like *Caladium* have had a long petiole. I have used it myself in this fashion, and without the petiole, it is useless. Purpus's photograph, attached to both the holotype and an isotype and published by Brandegee, shows perfectly round, deeply cordate leaves, raised and presumably supported by what must be long petioles.

The material from the type locality bears obovate or reniform leaves, moder-

ately lobed, with deeply cordate sinuses and long (exceeding 1 m) petioles. It resembles *G. insignis* (Oerst.) A. DC. from Costa Rica and Panama somewhat, and *G. kilipiana* very closely.

Further comparison of both types and material from the type locality of *G. mexicana* as well as additional material from central Chiapas and southwestern Guatemala shows great similarity in leaf surface features and inflorescence characters. Pubescence on the leaf surface is very similar to the above and much denser than that of the two other Central American species, *G. insignis* and *G. talamancana* Weber & Mora. Inflorescence characters, particularly in the thickness of the branches and the position, size and shape of their subtending bracts are also quite similar and consistent with synonymy.

I can find no real differences between material from the type locality for *G. mexicana* and Lundell's type. Lundell's description is a very good description of the Veracruz material. Since there can no longer be any conflict between Brandegee's and Lundell's short (58 and 28 word) descriptions, I can see no other alternative than to call them one species.

Even though Brandegee's description is based on fragmentary material and thus misleads, it is the earlier, and has priority, so *G. kilipiana* must be reduced to synonymy.

Material Studied: MEXICO: VERACRUZ: Sierra Chiconquiaco above Misantla, 26 Dec 1971, *Barrington 416a, 416b 417, 439* (GH); 18 Sep 1973, *Palkovic 767, 768, 769, 770, 771, 772, 773, 774, 775, 776, 777, 778, 779, 780* (GH); Jul 1912, *Purpus 8568* (UC holotype of *G. mexicana*, GH isotopes). CHIAPAS: Volcán Tacaná, 23 Mar 1939, *Matuda 2763* (GH, type of *G. kilipiana*).

This study represents a by-product of a dissertation completed at Harvard University under the supervision of Rolla M. Tryon with the support of NSF grants GB 27911 and GB 39866. I would also like to thank Drs. Richard M. Straw and Kenneth Wilson for their helpful reviews and comments.—LAWRENCE A. PALKOVIC, Department of Biology, California State University, Los Angeles, 90032.

FERNS OF THE NEW YORK MOUNTAINS, CALIFORNIA, WITH BIOGEOGRAPHIC COMMENTS.—Several chains of mountain ranges in the eastern Mojavo Desert are of particular biogeographic interest. The southernmost chain extends from the Granite Mountains through the Providence, Mid Hills, and New York Mountains to the northeast. North of the eastern part of this chain is another chain, comprising the Ivanpah, Mescal, and Clark Mountains. Still farther north is the Kingston Range, and finally, in adjacent Nevada, the very high Spring Mountains form the north end of this assemblage.

These mountains share several important features. They are high enough at their crests nearly or quite to emerge from the desert zone of the region. They regularly receive winter snow, and importantly, they generally intercept significant precipitation from the frequent late summer invasions of moist air from the Gulf of Mexico. This invests them with two rainy seasons, much like climatic regimens to the east. These ranges exhibit great tectonic complexity, and the array of exposed geological formations provides both chemical and physical edaphic diversity. Collectively, these ranges lie equidistant from ranges with comparable elevations to the east in Arizona (Cerbat and Hualapai Mountains) and to the southwest in California (Transverse Ranges).

These features favor a token intrusion of numerous biotic elements not otherwise a part of the fauna and flora of California. Particularly, plants and animals with ranges principally in the Arizona Uplands (Shreve, Publ. Carnegie Inst. Wash. 591:42-43, map 1. 1951) of the Sonoran Desert may reach California here. Also, some organisms with southern Rocky Mountain affinities and ranges across boreal Arizona form a part of this southeast California assemblage. This has been noted

briefly, without emphasis, for vertebrates by Johnson et al. (Univ. Cal. Publ. Zool. 48:248. 1948), for higher plants by Parish (Ecology 11:498. 1930) and most recently by Henrickson and Prigge (Madroño 23:164-168. 1975). There are a number of examples of similar distribution patterns known for invertebrates, chiefly insects, especially in the better known orders such as Lepidoptera (Emmel and Emmel, Los Angeles County Mus. Sci. Ser. 26:22-23, 46, 58, 60, 78, 84, 89. 1973; Ferguson, Moths of America North of Mexico 20.2A:133. 1971; MacNeill, unpubl.).

Recent collections of ferns from a section of the New York Mountains (California, San Bernardino Co.) reflect well the biogeographic patterns suggested by other segments of the flora and fauna. These collections have provided new records for the state and several additional records for this mountain range. Our observations further reaffirm that substrate strongly influences fern micro-distributions. Following is an annotated list of the species of ferns now known from the New York Mountains. Eight of the nine species of ferns recorded for the New York Mountains are rare or very uncommon in California as a whole and can be regarded as intrusive elements into California from the east (even though one, *Notholaena jonesii*, does extend westward to coastal counties). All eight occur in Arizona and generally southward or eastward, often much more commonly than in California.

Unless otherwise stated, collections are from the New York Mountains. Geological determinations have been provided through the kindness of B. C. Burchfiel, Rice University, and Pierina Nicholson, The Oakland Museum (here abbreviated OM).

*Polypodium hesperium* Maxon. 550 m NNE of New York Mt. Peak, 2130 m, MacNeill and Brophy 097510D11 (OM, UC), in shaded granite fissures and crevices;  $2n = 74$  II (voucher UC). Previously known in California from only a few collections in the Transverse Ranges. Records for *P. hesperium* from Placer Co. in the Sierra Nevada (Howell and Long, Four Seasons 3:8. 1970) and also northern California (see map in Lang, Madroño 20:58. 1969) require re-examination since Lang (Madroño 20:53-60. 1969; Madroño 21:235-254. 1971) and Lloyd (Fremontia 3:18-21. 1975) seem to imply that the diploid cytotype (*P. amorphum* Suksdorf) and the tetraploid cytotype (*P. hesperium*) are allopatric or nearly so south of British Columbia. *Polypodium amorphum* ranges south along the Cascade-Sierran axis to the central Sierra Nevada, where it is rare (Howell and Long, loc. cit.; reported as *P. montense* Lang). *Polypodium hesperium* evidently occurs along the intermountain face of the northern Cascades and extends south to Mexico along the Rocky Mountain system. It ranges west through Arizona and, unaccountably until now, is known from two stations in the Transverse Ranges of California. Our collection from the New York Mountains is tetraploid and lacks paraphyses and is thus not *P. amorphum*. The New York Mountain locality bridges the distributional gap between Arizona collections and those from western San Bernardino and Riverside Counties.

*Notholaena jonesii* Maxon. Keystone Basin, 1750 m, MacNeill and Smith s.n. (OM, UC), crevices of blue-gray limestone cliffs and boulders;  $2n = 54$  II (voucher UC). First collection from the New York Mountains. Previously known from scattered localities in southern California (including Providence and Clark Mts.), Utah, and Arizona. In Keystone Basin, this species was found associated only with the bluish-gray limestones of the Pennsylvanian Bird Spring Formation, most abundantly on a south-facing slope. On Clark Mountain we found this fern only upon a similar-appearing blue-gray limestone.

*Notholaena limitanea* Maxon var. *limitanea*. Keystone Basin, 1800 m, MacNeill 097512A2 (OM), s.n. (UC), 20 plants found in crevices of north-facing bluish-gray limestone of the Bird Spring Formation. First collections from California; previously recorded from southern Utah, Arizona, southern New Mexico, west Texas, Chihuahua, and Sonora, with an additional variety from southeastern Arizona and adjacent New Mexico to Hidalgo (Tryon, Contr. Gray Herb. 179:86. 1956).

*Cheilanthes feei* T. Moore. Keystone Basin, *MacNeill s.n.* (OM, UC), widespread throughout Keystone Basin from 1700 m to 2000 m in crevices of often north-facing limestone cliffs and boulders. Associated with both the bluish-gray and the white limestones of the Pennsylvanian Bird Spring Formation, but seemingly absent from a Triassic metamorphosed sandy limestone formation. A single plant was found on granite. Known from Texas to Iowa and west to Arizona, Nevada, British Columbia, Washington, and transmontane California in the Providence, New York, Clark, Panamint, and Inyo-White Mountains.

*Cheilanthes wootonii* Maxon. Keystone Basin, 1900 m, *MacNeill s.n.* (OM), bases of granitic outcrops under oaks. Found only among granitic rocks above 1825 m in Keystone Basin. Reported by Munz (op. cit.) from New York, Panamint, Inyo-White, and Providence Mountains in California, but we have seen specimens only from the two first-named ranges: New York Mts., Fourth of July Canyon, *Alexander and Kellogg 1411, 1412* (UC); Panamint Mts., *Munz 12571* (UC). Lloyd and Mitchell (A Flora of the White Mountains, California and Nevada. 1973) recorded it only as "to be expected" in the White Mountains. Otherwise known from Baja California, Sonora, Chihuahua, Arizona to Texas and north to Colorado and Oklahoma.

*Woodsia plummerae* Lemmon. Known from California only from a single ravine in Keystone Basin (Smith, Madroño 22:378. 1974); additional collections have now been made from the same locality (*Smith 673*, UC; *MacNeill s.n.*, UC). The species is found at 1900 m in soil at the base of north-facing granitic cliffs and boulders, often under the canopy of *Quercus chrysolepis*. Many of these plants show the characteristic forking or cresting of the blade apex mentioned for the species by Brown (Beih. Nova Hedwigia 6:106. 1964).

*Woodsia oregana* D. C. Eaton. Keystone Basin, 1900 m, *MacNeill s.n.* (OM), 097510D9 (UC), in soil at the base of granitic cliffs and boulders, generally well-shaded. Widespread throughout the higher elevations on intruded granite pluton that forms the crest of the range. In Keystone Canyon it grows with *W. plummerae* and in many other places on north-facing granitic slopes. The species ranges from British Columbia to Vermont in the north, south to New Mexico, Arizona and southern California. Nearly all records in California are transmontane. Howell and Long (op. cit., p. 9) cited only a single certain collection of this species from the southern Sierra Nevada.

*Pellaea truncata* Gooding (*P. longimucronata* of California and Arizona references; an illegitimate name, see Cronquist et al., Intermountain Flora 1:202, 1972). Keystone Basin, 1700 m, *MacNeill s.n.* (OM), mainly among granitic boulders and fissures in granite cliffs, but also frequent in a Jurassic formation of sheared volcanic and metamorphosed sedimentary rocks, and remarkably, the dominant fern (the only species found) throughout a formation of metamorphosed sandy limestone that may be Triassic. This latter formation seems not to support any of the several "limestone" ferns of the region. In the Keystone Basin area it ranges, on appropriate substrates, from 1600 m to 2150 m. It is rare on the Bird Spring limestones. Known with certainty in California only from the New York Mountains (also *Ferris and Bacigalupi 8076*, UC, *Alexander and Kellogg 1323a*, UC) and Providence Mountains (Pray, Amer. Fern J. 57:52-58. 1967). Its range beyond this part of California extends from Nevada to Colorado and Texas, Sonora, Arizona, and Baja California (Tryon, Ann. Missouri Bot. Gard. 44:155. 1957).

*Pellaea mucronata* D. C. Eaton. Fourth of July Canyon, *Alexander and Kellogg 1323*, pt. (UC). The locality cited is to the southwest of the region we sampled and is not far from a station in the Mid Hills (*Smith 682*, UC). This fern is also known from the Providence Mountains. It is very closely related to the preceding and, according to Pray (op. cit.), the two species hybridize in the eastern Mojave. *Pellaea mucronata* is one of several species that are much more prominent nearer the western margins of the desert regions. Indeed, this species is largely cismontane.

but does reach the desert, extending eastward barely into Nevada; it is not known from Arizona. *Pellaea mucronata* is here considered to be one of several "Californian" elements (discussed below) that extend eastward to meet elements from

Several additional ferns may ultimately be found in the New York Mountains. These fall into two categories: 1) those with distributions primarily to the south and east (Sonoran element); and 2) those with distributions in the eastern Mojave and Colorado Deserts and westward (Californian element). There are three such ferns in the first category:

*Notholaena cochisensis* Goodding occurs in limestone in the Providence Mountains and on a bluish limestone (much like that in Keystone Canyon) on Clark Mountain. It is to be expected on limestone in the New York Mountains but at elevations somewhat lower than the floor of Keystone Basin. Hevly (J. Ariz. Acad. Sci. 3:205-208. 1965) recognized this as a species separate from *N. sinuata* (Lag. ex Swartz) Kaulf., a distinction we support on morphological, geographical, and ecological grounds.

*Asplenium resiliens* Kunze has been reported recently in the Spring Mountains of Nevada (Fisher, Madroño 23:72. 1975), where it occurs on Navajo sandstone. The species may occur on shaded limestone or limey sandstone cliffs in other ranges of the eastern Mojave Desert at elevations somewhat below those of Keystone Basin.

*Cheilanthes fendleri* Hook. was reported from southern California by Cronquist et al. (Intermountain Flora 1:205. 1972), but Cronquist indicates (in litt.) that the inclusion of California was based on misidentified collections. Still, it is another Sonoran element that may occur in the eastern Mojave.

There are four ferns of the second category that may eventually be found in the New York Mountains. *Notholaena californica* D. C. Eaton and *Cheilanthes viscida* Davenport have not yet been recorded for the eastern Mojave ranges; they might be expected in the Granite Mountains. *Notholaena parryi* D. C. Eaton, a widespread fern of moderate elevations in the deserts, can be expected anywhere in the eastern Mojave ranges below 1550 m. We have seen specimens from the Providence Mountains (Bonanza Mine, Opler s.n., OM). *Cheilanthes covillei* Maxon has been collected in the Providence Mountains (Wolf 10688, UC) and may be present in the New York Mountains. This species is very closely related to *C. wootonii*. We expect all four species to be most prominent near the westernmost parts of the eastern Mojave ranges.—C. DON MACNEILL, The Oakland Museum, Oakland, CA 94607, WILLIAM BROPHY, Chabot College, Hayward, CA 94545, and ALAN R. SMITH, University Herbarium, Department of Botany, University of California, Berkeley, CA 94720.

DIPLOID CLAYTONIA PERFOLIATA FROM SOUTHERN MEXICO.—Prior studies of *Claytonia perfoliata* Willd. [*Montia perfoliata* (Willd.) T. Howell] (Miller, Syst. Bot. 1:20-34. 1976; Fellows, Madroño 23:296-297. 1976; Swanson, Ph.D. Dissertation, Univ. California, Berkeley, 1964) revealed two morphologically different diploids ( $2n = 12$ ), which were called "Channel Islands" or "Coastal" (referable to *C. perfoliata* ssp. *perfoliata*) and "Montane" [= *C. rubra* (T. Howell) Tidestrom]. These diploid species are easily distinguishable morphologically. The former is characterized by petals 3 to 4 mm long, linear juvenile basal leaves, deltoid mature basal leaves (with mucronate tips), green herbage, and a perfoliate to only slightly cleft cauline leaf disc. *Claytonia rubra* has petals similar in length to those of *C. perfoliata* ssp. *perfoliata*; and deltoid mature basal leaves. However, the juvenile leaves are never linear but instead are rhombic, and the cauline leaves are free or are united on only one side of the scape. As the name implies, *C. rubra* is characterized by livid beet-red foliage coloration, particularly on the abaxial leaf surfaces, although green-leaved morphs may be encountered in some populations.

Mexican populations at 3200 m on the slopes of Popocatepetl and 3000 m on Cerro Ajusco were examined cytologically ( $2n = 12$ ; México, Distrito Federal, Slopes of Cerro Ajusco, 2 km E of Estacion La Cima on Hwy. 95, *Miller 568*; Estado México: Slopes of Popocatepetl, 12.5 km E of Hwy. 115 junction on the road from Amecameca to Tlamacas, *Miller 570*; Slopes of Popocatepetl, 5.5 km W of Paso de Cortez on the road from Tlamacas to Amecameca, *Miller 571*; Municipio Amecameca, *Rodríguez 1460*). These populations are morphologically indistinguishable from diploid *C. perfoliata* ssp. *perfoliata* found in coastal California and on the Channel Islands. In contrast to *C. rubra*, which is common in drier northern montane and transmontane coniferous woodlands, diploid *C. perfoliata* ssp. *perfoliata* is more southern in distribution, ranging from coastal and cismontane California, through the Sonoran Desert, to high elevation coniferous forests of Mexico and Guatemala. Herbarium specimens examined from Durango, Queretaro, Hidalgo, Jalisco, Distrito Federal, Puebla, México, Morelos, and Cuesta El Caracol in Guatemala, indicate relative homogeneity of Mexican and Guatemalan populations, not only in their striking resemblance to the known diploid populations cited above but also in their elevational distribution and habitat preference.

Voucher specimens and permanent microslides for the chromosome counts reported here are deposited in OSC. Duplicate cytovouchers are deposited in CAS and ENCB. I am grateful to Dr. J. Rzedowski and Miss L. S. Rodríguez of the Escuela Nacional de Ciencias Biológicas for their help with field work and to the National Science Foundation for financial assistance (Doctoral Dissertation Research Grant DEB 76-06048).—JOHN M. MILLER, Department of Botany and Plant Pathology, Oregon State University, Corvallis 97331.

NOMENCLATRURAL CHANGES IN SPILANTHES, LYCOPERSICON, AND OPUNTIA FOR THE GALÁPAGOS ISLANDS.—Research on the endemic flora of the archipelago reveals that the following nomenclatural changes must be made:

(1). *Spilanthes diffusa* Hook. f. (Trans. Linn. Soc. London 20:214. 1847) is a later homonym of *S. diffusa* Poepp. & Endl. (Nov. Gen. Sp. Pl. 3:50. 1843). No other specific epithet being available for the former taxon, the following is proposed: ***Spilanthes darwinii*** D. M. Porter, *nomen novum* [Holotype: *Darwin*, end of Sept. 1835, Charles Island (CGE).].

(2). The widespread Galápagos tomato (*Lycopersicon cheesmanii* Riley) has long been recognized to consist of two infraspecific taxa, f. *cheesmanii* and f. *minor* (Hook. f.) Muller. However, recognition at a higher taxonomic rank is warranted, and the following combination is proposed: ***Lycopersicon cheesmanii*** var. ***minor*** (Hook. f.) D. M. Porter, *comb. nov.* [Basionym: *Lycopersicon esculentum* var. *minor* Hook. f., Trans. Linn. Soc. London 20:202. 1847. Holotype: *Darwin*, beg. of Oct. 1835, James Island (CGE).].

(3). ***Opuntia megasperma*** var. ***orientalis*** (J. T. Howell) D. M. Porter, *status novum* [Basionym: *O. megasperma* subsp. *orientalis* J. T. Howell, Proc. Calif. Acad. Sci., ser. 4, 21:48. 1933. Holotype: *Stewart 3003*, Hood Island (CAS).]. ***Opuntia echios*** var. ***gigantea*** (J. T. Howell) D. M. Porter, *status novum* [Basionym: *O. echios* subsp. *gigantea* J. T. Howell, op. cit. 51. 1933. Holotype: *Howell 9112*, Indefatigable Island (CAS).].

These two taxa inadvertently were included under the varietal rank in I. L. Wiggins and D. M. Porter's *Flora of the Galápagos Islands* (Stanford Univ. Press, Stanford, 1971) by E. F. Anderson and D. L. Walkington in their treatment of the Cactaceae, although new status was neither proposed nor effected. Recognition at the varietal level is desirable in order to conform with the classification of the genus in the archipelago. Where infraspecific taxa have been recognized in these species and in *O. galapageia* Hensl., they have been designated as varieties. Such trivial nomenclatural problems could be avoided if Raven, Shetler, and Taylor's "Proposals for the simplification of infraspecific terminology" (Taxon 23:828-831.

1974), which advocate recognition of a single infraspecific rank (subspecies), were incorporated into the *International Code of Botanical Nomenclature*.

A grant from the Penrose Fund of the American Philosophical Society which enabled me to examine Charles Darwin's Galápagos collections at Cambridge University and the Royal Botanic Gardens, Kew during the summer of 1976 is gratefully acknowledged.—DUNCAN M. PORTER, Department of Biology, Virginia Polytechnic Institute & State University, Blacksburg 24061.

**RARE TAXA IN THE LITERATURE.**—We were impressed while reading the July, 1977 issue of *Madroño* to note that three authors discussed three rare California taxa. However, we were equally impressed by the omission of any reference to the facts that these taxa are listed in the *Inventory of Rare and Endangered Vascular Plants* of the California Native Plant Society and that two of them are listed as candidates by the Office of Endangered Species, U.S. Fish and Wildlife Service, in the *Federal Register*. We respectfully submit that these omissions are serious oversights because presumably the authors have the best possible data concerning the status of the taxa they are studying relative to rarity and endangerment. Being very rare is a critical attribute of a plant possessing it.

As coordinators of the CNPS Rare Plant Project, we depend greatly upon the botanical community which includes you, the readers and writers of *Madroño* and similar publications. Please send your published and unpublished information about rare plants to either of us for use by the CNPS project.—W. ROBERT POWELL, Director, CNPS Rare Plant Inventory, Dept. of Agronomy and Range Science, Univ. of California, Davis 95616; and ALICE Q. HOWARD, Chair, CNPS Rare Plant Advisory Committee, Botany Herbarium, Univ. of California, Berkeley 94720.

**POLLEN SHED AS TETRADES BY PLANTS OF *ESCHSCHOLZIA CALIFORNICA* (PAPAVERACEAE).**—Mature pollen of *Eschscholzia*, and of the rest of the Papaveraceae, is normally shed from anthers as single grains (monads). In greenhouse-grown plants from two populations of *Eschscholzia californica* Cham. (*Clark 492*—California, Alameda Co.: ca. 2 mi SE of Livermore on S Livermore Rd, 24 May 1975; *Clark 503*—Butte Co.: Butte Canyon Rd, 0.9 mi E of junction with Manzanita Ave and Centennial Ave, 25 Jun 1975), I observed that pollen was shed not only as monads, but also as dyads, triads, and intact, generally tetrahedral tetrads. Individual plants of *Clark 492* present all monad pollen, or mixtures of monad, dyad, triad, and tetrad, or nearly all tetrad pollen. Of the two plants of *Clark 503* examined, one produced all monad pollen and the other a mixture of monad, dyad, triad, and tetrad pollen.

Scanning electron micrographs of intact pollen tetrads are presented in Fig. 1. Notice that individual grains are held together by bridges of pollen wall material. Sachar and Mohan Ram (Phytomorphology 8:114–124, 1958) state that "Wall formation [to form microspores] occurs by furrowing." In these populations furrowing evidently does not proceed to completion, leaving bridges of pollen wall and even cytoplasmic connections, which have been seen in light micrographs of pollen stained with cotton blue. Similar exine bridges have been reported in the Onagraceae (Skvarla *et al.*, Amer. J. Bot. 62:6–35, 1975) and in the fossil *Eomimosoidea* (Crepet & Dilcher, Amer. J. Bot. 64:714–725, 1977), but unlike those of *Eschscholzia*, their tetrads are also bound together at the margins of the apertures. Dyads and triads apparently result from furrowing which detaches only one or two grains from the tetrad.

Both populations have high pollen stainability in cotton blue; meiosis observed in *Clark 492* was normal. Tetrad pollen appears to be functional—pollen from an individual of *Clark 492* which sheds almost all tetrads was able to effect full seed set in other *E. californica* plants. The ability to form tetrads is evidently a heritable trait, appearing in F<sub>1</sub> progeny of crosses between *Clark 492* and other populations of *E. californica* and the closely related *E. mexicana* Greene, but appearing in none of

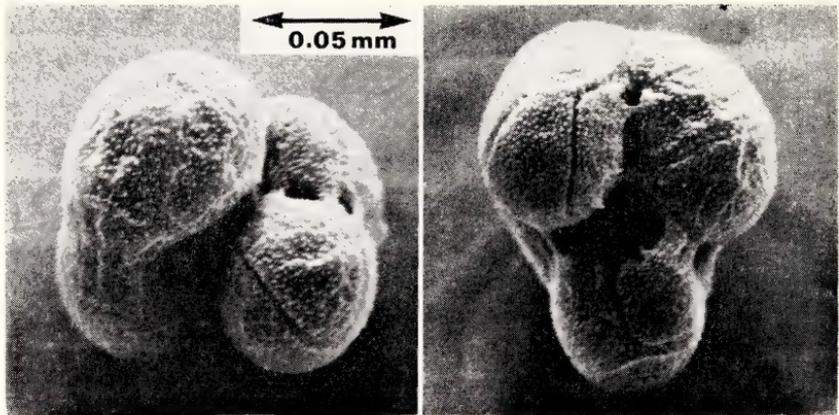


FIG. 1.—Scanning electron micrographs of tetrad pollen of *Eschscholzia californica*

over one hundred plants from 12 other populations of *E. californica* and their hybrids. However, the genetic basis of this inheritance cannot be estimated with the data available.

Examination of pollen of pressed voucher specimens of *Clark 492* (3 plants) and *Clark 503* (2 plants) and of flowers collected in April, 1977, from the approximate location of *Clark 492* revealed only monad pollen. Some greenhouse-grown plants of *Clark 492* present only monads, but it is somewhat surprising that there should be no evidence of tetrad pollen in the natural populations, since the trait is so common in their progeny. Perhaps these plants form tetrads in response to some condition of the greenhouse environment.

I wish to thank Judith A. Jernstedt for invaluable assistance with the scanning electron micrographs, and D. W. Kyhos for critical review of the manuscript. Pollen vouchers are deposited in the Department of Botany, University of California, Davis, and seeds for propagating the populations are available to interested investigators from the author.—CURTIS CLARK, Department of Botany, University of California, Davis 95616.

COMBINATIONS IN THE GENUS *ERIOGONUM* (POLYGONACEAE) NOT PROPERLY PROPOSED BY MUNZ IN "A FLORA OF SOUTHERN CALIFORNIA."—A few months after his death, "A Flora of Southern California" was published by the University of California Press (1974), and the final work and fitting tribute of Philip A. Munz was made available to his friends, colleagues, and to the people of California. He and I had collaborated on a treatment of the genus *Eriogonum* (Polygonaceae) for his "Supplement to A California Flora" (University of California Press, 1968), but as he wished to use the subspecific rank as his major infraspecific category in the 1974 book, I suggested he independently prepare the treatment and allow me to review it. This was done. I advised him in certain matters regarding the use of subspecies in *Eriogonum*, and he thereby avoided making some superfluous new combinations for taxa which occur beyond the limits of southern California. However, possibly through an oversight and no doubt aggregated by his illness, some of his proposed new combinations in the flora were not validly published in accordance with the International Code of Botanical Nomenclature, mainly because the basionym and its place of publication were not cited. I cannot take into consideration all of these various names, but as I communicated and talked with Dr. Munz on the names associated with *Eriogonum*, and knew his intentions, I feel the oversights can and should be corrected so that the names used in his flora are valid. Therefore the fol-

lowing combinations are made here: *Eriogonum kearneyi* Tidestr. ssp. *monoense* (S. Stokes) Munz ex Reveal, comb. nov., based on *E. nodosum* Small ssp. *monoense* S. Stokes, Leafl. W. Bot. 3:201. 1943; *E. spergulinum* A. Gray ssp. *reddingianum* (M. E. Jones) Munz ex Reveal, stat. nov., based on *Oxytheca reddingiana* M. E. Jones, Bull. Torrey Bot. Club 9:32. 1882. The first name was credited to Stokes by mistake, and in the second case the basionym was not cited. Several months before his death I called Dr. Munz and informed him that the type of *E. elatum* ssp. *glabrescens* S. Stokes was actually a specimen of *E. latens* Jeps., and that a new combination would be necessary. He agreed but apparently could not make the change for his Flora. The proper name, he concurred, would be as follows: *E. elatum* Dougl. ex Benth. ssp. *villosum* (Jeps.) Munz ex Reveal, stat. nov., based on *E. elatum* var. *villosum* Jeps., Fl. Calif. 1:421. 1913.

Supported by NSF Grant BMS75-13063.—JAMES L. REVEAL, Department of Botany, University of Maryland, College Park 20742; and National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

#### REVIEW

*The genus Epilobium (Onagraceae) in Australasia: a systematic and evolutionary study.* By PETER H. RAVEN and TAMRA ENGLEHORN RAVEN. With illustrations by Keith R. West. 321 pp. 1976. New Zealand Dept. of Scientific & Industrial Research Bulletin 216. Published by A. R. Shearer, Government Printer, Wellington, N.Z. \$20.00 NZ.

This sumptuous botanical monograph may be termed a labor of love both literally and figuratively: the authors who published on New Zealand *Epilobium* in 1971 as Raven and Englehorn are listed in 1976 as Raven and Raven. Although one hesitates to use the overworked word "mastpiece" for a taxonomic revision in the 20th century, this book with its superb illustrations (partly in color) by Keith West, attractive format, and meticulously detailed narrative harks back to the tradition of the great illustrated folio volumes by Hooker of the 19th century. The DSIR and the Government Printer merit applause from the botanical world for publishing a work of such exemplary merit.

The work consists of four chapters of discussion preceding a systematic treatment of the 50 species of *Epilobium* found in Australasia (mainly Australia, New Zealand, and New Guinea). The essay on crossing and ecological relationships published in 1972 (in Valentine, Taxonomy, Phytogeography, and Evolution) is here expanded to provide considerably more detail about the 45 native species.

The discussion of breeding systems in Australasian *Epilobium* owes a great deal to the work of the New Zealand botanist W. B. Brockie (1897-1972), who made over 900 crosses between the various taxa; the authors have appropriately dedicated the volume to his memory. Studies by the Ravens on the pollen fertility of Brockie's voucher specimens show that, in contrast to the Holarctic species of *Epilobium*, the Australasian ones readily form interspecific hybrids with a high degree of fertility. However, there is a surprising difference between the Australian species, which include a number of strongly outcrossing taxa, and the New Zealand species, which are predominantly (33 out of 37) autogamous. The authors regard the extraordinary radiation of *Epilobium* in New Zealand to be the result of extensive hybridization between sympatric populations that are kept apart by autogamous breeding systems and different habitat preferences (the latter graphically indicated in some detail).

An unusual feature of the Ravens' taxonomic interpretation of the New Zealand *Epilobiums* is their treatment of sympatric populations. No less than 40 of the 45 Australasian species occur sympatrically, and in New Zealand the Ravens found 9 or 10 taxa occurring together in the same local population! In a distinctly heterodox fashion, they have abandoned the conventional "subspecies displacement" rule, and

permit subspecies as well as species to have overlapping geographical distributions. This practice is counter to that followed by most taxonomists, who would treat sympatric variants as either distinct species or as simply genotypes in a variable population. To some extent, the situation in *Epilobium* may be unusual in that the large degree of microgeographic habitat variation in New Zealand can permit genetically miscible but strongly inbreeding taxa to maintain themselves as distinct. Then, too, as the authors candidly point out, there is an inherent degree of arbitrariness involved in assigning rank to these proteanly differentiated populations. In any event, researchers on other taxa might well reexamine the "sympatry rule" as it applies to closely related geographically overlapping taxa in regions both in and outside of New Zealand.

The phylogenetic model proposed by the authors involves a Holarctic origin of *Epilobium* and an invasion of Australasia in the Pliocene. The small comose seeds of *Epilobium* obviously "preadapt" the genus for long-distance dispersal, so that there is no difficulty in explaining the spread and differentiation of the genus within Australasia during the past 5-8 million years. The vagility of *Epilobium* is underscored by the Ravens' observation that 5 of the 9 Australian species also occur in New Zealand, and two of these species have made the crossing twice. In comparing occurrences of taxa in the region, one encounters one of the few deficiencies in this book: the lack of a table of the distributions. Since this can readily be extracted from the data, it is provided here (figures in parentheses indicate endemic species).

New Guinea & Moluccas	4 (3)	South Island	35 (11)
Australia	8 (0)	North & South I.	22 (9)
Tasmania	9 (1)	Chatham I.	12 (0)
New Zealand	36 (21)	Auckland/Campbell I.	4 (1)
North Island	23 (1)		

What is particularly striking about these figures is the low number of Australian native and endemic species and the very high number in the South Island of New Zealand. This seems especially anomalous in view of the fact that the Australian species, according to the Ravens, are the more primitive, and that New Zealand was invaded from Australia (and New Guinea). Evidently the autogamous but hybridizing breeding systems in the New Zealand taxa—as the authors suggest—have played a crucial role in adaptive response of the plants to the violent climatic fluctuations of the Pleistocene. Some curious aspects of these distribution patterns, in particular the notable focus of endemism in the South Island, still await explanation and may provide important clues to the Quaternary biogeographic history of the Australasian region.

Until speciation in other Australasian genera is analyzed as thoroughly as has been done for *Epilobium*, it will still be difficult to arrive at cogent generalizations regarding the recent phyletic history of the antipodal flora. In the meantime, this exemplary work of the Ravens will serve as a paradigm of the kind of study which needs to be done for a range of taxa with differing life forms and reproductive economies.—GRADY L. WEBSTER, Department of Botany, University of California, Davis 95616.

## BOOKS RECEIVED AND LITERATURE OF INTEREST

*Redwood national and state parks.* By DONALD F. ANTHROP. 70 pp. 1977. Nature-graph Publishers, Inc., Box 1075, Happy Camp, Cal. 96039. \$3.95 paper, \$7.95 cloth.

*An introduction to the botany of the major crop plants.* By A. M. M. BERRIE (ed.). x + 220 pp. 1977. Heyden & Son Ltd., Bellmawr, N. J. 08030.

*List of California herbaria and working collections 1977.* By THOMAS G. FULLER and G. DOUGLAS BARBE. California Dept. of Food & Agriculture, Div. Plant Industry—Botany Laboratory. 47 pp. This useful publication may be obtained free by writing to the Botany Laboratory at 1220 N Street, Room 340, Sacramento, Cal. 95841.

*Trees and shrubs of the United States: a bibliography for identification.* By E. L. LITTLE JR. and BARBARA H. HONKALA. U.S.D.A. For. Serv. Misc. Publ. 1336: 1-56. 1976.

*The flora of Canada.* By HOMER J. SCOGGAN. 4 vols., publication commencing in 1978. Available from the Museum of Natural Sciences of the National Museums of Canada as follows: Part 1 (General survey), 101 pp., 1978, \$11.00; Part 2 (Pteridophytes, Gymnosperms, and Monocotyledons), 460 pp., 1978, \$33.00; Parts 3 and 4 (Dicotyledons), c. 500, 575 pp., 1978, 1979. \$41.00, \$46.00.

*Vascular plants of British Columbia.* By ROY L. TAYLOR and BRUCE MACBRYDE. xxiv + 754 pp. 1977. Tech. Bull. 4, University of British Columbia Botanical Garden, Univ. Br. Col. Press. An interesting computer-generated checklist.

## REVIEWERS OF MANUSCRIPTS

The Editor of *Madroño* extends sincere thanks to the following persons who assisted as reviewers of manuscripts and in many other ways in connection with publication of Volume 24.—B.D.W.

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CALIFORNIA BOTANICAL SOCIETY

The California Botanical Society wishes to have an appropriate logo or emblem on brochures, official correspondence, etc. Persons with artistic ability are encouraged to submit a design (the theme need not be restricted to the Madroño, *Arbutus menziesii*) by 2 April 1978, to the address below. Designs should be simple and have a final size (after reduction) of approximately 7 by 7 or 7 by 10 cm. Designs will be evaluated by a panel of members of the Society; the winner will receive a \$25 prize and published recognition of his or her work. Good quality xerox copies of entries are acceptable, and none can be returned.—California Botanical Society, Dept. of Botany, Univ. of California, Berkeley, CA 94720.

ANNOUNCEMENT OF PROGRAM FOR MEETINGS OF  
THE CALIFORNIA BOTANICAL SOCIETY: SPRING, 1978

- Jan. 19. Dr. Eduardo Zeiger, Stanford U.  
How stomata respond to light: a new perspective.
- Feb. 8. Dr. Kenneth V. Thimann, U.C. Santa Cruz.  
Annual Banquet address: Some history of the study of plant growth and growth hormones. (Claremont Hotel, Berkeley).
- Mar. 16. Dr. Dan Cheatham, U.C. Berkeley.  
Floating down the River Amazon: a 400-mile journey from Iquitos, Peru to Leticia, Colombia.
- Apr. 20. Dr. Michael R. Mesler, Humboldt State U.  
The secret of subterranean sex of the Ophioglossaceae.
- May 18. Dr. Michael F. Baad, Sacramento State U.  
Adaptations of arctic vegetation.

All meetings held in Room 2003, Life Sciences Building, U.C. Berkeley, unless otherwise noted.

REPORT ON BOTANY GRADUATE STUDENT MEETING

On November 12–13, 1977, the Department of Botany, University of California, Berkeley, hosted the fourth annual Botany Graduate Student meeting, which is sponsored by the California Botanical Society. The meeting was attended by nearly 150 botany graduate students and professional botanists from California, Oregon and Washington. Graduate students presented papers on research projects in a wide range of botanical disciplines, including physiology, anatomy, morphology, mycology, phycology, pollination ecology, physiological ecology and systematics.

Each presentation was judged for content and presentation by a panel of graduate students. Robert N. Bowman, Botany Department, University of California, Davis, received an award of excellence for his paper titled "Phylogenetic implications from Cuticular Wax Analyses in *Epilobium canum* (section *Zauschneria*)."

The next Botany Graduate Student Meeting has been tentatively scheduled for Fall, 1978. Traditionally, the meetings have been hosted alternately by northern and southern schools, so a host for the 1978 meeting from the south or south-central area is being sought. Students or faculty of departments interested in hosting future meetings should contact L. R. Heckard, Department of Botany, University of California, Berkeley, 94720 (415-642-2465).—NANCY MORIN, Department of Botany, University of California, Berkeley, 94720.

Membership in the California Botanical Society is open to individuals (\$12.00 per year, regular; \$8.00 per year, student). Members of the Society receive MADROÑO free. Institutional subscriptions to MADROÑO are available (\$20.00 per year).

Back issues of Madroño are available at the following rates (some issues are out of print):

Vol. 1 (1916-1929) and Vol. 2 (1930-1934, each consisting of 17 numbers: \$1.50 per issue and \$25.50 per volume for members; \$3.00 per issue and \$51.00 per volume for institutions.

Vol. 3 (1935-1936) through Vol. 23 (1975-1976), each biennial, consisting of 8 numbers: \$3.00 per issue and \$24.00 per volume for members; \$5.00 per issue and \$40.00 per volume for institutions.

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Applications for membership (including dues), orders for subscriptions, requests for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the California Botanical Society, Inc., Department of Botany, University of California, Berkeley 94720.

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Short articles such as range extensions and other brief notes are published in condensed form under the heading "Notes and News". Authors of such articles should follow the format used in recent issues of MADROÑO.

Authors are allowed up to 10 pages per year without page charges; charge for additional pages is \$30.00 per page. Subject to approval by the Editors, articles may be published ahead of schedule, as additional pages of an issue, provided the author assumes complete costs of publication.





# MADRONÑO

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# MARITIME CHAPARRAL AND ENDEMIC SHRUBS OF THE MONTEREY BAY REGION, CALIFORNIA

JAMES R. GRIFFIN

Hastings Reservation, Carmel Valley, California 93924

Serious plant collecting started near Monterey in 1786, and the region's flora is now well known (Howitt and Howell, 1964, 1973; Thomas, 1961). Much has been written about the local manzanitas (Gankin, 1966, 1971; Hildreth, 1976; Hoover, 1964; Howell, 1952; Roof, 1961, 1964, 1976; Wells, 1968). The Monterey Peninsula closed-cone pine and cypress habitats as well as genetic and physiological features of conifers on these habitats have also been studied (Cannon, 1913; Duffield, 1951; Dunning, 1916; Forde, 1966; Lindsay, 1932; McDonald, 1959; McMillan, 1956; Vogl et al., 1977; Wolf, 1948). However, this knowledge about trees and shrubs is not matched by vegetative data, particularly for the maritime (or fog-belt) chaparral around Monterey Bay which has a conspicuous endemic element.

Chaparral patches dominated by endemic *Arctostaphylos* taxa along with *Adenostoma fasciculatum* appear locally within a coastal scrub-live oak forest-closed-cone conifer forest mosaic. Unfortunately, urban development is rapidly destroying this unique chaparral. For this reason, I surveyed species composition and relative dominance in the least disturbed maritime chaparral remnants between Larkin Valley, Santa Cruz County and Malpaso Creek, Monterey County (Fig. 1).

## METHODS

While surveying the Monterey Bay region for rare plants (Powell, 1974), I studied distributional patterns of six endemic shrubs (Table 1). That survey led to this project in which I sampled more carefully regions with major populations of one or more of the endemics (Fig. 1). Although the project did not specifically include *Ceanothus dentatus*, my sampling for the other endemic shrubs essentially covered the distribution of typical *C. dentatus*.

Between October 1975 and March 1977, 33 stands were analyzed with the Braun-Blanquet relevé method adapted from Muller-Dombois and Ellenberg (1974). Widespread disturbance in the maritime chaparral forced me to use stands with less than desirable homogeneity in aspect, slope, and soil depth. Relevés were placed in the least disturbed portions of each stand; a given stand covered several hectares. There was a total of 284 relevés, usually 6-10 per stand. All relevés were 10 m by 10 m squares. Cover-abundance ratings were assigned to all vascular plants on the first visit, and stands were revisited several times looking

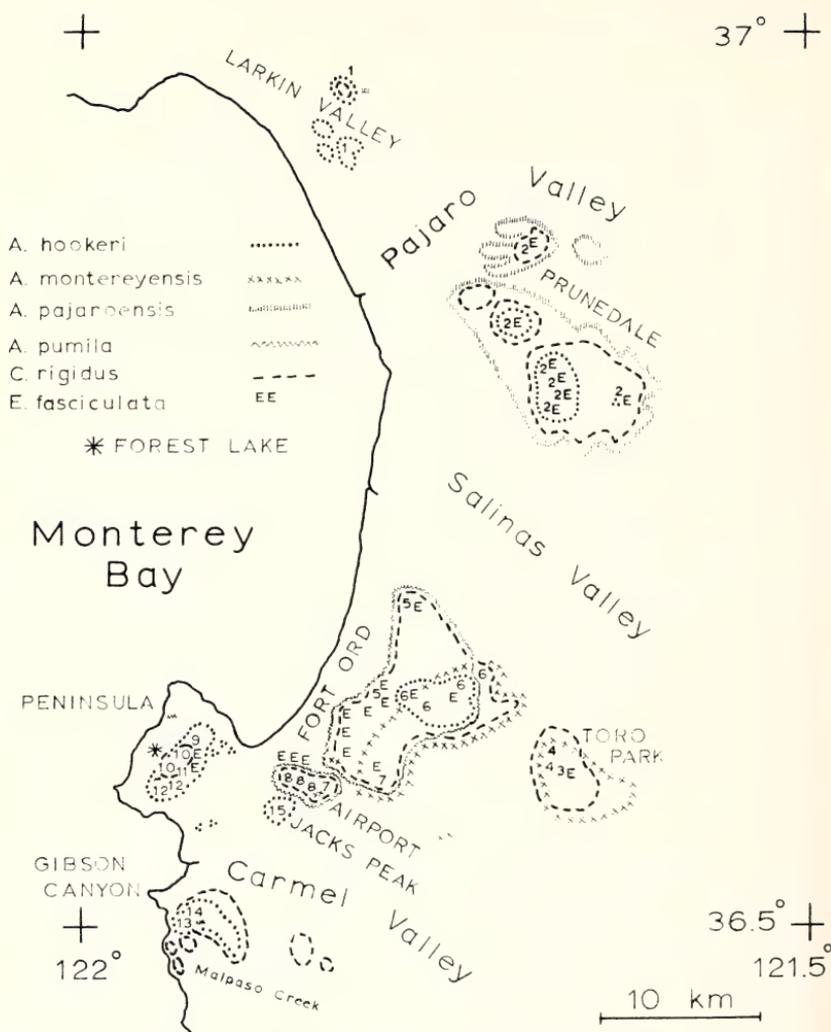


FIG. 1. Present distribution of six Monterey Bay endemic shrubs, extinct populations in urban areas not included; relative positions of the 33 sample stands indicated by the "locality" numerals.

for additional herbs and errors in cover estimates. Vouchers for most taxa are filed at the Pacific Grove Museum of Natural History; some particularly interesting specimens are at JEPS.

Dr. Dean W. Taylor produced an association table from the stand data by a modified algorithm method of Ceska and Roemer (1971). Stands with similar ranges of geological and topographic conditions were grouped into 15 "localities" for convenience of some analyses and discussion (Fig. 1, Table 2)

TABLE 1. SHRUB SPECIES WHICH IN TYPICAL FORM ARE ENDEMIC TO MONTEREY BAY; in some cases the differentiation between the Monterey taxon and related coastal taxa is controversial.

---

*Arctostaphylos hookeri* G. Don  
 Excluding ssp. *ravenii*, *A. franciscana*, and *A. hearstiorum*  
 (Hoover and Roof 1966, Roof 1976, Wells 1968)

*A. montereyensis* Hoover  
 THREATENED (Smith. Inst. 1974)

*A. pajaroensis* Adams (*A. andersonii* var. *pajaroensis* Adams ex McMinn)

*A. pumila* Nutt.  
 ENDANGERED (Dept. Int. 1976, Howell 1952, Roof 1961)

*Ceanothus dentatus* T. and G.  
 Excluding *C. hearstiorum* and intermediates with *C. foliosus* and *C. papillosus*  
 (Hoover and Roof 1966, McMinn 1961)

*C. rigidus* Nutt.  
 THREATENED, excluding *C. ramulosus*  
 (Hoover 1970, Nobs 1957, Smith 1976, Smith Inst. 1976, Thomas 1961)

*Ericameria fasciculata* (Eastw.) McBride (*Haplopappus eastwoodae* Hall)  
 ENDANGERED (Dept. Int. 1976)

---

TABLE 2. AVERAGE SEASONAL PRECIPITATION, AVERAGE SLOPE, ELEVATIONAL RANGE, DISTANCE INLAND, ESTIMATED ABSOLUTE TREE AND SHRUB COVER, AND AVERAGE NUMBER OF SPECIES PER RELEVÉ FOR MARITIME CHAPARRAL LOCALITIES.

Locality and (no. relevés)	Seas. prec.	Slope	Elev.	Dist.	Cover		Ave. no. sp./relevé
					Tree	Shrub	
	cm	%	m	km	%	%	
1 Larkin V.(20)	55	7	120-145	4-6	1	84	7.7
2 Prunedale(62)	52	17	75-160	9-14	2	85	8.2
3 Toro Park(10)		13	310	15	0	81	17.4
4 Toro Park(22)		27	230-290	15	0	79	5.2
5 Fort Ord(20)		11	60-150	6-11	2	84	10.0
6 Fort Ord(28)	35	2	45-140	3-4	0	85	10.4
7 Airport(17)		13	60-180	4-7	1	95	6.2
8 Airport(29)	31	7	75	2-4	7	77	11.0
9 Penin.(6)	42	38	210	3	35	54	11.0
10 Penin.(12)		13	120	3	11	84	15.7
11 Penin.(6)	46	9	105	2	20	68	15.0
12 Penin.(12)		7	120	2	40	82	15.5
13 Gib. C.(10)	53	11	105	1	8	63	7.7
14 Gib. C.(10)		26	150-210	1	0	90	8.2
15 Jacks P.(20)		24	170-210	5	1	83	3.3

---

## ENVIRONMENTAL FEATURES

*Climate.* Abundant precipitation data are available for the Monterey region. Marginal records for the city of Monterey go back to 1847, and reliable records started at Forest Lake in 1896 (Fig. 1). The Forest Lake 80-year seasonal average was 457 mm; the extreme low 191 mm, extreme high 855 mm. In 1957 the Meteorology Department at the U.S. Naval Postgraduate School, Monterey began compiling rainfall data from a network of over 40 stations around Monterey. Preliminary summaries from this unpublished data suggest large differences between study localities (Table 2). The 1975-76 season in which this project started was dry and most stations received about 50% of average rainfall. The airport had only 175 mm of rain in 1975-76.

All localities have summer drought moderated by fog. Quantitative data on amounts of fog are limited to the Monterey climatological station and the airport. Unpublished records at the Monterey station from 1963-76 averaged 135 foggy days per year. Monthly distribution of fog during the summer averaged:

	days with fog	hours fog/fog day
June	14	9
July	20	13
August	22	14
September	17	12

At the airport fog is most frequent at 0600, and it remains until 1000 on 25% of the days. Farther inland the fog dissipates sooner. Toro Park probably has the least summer fog, followed by Prunedale.

McDonald (1959) estimated fog drip at many Peninsula spots. Maximum drip during McDonald's superficial single-season study was recorded on Huckleberry Hill in the central Peninsula where 144 mm accumulated during a one-week period in August. I have observed wet spots on the ground under *Pinus radiata* trees in the same area on August mornings. But the major fog effect must be the widespread reduction of evaporative stress and not the localized addition of soil moisture. Most of the closed-cone forests and maritime chaparral stands do not have enough fog drip to wet the soil.

Temperature data for specific study localities are not available. From 1952-76 the Monterey climatological station had a mean annual temperature of 13.5° C. Average minimum and maximum for January, the coldest month, were 5.9° and 15.5° C; for September, the warmest month, 11.3° and 22.2° C. The daily extremes ranged from -5.0° to 38.3° C. Temperature fluctuations would be greater at the more inland localities.

*Geology and soils.* General geologic features of the study localities were shown by Jennings and Strand (1958). Youngest soil parent materials

are late Pleistocene dunes which blew off the Monterey Bay shore. These stabilized "pre-Flandrian" dunes extend from near Larkin Valley south across Fort Ord to the airport (Cooper, 1967). Chaparral covered soils on the dunes were mapped as Baywood sand; a few spots might be Océano loamy sand (Soil Cons. Serv., 1975).

The loosely consolidated "red sand" beds of the mid-Pleistocene Aromas formation (Allen, 1946) are important to this project; 60% of the relevés were either directly on this material or on a thin layer of pre-Flandrian sand over Aromas sandstone. Aromas sandstone extends from Larkin Valley through the Prunedale hills and Fort Ord to the airport. Aromas sandstone underlies the pre-Flandrian dunes at Fort Ord and the airport (Bowen, 1966). The Monterey County chaparral soils on Aromas sandstone were mapped as Arnold loamy sand (Soil Cons. Serv., 1975). Storie et al. (1944) mapped the chaparral soils near Larkin Valley as Moro Cojo loamy sand, which is now synonymous with Arnold series in Monterey County.

The lower portion of Toro Park lies on Plio-Pleistocene Paso Robles formation sand and gravel deposits (Bowen, 1966). Aromas formation was not mapped at Toro Park, but one sandy swale in the Paso Robles sediment area resembles Aromas sand. In fact, the chaparral soils on Paso Robles formation were also mapped as Arnold loamy sand (Soil Cons. Serv., 1975). The upper Toro Park slopes are on garnetiferous quartz monzonite (Ross, 1977); chaparral soils on these granitics were mapped as Cieneba fine gravelly sandy loam.

The basement rocks of the Peninsula and Gibson Canyon are porphyritic granodiorite (Ross, 1977). During the Pleistocene a series of marine terraces were cut into these granitics (Bowen, 1966; Hart, 1966). The Peninsula localities were either on these terrace sands or the adjacent granitics from which the terrace deposits have been eroded away. Granitic soils with chaparral were mapped as Sheridan sandy loam; soils on the terrace deposits were Narlon fine sand and often have a strong claypan. (Soil Cons. Serv., 1975).

Gibson Creek drains a granitic basin and crosses a small area of Paleocene Carmelo formation conglomerate-sandstone (Bowen, 1966). Terrace deposits must have been eroded off the lower slopes here, for all the relevés had rounded cobbles scattered on the granitic outcrops. The granitic slopes with chaparral were mapped as Cieneba fine gravelly sandy loam (Soil Cons. Serv., 1975). Soils on the Carmelo formation were mapped as San Andreas fine sandy loam; however, so much rock outcrops that there is no "soil" in an agricultural context.

I found maritime chaparral on shale only near Jacks Peak Regional Park within an area mapped as upper Miocene Aquajito shale (Bowen, 1966). Soils on the shale have been described as Santa Lucia shaly clay loam (Soil Cons. Serv., 1975), but there are some sandstone strata within the shale beds with sandy loam soils.

## REGIONAL VEGETATION PATTERNS

The unpublished maps and notes of the Vegetation Type Map (VTM) survey for quadrangles 105 A,B,C,D and 106 B are important vegetation descriptions. Colwell (1977) discussed the background of this old survey. Field maps and rough type descriptions were completed between 1930 and 1934.

The study localities are associated with a gap in the Coast Range ridge and there is also a gap in well developed coastal forests here. Redwood forest in the Santa Cruz Mountains grew south to Larkin Valley prior to logging (Gordon, 1974), and scattered *Sequoia sempervirens* trees still grow near the Larkin Valley locality. Redwoods are absent across the lowland, and the northern outpost of the Santa Lucia Range redwood forest is on San Jose Creek near Gibson Creek.

*Closed-cone conifer forest.* The Monterey and Point Lobos Peninsulas lie at the southern end of the lowland and are covered with closed-cone conifer stands. These stands, which include two pine and two cypress species, are more extensive and better developed than the other disjunct closed-cone communities along the central California coast (Vogl et al., 1977). Conifer stands relevant to maritime chaparral are *Pinus radiata* woodland, *P. muricata* woodland, *P. muricata-Cupressus goveniana* dwarfed woodland, and *C. goveniana* dwarfed woodland. *Pinus radiata* local distribution occurs between the airport, where the dunes meet the steeper Peninsula hills, and Malpaso Creek to the south. Within this range the woodlands with chaparral understories are mostly associated with poorly drained Narlon clay-pans or very rocky soils.

*Live oak forest.* Depauperate forms of mixed hardwood forest (Sawyer et al., 1977) occur on north slopes and well-drained canyon bottoms across the Monterey Bay lowland. *Arbutus menziesii* is rare and *Lithocarpus densiflorus* is absent from these forests; *Quercus agrifolia* is the only dominant tree. These live oak stands differ little from live oak communities in other central coast lowlands. The live oak stands are better developed in the Prunedale hills than in the Fort Ord area. On the Peninsula, live oaks shift to a subdominant position in the *P. radiata* communities. Oaks are negligible in the dwarfed conifer woodlands.

*Chaparral.* Typical chaparral does not approach the coast closely on shale, but maritime chaparral penetrates well into the scrub zone on the sandhills. Cooper (1922) noted that Monterey Bay chaparral had a high species diversity, and he considered *Ceanothus rigidus*, *Arctostaphylos hookeri*, *A. pumila*, and a form of *A. tomentosa* (*A. vestita* Eastw.) as endemic to Monterey. Shreve (1927) discussed five types of chaparral in the Santa Lucia Range. His comments relating to Monterey Bay chaparral were: "*Adenostoma* type" was uncommon within 5 km of the coast;

"*Arctostaphylos* type" with *A. tomentosa* was common only along the coast, and near Monterey other manzanitas were added to it; "mixed coastal type" had much *Toxicodendron diversilobum* and scattered *Salvia mellifera* and *Ericameria ericoides* in it.

Near Larkin Valley *Arctostaphylos tomentosa* ssp. *crinita* dominates a tall chaparral. To the south less typical forms of this Santa Cruz Mountains taxon are rare on Fort Ord and the Peninsula. The VTM survey mapped a xeric phase of the ssp. *crinita* chaparral near Larkin Valley which included *A. hookeri* as a local dominant. In areas transitional to woodland, shrubs such as *Corylus cornuta* and *Ceanothus thrysiflorus* intermingle with the manzanitas. These thickets are similar to Shreve's (1927) "*Ceanothus* type" of chaparral. The *Corylus* is absent to the south except for a few shrubs near Prunedale.

In the Prunedale hills the VTM survey recognized two chaparral types—a dwarfed "chamise" type and a mixed "chaparral" type. The latter had *Arctostaphylos pajaroensis* and *A. tomentosa* ssp. *crustacea* as important elements. Both types, which were in the foggy zone, were distinguished from a widespread inland non-foggy type. The VTM survey noted that *Ceanothus rigidus* was widely scattered near Prunedale and was favored by occasional fires. Davis (1972) studied the structure of 11 *A. pajaroensis* stands in detail.

Fort Ord chaparral has strong similarities to Prunedale chaparral even though *A. pajaroensis* is absent. Several forms of *A. tomentosa* grow at Fort Ord, and *A. montereyensis* and *A. pumila* are locally important. Critchfield (1971) published a VTM profile transect across the Peninsula that included one corner of Fort Ord.

The Toro Park region has chaparral covering several thousand hectares of steeper terrain rising to 700 m. From a distance this brushland appears to be typical chaparral, and the VTM survey mapped it all as "*Adenostoma* type". However, endemic shrubs are locally common along with scrub species. The endemic shrubs have not been reported farther inland than Toro Park. The Toro Park chaparral is separated from Fort Ord chaparral by a zone of grassland and savanna on Santa Ynez clay-pan soils (Soil Cons. Serv., 1975).

Maritime chaparral with Monterey endemics does not continue far to the south of Malpaso Creek. Another endemic *Arctostaphylos edmundsii* starts a few kilometers farther south, but this coastal bluff manzanita does not seem to have as close an ecological connection with the sandhills as do the other endemic shrubs. *Ceanothus rigidus* is scattered into typical chaparral east of Gibson Creek, and the VTM survey mapped it as a minor chaparral component 8 km inland. *Ceanothus rigidus* appears in less typical form as far south as Big Sur. To the south *Ceanothus dentata* merges into *C. papillosus*.

*Coastal scrub.* Scrub types have a greater continuity across the lowland than either chaparral or live oak forest. To the lee of the active dunes wind-pruned scrub was almost continuous prior to agricultural development. Farther inland scrub is more conspicuous on shale than on the sandhills. Elements of both the northern coastal scrub (Heady et al., 1977) and coastal sage scrub (Mooney, 1977) are included. Shreve (1927) noted that *Artemisia californica*, *Salvia mellifera*, *Ericameria ericoides*, and shrubby *Lupinus* spp. were important in the "xerophytic scrub" near Monterey. He was impressed with the dense stands of *E. ericoides* along the coast, and he noted that this shrub extended inland on sandy soils. The VTM survey made similar observations.

At low elevations the VTM survey often mapped *Artemisia californica* as a dominant on south-facing slopes. Higher on the slopes or on north aspects *Baccharis pilularis* was important along with *Toxicodendron diversilobum*, *Mimulus aurantiacus*, and *Rubus vitifolius*. On the VTM maps *Salvia mellifera* was often shown as a minor associate of the chaparral species.

#### MARITIME CHAPARRAL STRUCTURE

*Tree stratum.* Pine stands around Monterey have gone through several generations since the Spanish came, and current urbanization makes it impossible to determine the density of "natural" stands. The present pine woodland on most of the Peninsula localities regenerated after a severe fire in 1901, and woodcutters have lightly thinned some stands in recent times. The scattered pines at the Airport are younger, mostly less than 50 years old. In any case, endemic shrubs currently grow under the more open pine woodlands; tree canopy did not exceed 40% cover on the relevés. These shrubs are also absent under the remaining examples of closed-canopy, rapidly growing pine forest.

The non-conifer localities all had live oak forest nearby, but on my relevés *Quercus agrifolia* consisted of tall shrubs or scattered small trees. Live oaks grew on only 24% of the relevés and seldom formed more than 5% cover. Some live oaks in the pine localities may become medium-sized trees in time, but the scrubby oaks on the exposed sandstone ridges show little sign of forming real trees. Several early naturalists commented on the low stature of live oaks on the sandhills.

*Shrub stratum.* Collectively the relevés had 31 shrub taxa. The sandy locality at Toro Park had the greatest shrub diversity with 15 shrub taxa; one relevé there had 11 shrub species. In contrast, the adjacent Toro Park locality with shallower, less sandy soils had many relevés with only two shrub species. Climate, cultural history, and recent fire history were the same for both localities. One Jacks Peak relevé had only a single shrub species; Jacks Peak was the only locality involving shale parent

TABLE 3. RELATIVE DOMINANCE OF COMMON SHRUBS IN MARITIME CHAPARRAL AS EXPRESSED IN PERCENTAGE OF RELEVÉS IN COVER-ABUNDANCE CLASSES AND THE PERCENT OF ALL RELEVÉS WHICH CONTAINED EACH SPECIES (CONSTANCY)

	R	+	Cover-abundance class					Constancy
			1	2	3	4	5	
			%					%
<b>SCLEROPHYLLS</b>								
<i>Arctostaphylos tomentosa</i>		1	7	27	33	12	2	82
<i>Adenostoma fasciculatum</i>		6	20	28	15	8	1	78
<i>Arctostaphylos hookeri</i>		1	7	12	16	5	2	43
<i>Ceanothus rigidus</i>		5	18	9	3			35
<i>Arctostaphylos pumila</i>		1	3	3	6	6	3	22
<i>Arctostaphylos pajaroensis</i>				1	8	8	5	22
<i>Heteromeles arbutifolia</i>	1	3	11	3				18
<i>Arctostaphylos montereyensis</i>		1	4	6	4	1		16
<b>NON-SCLEROPHYLLS</b>								
<i>Salvia mellifera</i>		2	5	20	16	1		44
<i>Mimulus aurantiacus</i>		1	21	20	1			43
<i>Baccharis pilularis</i>		3	9	11	4			27
<i>Ericameria fasciculata</i>		2	7	11				20
<i>Toxicodendron diversilobum</i>		2	7	8	2			19
<i>Ericameria ericoides</i>		3	7	2				12

materials. No introduced shrubs grew on the relevés, but *Cytisus monspessulanus* was common on seriously disturbed sites near several stands.

Average absolute shrub cover for all localities was 80% (Table 2), and only 6 of 284 relevés had less than 50% shrub cover. Sclerophylls usually dominated over scrub species (Table 3). Collectively the scrub species probably did not exceed 25% cover on any relevé, and single scrub species seldom had more than 5% cover (Table 3).

The height and density of the chaparral varied considerably within stands. On parts of the most exposed ridges old-growth chaparral was less than 1 m tall with bare spots between shrubs. Such low chaparral included similar looking dwarfed *Adenostoma fasciculatum*-*Arctostaphylos hookeri* patches on granitic, Aromas sandstone, and shale outcrops. On adjacent slopes with deeper soils the manzanitas were often impenetrably dense and over 3 m tall. I found some *A. montereyensis* shrubs about 6 m tall on Fort Ord, and Davis (1972) reported *A. pajaroensis* up to 7 m tall near Prunedale.

Every relevé had at least one manzanita species; some had three. The burl-forming *Arctostaphylos tomentosa* complex (Wells, 1968) was the most widespread and dominant shrub studied (Tables 3, 4). In localities with *A. tomentosa* ssp. *tomentosa* the tomentose twig, tomentose leaf f.

TABLE 4. GEOGRAPHIC TRENDS IN DOMINANCE EXPRESSED BY CONSTANCY/MODAL COVER-ABUNDANCE CLASS FOR SELECTED WOODY SPECIES AT EACH LOCALITY.

Locality	Arct. tome. tome.	Arct. tome. crus.	Arct. tome. crin.	Aden. fasc.	Cean. rigi.	Eric. fasc.	Arct. hook.	Arct. pumi.	Arct. mont.	Arct. paja.	Pinus radi.	Cupr. gove.
1 Larkin V.			95/3	80/1	10/2		100/3					
2 Prune.		60/3		56/1	32/1	11/+	44/3			100/4		
3 Toro P.		18/1		100/4	18/1				64/2			
4 Toro P.		90/3		90/3	50/1	100/1			80/2			
5 Fort O.	57/3	39/3		89/2	75/2	46/1	21/1	36/3	61/1			
6 Fort O.	100/3			100/3	55/2	50/1		65/1				
7 Airport	100/4			88/2	35/+	12/1		65/3	56/3		62/2	
8 Airport	93/2			79/1	38/1	38/1		100/4				
9 Penin.	83/2			50/2			100/3				100/3	
10 Penin.	100/3			100/2	92/1		100/3				92/1	25/1
11 Penin.	100/4			67/+	50/1	83/+	100/2				17/1	17/2
12 Penin	100/2						100/4				100/3	17/3
13 Gib. C.	90/2			100/2			90/2				10/1	100/2
14 Gib. C.	100/4.			100/3	50/1		80/1	20/2				
15 Jacks P.	95/2			95/2			80/3				15/1	

*tomentosa* was most common; the glandular-setose twig, tomentose leaf f. *trichoclada* was uncommon; the glabrescent f. *hebeclada* did not appear on the relevés. An undescribed setose twig, glabrous leaf form was conspicuous near Jacks Peak. Although it becomes locally common south of Gibson Canyon, ssp. *rosei* was not on or near the localities.

*Adenostoma fasciculatum* was the only conventional chaparral species that was widespread and important in the maritime chaparral (Tables 3, 4), but it exceeded 50% cover only in Toro Park. A number of sclerophyll shrubs with broad distributions elsewhere were present in the maritime chaparral in minor amounts: *Ceanothus papillosus*, *Dendromecon rigida*, *Garrya elliptica*, *Lepechinia calycina*, *Pickeringia montana*, *Quercus wislizenii*, *Rhamnus californica*, and *R. crocea*.

*Salvia mellifera* and *Mimulus aurantiacus* were the most important scrub species. *Salvia* was absent in the pine woodland stands; *Mimulus* was present everywhere but was most vigorous in the pine woodland. *Artemisia californica* grew near several stands but did not appear on any relevé.

*Herb stratum*. The herb flora did not develop fully during the 1975-76 drought; only some 80 species were identifiable. The most diverse herb flora was under the pine woodland on the Peninsula and the sandy locality at Toro Park. One relevé on the Peninsula had 16 herb species; one at Toro Park had 13. The most widespread herb was *Carex brevicaulis* which grew in 13 localities but with a cover usually less than 1%. *Eriophyllum confertiflorum*, *Gnaphalium californicum*, and *Zygadenus fremontii* were also common in low densities. None of the herbs reached significant cover in any stand. The rhizomatous grass *Agrostis hallii* was the only herb to have 100% constancy in any stand and over 5% cover.

Introduced species were inconspicuous in intact maritime chaparral. *Aira caryophylla* and *Vulpia myuros* were most common in sandy openings at the airport, but they still had less than 1% cover. Only a few annual *Bromus* spp. plants were present. On disturbed spots adjacent to several stands *Carpobrotus edulis* and *Cortaderia jubata* were serious invaders.

*Species Groups*. Since my sampling was biased towards stands containing endemic shrubs, classification of regional vegetation types is inappropriate from this data. However, the association table derived from the maritime chaparral data does reveal several associative tendencies worth mentioning.

The most conspicuous group of associated species grew on the Peninsula stands. Differential species in this closed-cone forest species group in addition to the pines and cypress included: *Vaccinium ovatum*, *Agrostis hallii*, *Sanicula laciniata*, *Achillea borealis* ssp. *californica*, and *Iris douglasiana*.

Several species groups were rare on the Peninsula and grew on either the pre-Flandrian dunes, the Aromas sandstone hills, or some combination of the two sandy habitats. An airport-Fort Ord group included *Ceanothus dentatus*, *Arctostaphylos pumila*, *Ericameria ericoides*, and *Corethrogyne flaginifolia*. A more widespread airport-Fort Ord-Prunedale group had *Lotus scoparius*, *Ericameria fasciculata*, *Helianthemum scoparium*, and *Horkelia cuneata*.

A group of three associated taxa occurred in both the Peninsula and sandhill habitats: *Arctostaphylos tomentosa* ssp. *tomentosa*, *Lomatium parvifolium*, and *Galium californica* ssp. *californica*.

One species group which appeared in a variety of localities but was never dominant was *Toxicodendron diversilobum*, *Baccharis pilularis* var. *consanguinea*, *Rhamnus californica*, and *Pteridium aquilinum*.

*Dudleya lanceolata*, *Pellaea mucronata*, and *Selaginella bigelovii* were too rare to show as a species group on the association table, but were scattered on rock outcrops.

Of eight well defined endemic herb taxa in the Monterey area only *Cordylanthus littoralis* seems to have been associated with the maritime chaparral localities. This herb was collected in the past in many maritime chaparral localities. Now only one stand of typical material remains near the airport, and it is considered endangered (Dept. Int., 1976). From historical sources it appears that *Cordylanthus littoralis* often grew with or at least near *Ericameria fasciculata* in sandy habitats.

#### SUCCESSIONAL TRENDS

Cooper (1922) felt that succession on the Fort Ord sandhills would lead from scrub, to *Adenostoma-Arctostaphylos pumila* chaparral, then to *A. tomentosa* chaparral, and finally to a "climax" live oak forest. Gordon (1974) also viewed the "potential natural vegetation" of these sandhills as live oak forest. On the dunes of the Peninsula, Cooper (1922, 1967) thought that pine would be important in the climax forest, but McBride and Stone (1976) concluded that with the present degree of fire protection live oak forest would replace the pine here.

I agree that live oak forest would eventually dominate much of the sandhill landscape, but the poorly developed soils on the ridges will have chaparral patches for a long time. Both the VTM survey and Davis (1972) suggested that chaparral is often climax on south-facing slopes and ridges. The ridgetops where old-growth *Adenostoma* grows less than 1 m tall are unlikely to support live oak forest under the present climate.

We have few historical details on relative distribution of live oak forest and brushland. However, a comment by an early naturalist suggests that chaparral and scrub have long been obvious on the sandhills. In 1792 Archibald Menzies observed that the hills behind the Fort Ord area had ". . . Clumps of Trees thinly scattered of the Holly-leavd (sic)

Oak . . . but the greatest part of the Country here was covered with stiff low Shrubs, many of them evergreen . . . many of these shrubby Plants . . . were of a fragrant quality" (Eastwood, 1924). Stiff low shrubs, many evergreen, many aromatic is a good description of the maritime chaparral-scrub mosaic on the ridges. Many of the presently living *Adenostoma* and *Arctostaphylos tomentosa* burls probably were growing on these sandhills when Menzies visited.

On the Peninsula, maritime chaparral seems to grow where unfavorable soils in conjunction with disturbances such as fire, bark beetle and dwarf-mistletoe attack, or wind throw have kept the pine and cypress canopies open for long periods. One of the few historical observations on chaparral within this Peninsula forest was by Hartweg (1848) who mentioned a "thick brushwood" of *Arctostaphylos*, *Ceanothus* (including *C. rigidus*), and *Chrysolepis* near the *P. muricata*-*C. goveniana* dwarfed woodland.

This dwarfed conifer woodland at the Morse Botanical Reserve (Griffin, 1972) represents the extreme in unfavorable soils on the Peninsula. Here the Narlon clay-pan closely resembles the aborigine clay-pan of the Mendocino County coastal pygmy forest (Jenny, Arkley, and Schultz, 1969). The marine terrace and dune deposits have produced the most mature soils on the Peninsula, and both live oak and *P. radiata* forests are excluded from these podsolized soils. Maritime chaparral species can tolerate the poor drainage and sterile, acid conditions.

When either maritime chaparral or live oak forest is disturbed, scrub species such as *Baccharis pilularis* and *Ericameria ericoides* invade. Short-lived chaparral species such as *Ceanothus dentatus* and *C. rigidus* may also increase. In time, manzanita sprouts and seedlings will replace much of the scrub and ceanothus. *Salvia mellifera* seems to persist in chaparral longer than other scrub species, particularly in *Adenostoma* stands. Although *A. hookeri* and *A. pumila* are often thought of as low mound formers, they can exceed 2.5 m and may survive in mixed chaparral for long periods. However, they do not have the height potential of *A. tomentosa*, *A. montereyensis*, or *A. pajaroensis*. Davis (1972) emphasized the role of tall manzanitas in Prunedale hills chaparral succession.

Near San Luis Obispo, Wells (1962) noted that fine textured soils on shale favored grassland, whereas either deep sand or rockland favored chaparral and live oak forest. He emphasized that these substrate trends were reinforced by frequent fires. The Monterey Bay situation is compatible with this theme.

#### CONCLUSIONS AND RECOMMENDATIONS

Maritime chaparral consists of variable sclerophyll shrub communities within a scrub-live oak forest region that is best developed on sandy soils within the summer fog zone. This chaparral is frequently dominated

by forms of *Arctostaphylos tomentosa* plus one or more of four endemic manzanita taxa. *Adenostoma fasciculatum* is a common sub-dominant. These shrubs of the sandhill brushland also form a conspicuous part of the understory of the closed-cone conifer forest on some marine terraces and rocklands on the Peninsula. There are close floristic ties between the chaparral on the sandhills and the closed-cone forest understory chaparral on the Peninsula.

Maritime chaparral on the airport and Fort Ord sandhills receives substantially less rainfall than the closed-cone forests on the Peninsula. The water relations of sclerophyll shrubs on the sandhills should be compared with those on clay-pan or rockland habitats within the closed-cone conifer forest as well as with the conventional chaparral farther inland out of the fog zone.

Many aspects of the Monterey Bay maritime chaparral resemble those of coastal lowlands to the south. Near Morro Bay and the Nipomo Mesa, San Luis Obispo County and the Point Sal, Orcutt, Burton Mesa areas, Santa Barbara County are similar sandy soils, foggy climate, and concentrations of endemic manzanitas within scrub-live oak forest remotely connected with closed-cone pine forest. The vegetative and floristic homologies between Monterey Bay and southern coastal lowlands should be specifically studied while some intact landscape samples remain in both regions.

Pressures for development are so great around Monterey Bay that maritime chaparral stands need legal protection to survive. For example, areas at the airport were advertised for sale as industrial sites, and one area was developed during the sampling period. One Prunedale sample area was bulldozed bare after sampling, and another is within a rapidly expanding county dump.

The opportunity for new chaparral "reserves" is so limited that maximum support should be given to present areas with any sort of administrative protection. The Gibson Creek annex (Point Lobos State Reserve) and the S.F.B. Morse Botanical Reserve (Pebble Beach Corporation) protect samples associated with dwarfed closed-cone conifers. The fate of maritime chaparral on the Monterey Presidio (U.S. Army) is not known. Human impact at Veterans Memorial Park (City of Monterey) is probably too great to maintain natural chaparral. Development at the airport and surrounding industrial park is so extensive that chaparral can not survive. Despite an increasing level of military activity, Fort Ord (U.S. Army) provides the best opportunity for maintaining maritime chaparral communities on the sandhills (Griffin, 1976). Toro Regional Park (Monterey County) protects some relatively interior samples. No adequate sample of chaparral near Prunedale has formal protection now. The few scraps of maritime chaparral near Larkin Valley also have no protection.

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## CIRCUMSCRIPTION AND GENERIC RELATIONSHIPS OF GALINSOGA (COMPOSITAE: HELIANTHEAE)

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In 1894, B. L. Robinson commented that (p. 325): "Few genera have been subject to so much doubt as to proper limitations as *Galinsoga*. Satisfactory generic limitations can perhaps only be obtained by a monograph including not only the plants hitherto ascribed to *Galinsoga*, but several neighboring genera . . ."

During a recent study of the specific limits and relationships in *Galinsoga*, it became apparent that Robinson had indeed assessed the situation correctly. The genus has been known only superficially and therefore, has not been well defined from a number of closely allied genera in the subtribe Galinsoginae. This circumstance has prevailed even though related genera have been monographed recently: *Sabazia* Cass., *Selloa* H.B.K., and *Tricarpha* Longpre (Longpre, 1970), *Tridax* L. (Powell, 1965), and *Stenocarpa* S. F. Blake (Turner, 1965).

The first objective of this paper is to consider the circumscription of *Galinsoga*. I believe that the taxonomic changes discussed here, based on morphological, chromosomal, and geographical criteria, reflect the close phenetic and inferred phylogenetic relationships of the taxa involved. A second objective is to discuss and re-evaluate the relationships of *Galinsoga* with closely allied genera in the Galinsoginae.

### HISTORY OF THE GENERIC CONCEPT OF *Galinsoga* S. STR.

When Ruiz and Pavon (1794) first described *Galinsoga* (s. str.), they emphasized the following characters as diagnostic: plants annual, herbaceous, with a paleaceous receptacle, pappus of ciliate scales, and ray

florets 4–6, with corollas trifid. Later authors have characterized the genus by a combination of the above features plus the following characteristics (Candolle, 1836; Bentham and Hooker, 1873; Hoffmann, 1890): heads small (to 8 mm diam.), on short peduncles (to 4 cm long); involucre 2-seriate; and achenes black and somewhat angular. Both Candolle (1836) and Bentham (1844) also noted a characteristic typical of most *Galinsogas*: each ray floret is enclosed by a phyllary and two or three pales. This aggregation falls from the receptacle as a unit at maturity.

As additional species of *Galinsoga* were described in the latter half of the 19th century and into the present decade, the genus came to include species with eligulate ray florets (*G. eligulata* Cuatrecasas, 1954) and, in the case of some specimens of *G. subdiscoidea* Cronquist (1965), even discoid plants. However, the generic concept of *Galinsoga* was not significantly altered until the publication by McVaugh (1972) of *Galinsoga mollis*. Plants of this species differed notably from previously recognized *Galinsogas* in: height to 1.5 m; elongate internodes; heads to 2 cm diam.; large number of disc florets (125–150, compared with 10–60 in other species of *Galinsoga*); ray florets 8 rather than 5 per head; and disc and ray corollas twice the length of those in other species. Despite these differences, *G. mollis* possessed many of the diagnostic features of the genus mentioned earlier and so was related to the other *Galinsogas* as a somewhat anomalous species.

In a recent revisionary study of *Galinsoga* (Canne, 1977b), several newly described species were recognized that bridge the morphological gap between the small-headed, short-statured *Galinsogas* and *G. mollis*. Three species, *G. triradiata*, *G. longipes* and *G. elata*, possess the following characteristics that approach the condition found in *G. mollis*: (1) heads to 1.5–2.0 cm diam; (2) heads many to few on elongate peduncles in open, cymose clusters; (3) phyllaries with scarious margins; (4) plants to 55–90 cm tall with elongate internodes; (5) leaves elliptic-lanceolate to ovate-lanceolate with serrate to remotely denticulate margins; and (6) ligules tridenticulate to deeply divided, to 8 in number, and 8 mm in length.

As revised, *Galinsoga* includes 14 species in 3 sections. The fact that 6 of these species are described as new is a reflection of an absence of previous taxonomic study. The transfer of 3 species to *Galinsoga* from 3 other genera is an indication, as well, that generic concepts have been inadequately defined among these genera of the Galinsoginae. While I believe a morphological examination of the new species and combinations leaves no doubt that they are indeed *Galinsoga*, their inclusion does broaden the limits of the genus somewhat and brings *Galinsoga* closer to other members of the Galinsoginae, most notably *Sabazia*, with regard to certain characteristics.

*Galinsoga* and the genera that are morphologically, chromosomally,

and distributionally most similar to it form a rather close-knit unit. Morphological features which in general are characteristic of a given genus occur regularly in some members of other genera. However, in my view, the rather confusing mosaic of character state distributions among genera does not severely alter the integrity of most generic boundaries. *Stenocarpha* and *Tricarpha*, with one and two species respectively, are exceptions. Table 1 provides a comparison of the differences and similarities among the genera discussed here. A key to these taxa is presented below.

1. Annual herbs with slender stems; heads solitary or in cymose clusters . . . . . 2.
2. Heads solitary or occasionally in subcymes; ligules bilabiate or if absent then disc corollas bilabiate; pappus of plumose bristles . . . . . *Tridax*
2. Heads in dense to loose cymes or cymose panicles, occasionally solitary in *Sabazia*; ligules rarely bilabiate, sometimes absent or disc-like; pappus of scales, rarely of setose bristles, or absent . . . 3.
3. Heads in cymose panicles; disc corollas white . . . *Cymophora*
3. Heads in dense to loose cymes or solitary; disc corollas yellow to occasionally reddish-purple . . . . . 4.
4. Plants erect and single-stemmed; heads in cymes; each ray floret usually enclosed within a phyllary-pale association; involucre 1-2 seriate of ovate phyllaries, and a pappus of obtuse to aristate scales or absent; or involucre 2-3 seriate and a pappus of setose bristles . . . . . *Galinsoga*
4. Plants decumbent to ascending and multistemmed or much branched near the base; ray florets usually not enclosed within a phyllary-pale association; involucre 2-3 seriate and a pappus of obtuse scales; or stems erect, branched or not; involucre 3-5 seriate and pappus of delicate, linear scales . . . . . *Sabazia*
1. Shrubs or perennial herbs with stems from thickened rootstocks or rhizomes; heads solitary, in loose cymes, or in corymbose or umbellate clusters. . . . . 5.
5. Herbs: heads radiate; phyllaries parabolic; disc corollas 1.5-4(-5) mm long; disc style branches 0.3-1.2 mm long with acute or rhomboid tips . . . . . 6.
6. Leaves cauline and basal; pales of setose bristles to 0.2 mm wide; style tips rhomboid . . . . . *Selloa*
6. Leaves cauline; pales of linear or lanceolate scales more than 0.2 mm wide; style tips acute . . . *Sabazia*
5. Shrubs and herbs; heads radiate or discoid; phyllaries linear-lanceolate to oblong or obovate; disc corollas 4-10 mm long; disc style branches 1-3 mm long with obtuse, truncate or subulate tips . . . . . 7.

7. Herbs; ray corollas bilabiate; achenes densely pilose, rarely glabrous; pappus of plumose bristles, rarely of deeply fimbriate scales; style tips long subulate . . . . . *Tridax*
7. Shrubs and herbs; ray corollas not bilabiate; achenes strigose or glabrous; pappus usually of spinulose-fimbriate, linear-lanceolate scales, occasionally of blunt scales or setose; style tips obtuse to truncate . . . . . *Calea*

#### RELATIONSHIP TO *Tricarpha*

The 3 new species of *Galinsoga* mentioned above are remarkable in their resemblance to *Tricarpha durangensis* Longpre. *Tricarpha durangensis* and a second species, *T. purpusii* (Brandg.) Longpre, were considered by Longpre to represent a distinct genus on the basis of scarious-margined phyllaries, deeply trifold pales, and shallowly lobed ray corollas. These characters are found not only in numerous species of *Galinsoga*, in which scarious-margined phyllaries and trifold pales are common, but some representatives of the related genus *Sabazia* [e.g., *S. humilis* (H.B.K.) Cass. and *S. multiradiata* (Seaton) Longpre] also possess these characteristics as Urbatsch and Turner (1975) noted. In vegetative features *Tricarpha* cannot be distinguished from *Galinsoga*. The chromosome number of *Tricarpha purpusii* is unknown. *Tricarpha durangensis* was reported to be  $n = 8$  by Keil and Stuessy (1975) and Turner and Flyr (1966, as *Sabazia microglossa* DC., Flyr 292, the type collection for *T. durangensis*). This is also the base chromosome number for *Galinsoga* (Turner and Flyr, 1966; Canne, 1977b).

The similarity in vegetative and floral characters between *Galinsoga* and *T. durangensis* is so great that I have transferred *T. durangensis* to *Galinsoga* (Canne, 1977b). This transfer is contrary to that made by Urbatsch and Turner (1975) who placed *T. durangensis* in *Sabazia* because, as noted above, a few species of *Sabazia* possess two of the three diagnostic characters used as generic markers for *Tricarpha*. Clearly, the generic boundaries of *Sabazia* and *Tricarpha* overlap, at least with regard to these characters. A similar overlap exists with *Tricarpha* and *Galinsoga*, and in the case of *T. durangensis* (but not *T. purpusii*) the overlap is more extensive with *Galinsoga* than it is with *Sabazia*. *Tricarpha durangensis* shares with nearly all species of *Galinsoga* those features that were used as generic markers for *Tricarpha*. In addition, this species is a slender-stemmed annual as is *Galinsoga*, but most *Sabazias* are either weak-stemmed, lax perennials or firm-stemmed, erect perennials with rhizomes or caudices. Yellow anthers and ovate, scarious-margined phyllaries, characteristic of *Galinsoga*, are found in *T. durangensis* whereas *Sabazias* characteristically have red anthers and parabolical, herbaceous phyllaries. *Tricarpha purpusii*, however, differs from *Galinsoga* in several features of the head. The 3-4 seriate involucre of sharply acute phyl-

laries, ray ligules to 11 mm long with tubes to 4 mm long, shiny achenes, disc corollas to 3.7 mm long and anthers to 1.8 mm long are characteristics not found in *Galinsoga*. *Tricarpha purpusii*, a species known only from the type collection (*Purpus* 3961) gathered in Baja California Sur in 1901, has close affinities with *Sabazia*, as Brandegees (1903) originally suggested.

#### RELATIONSHIP TO *Stenocarpha*

*Stenocarpha* was described in 1915 by S. F. Blake, based upon *Galinsoga filiformis* Hemsley. Blake distinguished *Stenocarpha* from *Galinsoga* by the former's tall, narrowly conical receptacle, narrow pales, alternating truncate and aristate pappus scales, and smaller heads. Turner (1965) concurred with Blake in maintaining *Stenocarpha* as distinct, emphasizing that this genus differed from *Galinsoga* by having heads on long peduncles arranged in an open capitulescence, and 8 ray florets with narrow ligules. However, all the features mentioned above, with the exception of the dimorphism of the pappus, occur commonly in various species of *Galinsoga* (Canne, 1977b).

Plants of *Stenocarpha filiformis* differ most strikingly from *Galinsoga* by having linear pales, relatively few cauline leaves, and usually some basal leaves. Nevertheless, I have observed the similar formation of basal leaves in *G. quadriradiata* Ruiz & Pavon grown under greenhouse conditions. Conversely, a specimen of *S. filiformis* grown from seed at Stanford from a *Breedlove* 1668 collection (DS) shows many pairs of well-formed cauline leaves. The pales of *S. filiformis* are narrower than those in *Galinsoga* but are approached by those of *G. mollis* and *G. triradiata*, which reach only 1 mm in width. The character states that distinguish *S. filiformis* as a species do not warrant generic recognition as well. I agree with Hemsley's original decision to place this species in *Galinsoga* where it is located in the monotypic section *Stenocarpha*. Turner and Fly (1966) reported  $n = 8$  for *G. filiformis* while Solbrig et al. (1972) reported  $n = 9$ , indicating the possible existence of intraspecific aneuploidy.

#### RELATIONSHIP TO *Sabazia*

In his discussion of generic relationships, Longpre (1970) indicated the following character states by which *Galinsoga* was thought to differ from *Sabazia*: plants annual in *Galinsoga* vs. perennial in *Sabazia*; heads 3-5(-7) mm diam. vs. 6-23 mm diam.; 5 vs. 8-17 ray florets per head; and ray florets enclosed by a phyllary-pale association in *Galinsoga* but not in *Sabazia*.

All species of *Galinsoga* are considered to be annuals (although possibly perennial in *G. mollis*) but more than three-fourths of the species of *Sabazia* are perennial. The large overlap in capitulum size (including rays) between *Galinsoga* (3-20 mm diam.) and *Sabazia* [6-25(-35) mm diam.] makes this character of limited use for generic differentiation.

The ray floret number was first noted as a variable character in *Galinsoga* by Ruiz and Pavon (1798) when only two species were known

TABLE 1. COMPARISON OF SELECTED CHARACTERISTICS OF *Galinsoga*, *Sabazia*, *Selloa*, *Tridax*, *Cymphora* AND *Calea* ILLUSTRATING DIFFERENCES AND SIMILARITIES IN MORPHOLOGY AND BASE CHROMOSOME NUMBER.

GALINSOGA	SABAZIA	SELLOA
Annual herbs; stem erect, rarely decumbent, from a slender taproot	Perennial or less often annual herbs; stem erect, decumbent or procumbent, from a taproot or often a short rootstock or rhizome	Perennial herbs; stem erect or often decumbent or ascending, from a short rootstock
Heads in few to many-headed cymose clusters, never solitary	Heads solitary or in few-headed cymose clusters	Heads solitary or in few-headed subcymes
Involucre 1-2(-3) seriate; inner phyllaries ovate, usually with 2-3 pales attached at the base and enclosing a ray floret	Involucre (1-)2-5 seriate; phyllaries parabolical, less often ovate, usually free from adjacent pales	Involucre 2-3 seriate; phyllaries parabolical and free from pales
Ligules usually 5 or 8, quadrate to obovate or less often rectangular, occasionally bilabiate in one species	Ligules usually 8-16, less often 5, rectangular, sometimes quadrate-obovate, not bilabiate	Ligules 6-19, rectangular, quadrate-obovate in one species, not bilabiate
Disc corollas yellow, 1.0-3.2 mm long	Disc corollas yellow, 2-5 mm long	Disc corollas yellow or greenish-yellow, 1.5-4.8 mm long
Anthers yellow or less often pale brown, rarely red; apical appendage with glands in two species	Anthers red, rarely yellow, aglandular	Anthers reddish, aglandular
Disc style branches 0.2-0.6 mm long, tips acute	Disc style branches 0.4-1.2 mm long, tips acute	Disc style branches 0.3-1.2 mm long, tips abruptly rhomboid
Pappus of broad, obtuse or aristate, fimbriate or ciliate scales, of setose bristles in one species, or absent	Pappus usually of spinulose-fimbriate, linear-lanceolate scales or of obtuse, fimbriate scales, occasionally absent	Pappus of setose bristles or absent
Base chromosome number, $x = 8$	Base chromosome number, $x = 8$ (4?)	Base chromosome number, $x = 8$

## TRIDAX

Annual and perennial herbs, sometimes woody near the base; stem procumbent, decumbent, or erect, from a taproot, sometimes with woody thickenings, or rhizomatous

Heads solitary or in few-headed subcymes

Involucre 2-5 seriate; phyllaries oblong to lanceolate or ovate, with attached pales in one species

Ligules 0, 3-8(-13), usually obovate to suborbicular, or broadly oblong, bilabiate

Disc corollas yellow or greenish-yellow, (3-)4-10 mm long

Anthers brown to red, apical appendage usually with glands

Disc style branches 1-3 mm long, tips subulate

Pappus usually of plumose bristles, less often of deeply fimbriate scales, rarely absent

Base chromosome number,  $x = 9, 10$

## CYMOPHORA

Annual herbs; stem erect, from a taproot.

Heads in several- to many-headed cymose panicles

Involucre 1-2(-3) seriate; phyllaries oblong to ovate and free from pales or pales absent

Ligules 0-5, obovate, bilabiate

Disc corollas white, 2.8-3.5 mm long

Anthers pale brown to red, apical appendage with glands in one species

Disc style branches 0.6-1.2 mm long, tips subulate

Pappus of obtuse fimbriate or plumose-fimbriate scales or absent

Base chromosome number,  $x = 8$

## CALEA

Shrubs, rarely perennial herbs; stem erect, less often prostrate or climbing

Heads solitary or in few to many-headed cymose, corymbose or umbellate clusters

Involucre 3-multi-seriate, phyllaries oblong, oblanceolate, obovate and free from pales

Ligules 0-8, 10-25, oblong-rectangular to obovate, not bilabiate

Disc corollas yellow, orange or white. ca. 4-7 mm long

Anthers yellow to reddish-brown; of the taxa seen, none with glands as in *Tridax*

Disc style branches 1-2 mm long, tips obtuse or truncate

Pappus usually of spinulose-fimbriate, linear-lanceolate scales

Base chromosome number,  $x = 8$  and/or 9?

in the genus. In the more common weedy species (e.g., *G. parviflora* Cav., *G. quadriradiata*, and *G. mandonii* Sch.-Bip.) ray number varies from 3 to 10, with 5 the usual number, and the characteristic number for many species. *Galinsoga filiformis*, *G. durangensis*, *G. mollis*, and *G. elata* are exceptions and have 6–12 ray florets per head with 8 the usual number. Eight or more ray florets per head is common in *Sabazia* but *S. micropermoides* Longpre, *S. humilis*, *S. acoma* (S. F. Blake) Longpre, *S. sarmentosa* Less., *S. liebmannii* Klatt (Longpre, 1970), and *S. tridacioides* Urbatsch & Turner (1975) sometimes have 5 ray florets per head. In general, then, *Galinsoga* has 5–8 ray florets per head whereas in *Sabazia* there are usually 8 or more.

The phyllary-pale enclosure of the ray florets in *Galinsoga* is a trait that has been used by a number of authors (Candolle, 1836; Bentham, 1844; Longpre, 1970; and Urbatsch and Turner, 1975) to distinguish *Galinsoga*. McVaugh (1972) has been the only author to point out that this feature also occurs in *Tridax* (e.g., *T. dubia* Rose). I have observed it in *Sabazia sarmentosa*, *S. pinetorum* S. F. Blake, and *S. trianae* (Hieron.) Longpre. It is, however, a fairly consistent feature in *Galinsoga* except for its absence in *G. glandulosa*, *G. filiformis*, and *G. durangensis*, and its weak occurrence in *G. subdiscoidea* and some representatives of *G. mandonii*. Thus, the phyllary-pale association is characteristic of *Galinsoga* in general, but does not occur in all species and is not restricted to *Galinsoga*.

The morphological closeness of *Galinsoga* and *Sabazia* is emphasized further by the morphology of *Sabazia trifida* Fay. The annual *S. trifida* is of particular interest because in overall vegetative and floral morphology it is much like *G. durangensis*, *G. elata* and *G. mollis*, differing from them significantly only by having a setose pappus. Accordingly I have transferred to this species to *Galinsoga* (Canne, 1977b).

Little doubt exists that *Sabazia* is the genus most closely related to *Galinsoga*. The genera are alike in chromosome number, distribution and habitat, and they share a number of morphological features (Table 1). Characters typical of one genus are found sporadically in the other, but when combinations of characters are considered the two genera can be recognized as separate entities. Until additional data can indicate a more taxonomically sound alternative, it is best to note the morphological overlap that exists and maintain the genera as distinct.

McVaugh (1945), Gillis (1971) and Grashoff (1975) have noted that homogeneity within a genus is a most important consideration, even if in the present situation by including in *Galinsoga* the new species mentioned previously and *Tricarpha durangensis*, *Stenocarpha filiformis*, and *Sabazia trifida*. These taxa are clearly, on morphological grounds, most closely related to *Galinsoga*, but within that genus are conveniently rec-

ognized as units at the sectional level. *Tricarpha durangensis*, *Sabazia trifida*, *Galinsoga elata* and *G. mollis* are recognized in section *Elata*. Section *Stenocarpa* accommodates the transfer of *Stenocarpa filiformis*, and the remaining nine species are placed in section *Galinsoga* (see Table 1 for a comparison of *Galinsoga* and *Sabazia*).

#### RELATIONSHIP TO *Selloa*

*Selloa*, in terms of overall morphology (particularly shape and size of the ray corollas, number of heads per plant, decumbent stems, and parabolic phyllaries) must be considered closely related to *Sabazia*, as Longpre (1970) maintained. The relationship of *Selloa* to *Galinsoga* seems to be through *Sabazia* rather than directly. *Selloa* can be best distinguished from *Galinsoga* by the former's elliptic-obovate leaves, setose pales, and rhomboid style tips. Additional differences are listed in Table 1.

#### RELATIONSHIP TO *Tridax*

Powell (1965) noted in his revision of *Tridax* that *Galinsoga* is probably the genus most closely related to *Tridax*. *Tridax* comes closest to *Galinsoga* through *T. dubia* Rose. This species has the habit, head size, ciliate pappus scales, and phyllary-pale association similar to *Galinsoga* but *T. dubia* differs conspicuously from all *Galinsogas* by its orange or golden-yellow ray corollas, brownish to rose-color of the pappus, large disc corollas (5–6 mm long), densely pilose ray achenes, and  $n = 9$  chromosome number.

*Galinsoga glandulosa* Canne most closely resembles *Tridax*. The glands of the anther appendages noted by King and Robinson (1970) to occur in many *Tridax* are also presented in this *Galinsoga*. The phyllaries of *G. glandulosa* are intermediate in shape between those of *Tridax* and *Galinsoga* and more densely pilose than in other species of *Galinsoga*. The tubes of the ray corollas are longer than in other *Galinsogas* and much like those in *Tridax*. *Galinsoga* differs from *Tridax* by numerous characteristics (listed in Table 1).

#### RELATIONSHIP TO *Cymophora*

*Cymophora* was established by Robinson (1907) to accommodate the single species *C. pringlei*. Anderson and Beaman (1968) later submerged *Cymophora* into *Tridax*, noting its similarities with *T. accedens*, a species in which I have a special interest because of its likeness to *Galinsoga*. Recently Turner and Powell (1977) have advocated the transfer of *T. accedens* to *Cymophora*. I concur with these authors that *T. accedens*, *C. pringlei*, and a species newly described by them (*C. hintonii*) form a coherent generic unit, but feel that *Tridax venezuelensis* Aristequieta & Cuatrecasas belongs in *Cymophora* as well (Canne, 1977a). The zygomorphic outer disc corollas, white corolla color, and the paniculate-

cymose capitulescence differentiate *Cymophora* as a well-defined genus. On the basis of morphological similarity, *Cymophora* stands near both *Galinsoga* and *Tridax*. The  $n = 8$  chromosome number of *C. pringlei* (Turner *et al.*, 1973) suggests a somewhat closer tie with *Galinsoga* ( $x = 8$ ) than with *Tridax* ( $x = 9, 10$ ), as noted by Turner and Powell. That *Cymophora* and *Galinsoga* are erect, small-headed annuals whereas most *Tridax* are decumbent, larger-headed perennials supports the view that the former genera are more closely related to each other than to *Tridax*.

#### RELATIONSHIP TO *Calea*

The poorly known genus *Calea* L. was revised in part by Robinson and Greenman (1896). At that time the genus was estimated to contain about 85 species, but numerous species have been described since then and 110–120 species is probably now a more accurate estimate.

*Calea* seems more distantly related to *Galinsoga* than the genera discussed previously and differs from *Galinsoga* in a number of ways (listed in Table 1). The two genera also differ in shape of achenes, pubescence and lobing of the disc corollas, and shape of corolla tubes. The shrubby, small- and many-headed *Caleas* seem most closely related to *Galinsoga*, while the large- and solitary-headed species with truncate style branches (e.g., *C. pennellii* S. F. Blake, *C. monocephala* Dusen, *C. lucidivenia* Gleason & S. F. Blake) may deserve generic ranking apart from *Calea*. The base chromosome number for *Calea* is not readily apparent from the reported counts of  $n = 16, 17, 18, 19, 24, 32$  (Federov, 1969; Moore, 1973, 1974) and this also is perhaps an indication of the heterogeneity of the genus. A clear view of how *Calea* relates to *Galinsoga* and other genera of the Galinsoginae must await a comprehensive systematic study of the former genus.

#### SUMMARY

A diagrammatic interpretation of generic relationships as discussed above is shown in Fig. 1. *Stenocarpa*, *Sabazia trifida*, and *Tricarpha durangensis* have been transferred to *Galinsoga*. Similarities between *Galinsoga* (particularly sect. *Elata*) and *Sabazia* are numerous, but morphological overlap is insufficient to demand merger of the two genera.

*Selloa* seems closest to *Sabazia* but is rather clearly defined. It is placed in the diagram near *Sabazia*, *Galinsoga*, and *Calea* since two species, [*S. obtusata* (S. F. Blake) Longpre and *S. breviligulata* Longpre], resemble *Galinsoga* and *Sabazia* while the third species, (*S. plantaginea* H.B.K.), resemble those species of *Sabazia* that are closest to *Calea*.

For the most part, the boundary between *Galinsoga* and *Tridax* is a clear one, although the similarities of *T. dubia* to *Galinsoga* and the *Tridax*-like features of *Galinsoga glandulosa* emphasize the closeness of the two genera.

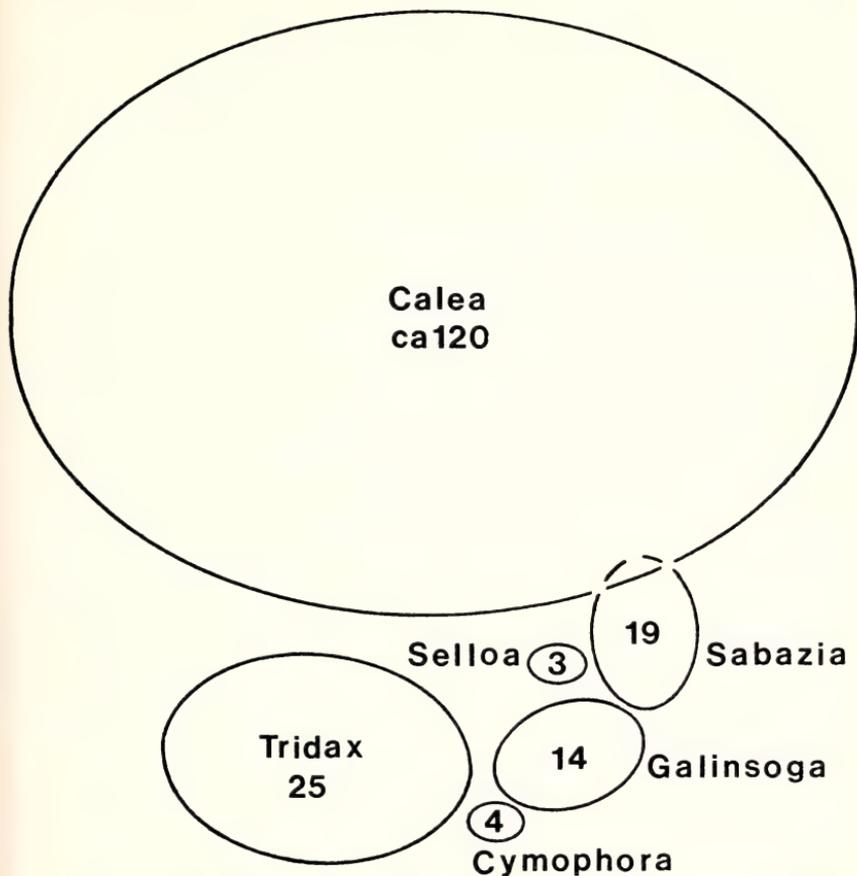


FIG. 1. Relationships among *Galinsoga*, *Sabazia*, *Selloa*, *Tridax*, *Cymophora*, and *Calea*. Numbers and relative sizes of ellipses designate present number of species per genus. Relative placement of ellipses infers closeness of relationship. Overlap indicates uncertainty of generic boundaries.

The relationship between *Tridax* and *Sabazia* seems more distant than that between these genera and *Galinsoga*. Several species of *Tridax* and *Sabazia* possess large solitary heads and are decumbent in habit but otherwise differ in most vegetative and floral characteristics.

The relationship of *Tridax* and *Calea* is unclear. *Tridax* is more distinct from *Calea* in total morphology than is *Sabazia*. However, similarities in pale and phyllary shape among some species suggest a not too distant relationship.

Urbatsch and Turner (1975) discussed the relationship of *Sabazia* and *Calea* and noted that *Caleas* such as *C. caracasana* O. Ktz., *C. integrifolia* Hemsl., *C. scabra* Robins., and *C. colimensis* McVaugh resemble

*Sabazia*. The uncertainty of the *Calea-Sabazia* relationship is indicated in Fig. 1 by the overlapping and broken boundaries of the two taxa.

Finally, the small genus *Cymphora* is similar to *Tridax* and *Galinsoga* and so is positioned in Fig. 1 close to both genera. Morphology and chromosome number suggest a somewhat closer relationship of *Cymphora* to *Galinsoga* than to *Tridax*.

#### ACKNOWLEDGMENTS

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## ON THE TAXONOMIC STATUS OF FRITILLARIA PHAEANTHERA EASTW. (LILIACEAE)

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The identity and geographical distribution of *Fritillaria phaeantha* Eastw. and *Fritillaria phaeantha* Purdy have been the subject of some confusion. Several issues involved have been discussed by Furse (1969). It is pointed out here that these two homonyms apply to different taxa, and the question of priority is resolved by renaming the later homonym *F. phaeantha* Eastw., to which I give the name *F. eastwoodiae*. The probable origin of *F. eastwoodiae* as a hybrid between *F. recurva* Benth. and *F. micrantha* Heller is explored. Pollination experiments were carried out to confirm the interfertility of the latter two species, and seeds of the cross *F. recurva* (♀) × *F. micrantha* (♂) have been germinated.

The confusion began when Purdy (1932) published a photograph labelled *F. phaeanthera*, together with a brief diagnostic description, following one of *F. lanceolata*. No type was cited, so the type of *F. phaeanthera* Purdy is here designated as the photograph and original description. Both photograph and description ("*F. phaeanthera*, a slender related species, in which the anthers are red, and the petals rather twisted") are those of *F. lanceolata* Pursh var. *gracilis* Wats. (Watson, 1879) from Napa Co., California. As Furse has noted, the publication of Purdy's description precedes that of Eastwood (1933).

A study of Purdy's correspondence to Eastwood, in the archives of the California Academy of Sciences, reveals the reason for this confusing situation. On 22 March, 1932, Purdy sent a specimen of *Fritillaria* from east of Middletown (Lake Co., California) to Eastwood for identification. A few weeks later, the type material of *F. phaeanthera* Eastw. was collected by Mrs. J. H. Morrison near Durham (Butte Co.), and Eastwood recognized the Durham plant as a new species. She apparently wrote to Purdy, incorrectly identifying his plant as *F. phaeanthera*, an as yet unpublished name. Although Eastwood's letter making the identification cannot be found, its content can be inferred from Purdy's reply of 7 May, 1932, acknowledging her identification and noting that he had a good photograph of his plant which he intended to publish in an article in the R.H.S. Lily Year Book (Purdy, 1932). A possible reason for Eastwood's misidentification is that one of the diagnostic characters used by her (indeed the source of the epithet '*phaeanthera*') is the dark red color of the anthers, a character which is also found in *F. lanceolata* var. *gracilis*.

The taxonomic confusion was continued by Beetle (1944) and Munz (1959) who cite locations for *F. phaeanthera* Eastw. in Butte Co. (the type locality of *F. phaeanthera* Eastw.) and in Napa Co. (a locality of *F. lanceolata* var. *gracilis* Wats.). In the text of Beetle's monograph she gives a further location as Plumas Co. but does not cite a specific specimen. However, a specimen from Quincy, Plumas Co. (*Luke Gill s.n.*, DS) was annotated by Beetle as *F. phaeanthera* Eastw. but is *F. atropurpurea* Nutt. with linear, ascending, scattered leaves and open campanulate flowers.

Eastwood's plant (*F. phaeanthera* Eastw.) is a distinct species belonging to a rather difficult taxonomic unit, intermediate between *F. recurva* Benth. and *F. micrantha* Heller. It has been suggested by Beetle (1944) that it arose as a hybrid between *F. recurva* and *F. micrantha*. Although there is little experimental or definitive cytological evidence to establish this as yet, the circumstantial evidence in favor of the hypothesis is compelling and will be reviewed below. Since the epithet *phaeanthera* was previously used by Purdy, I propose a new name for Eastwood's plant, and include an expanded description.

*Fritillaria eastwoodiae* Macfarlane = *Fritillaria phaeanthera* Eastwood, Leaf. West. Bot. 1:55, 1933, not *F. phaeanthera* Purdy, Roy. Hort. Soc. Lily Year Book 1:97, 1932.

Perennial herb. Bulb 1.5–2.5 cm diam., a sub-conical, enlarged stem base, surrounded by several fleshy scales and numerous rice-grain bulb-lets. Stem 20–80 cm tall, simple, terete, glaucous, flecked with purple near the base. Leaves on upper  $\frac{2}{3}$  of stem, in 1–2 whorls of 3–5 below, scattered above, blades linear to narrowly lanceolate, 4–9 mm wide, 5–10 cm long, often glaucous. Flowers (2)3–5(7), racemose, nodding, campanulate, ca 15 mm long and as broad, pale greenish-yellow, apricot, to red. Perianth segments six, narrowly elliptic, 3–5 mm wide, 10–17 mm long, flaring to partially recurving at the tips, sepals narrower and more acute than petals. Nectary lanceolate, less than  $\frac{1}{3}$  the length of tepals. Androecium: filaments contiguous near their base, attenuate to the tips, stamens equalling or exceeding pistil before anther dehiscence, but not after; anthers cultrate, ca 5 mm long before dehiscence, red; pollen rust to yellow in color. Gynoecium: style divided in three less than  $\frac{1}{2}$  its length, style branches recurving somewhat; pistil often absent in upper flowers. Capsule 6-angled, winged, truncate, ca 15 mm tall and as wide. Chromosome numbers:  $n = 18$ , near Cherokee, Butte Co. RM 202536 (Beetle 1944);  $n = 12$ ,  $12 + f$ , near Magalia, Butte Co. JEPS 55690,  $n = 17$ ,  $18 + f$ ,  $16 + 2f$ , Pinkston Canyon, Butte Co. (Cave 1970);  $2n = 24 + 2f$ , near Magalia, Butte Co. (Marchant, pers. comm.).

TYPE: Near Durham, Butte Co., California, 17 Apr 1932, Mrs. J. H. Morrison (Holotype CAS 194148!; isotypes: CAS!, K!, GH!).

DISTRIBUTION AND HABITAT: California, Butte Co. and S Shasta Co. Dry slopes, chaparral, foothill woodland, in sun to partial shade, in stony soil with leafmold, on serpentine formations, 400m–1000m. Flowering April–May.

SPECIMENS EXAMINED: CALIFORNIA: De Sabla May 1917, Helen M. Edwards (NY); Feather R. near Yankee Hill, Butte Co., 23 Apr 1922, A. A. Heller 13618 (DS, WTU); occasional about shrubbery in leafmold in the Yellow Pine forest . . . above the reservoir beyond Magalia, 1 May 1938, A. A. Heller 15058 (DS, MO, WTU); on a serpentine outcrop about 4 mi from Magalia on the Coutolenc Rd., Butte Co., 8 Apr 1939, A. A. Heller 15367 (DS, MO, NY, PH, UC, WTU); near Cherokee (pres. Butte Co.), a few in clusters, serpentine soil, 1 Mar 1942, V. Holt (RM); in ponderosa pine woods S of Shingletown, Shasta Co., 21 Apr 1959, R. Bacigalupi 7019 (JEPS); Pinkston Canyon, Big Bend Rd to Yankee Hill, Butte Co., 1800 ft, with *Arctostaphylos viscida*, *Berberis dictyota*, *Dichelostemma volubile*, *Brodiaea californica*, 18 Jun 1960, G. E. See and H. M. Beard s.n. (JEPS); near Magalia, Butte Co., 15 Apr 1967, Margaret Williams s.n. (RENO); near Magalia, Butte Co., E slope amongst bunch grass in the open at the S end of cypresses (a few scattered Douglas Fir and pines), growing in sand and humus amongst serpentine gravel, 16 Apr 1967, W. Roderick s.n. (JEPS); N side of Butte Ck. near Honey Run covered bridge, Butte Co., in wet area, soil a sandy clay, associates *Meconella californica*, *Brodiaea laxa*, 26 Mar 1971, T. C. DeWitt 8 (HSC).

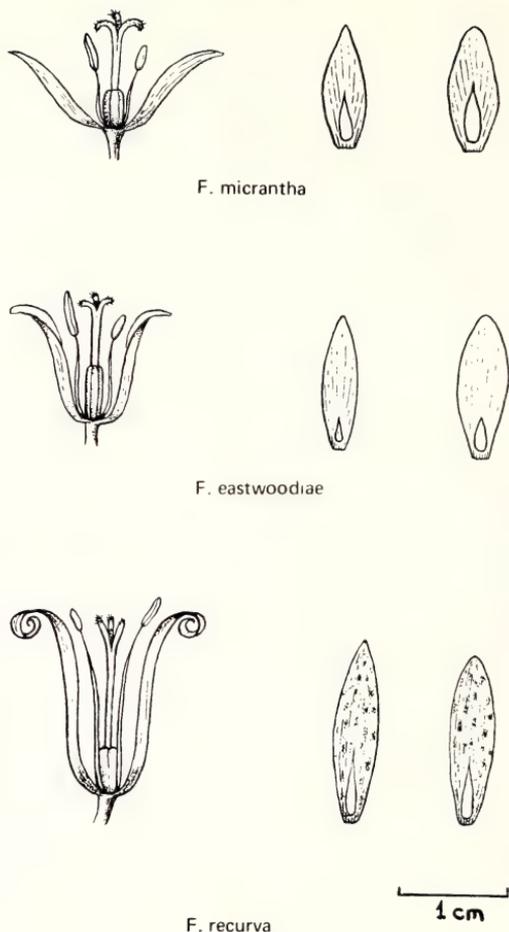


FIG. 1. Floral characters of *Fritillaria micrantha*, *F. eastwoodiae* and *F. recurva* showing (left to right) a) longitudinal section of flower with dehisced and undehisced anthers; b) sepals with nectary in outline; c) petals with nectary in outline.

It will be seen from the above that the first collection of *F. eastwoodiae* was in 1917 at De Sabla, about 20 mi NE of the type locality (it was then identified as *F. coccinea*). In view of the confusion between Eastwood and Purdy, it is interesting to note that the next collection of *F. eastwoodiae*, by Heller in 1922, was identified by him as *F. lanceolata* var. *gracilis* Wats.

The name *Fritillaria eastwoodiae* commemorates Alice Eastwood, long time curator of the California Academy of Sciences herbarium, and author of *Fritillaria brandegei*, *F. eximia*, *F. purdyi*, and *F. striata*.

Without flowers there are few reliable morphological characters separating the species *F. recurva*, *F. micrantha*, *F. eastwoodiae* and *F. lanceo-*

*lata* var. *gracilis*. A diagnostic key is given below based on floral characters, some of which are illustrated in Fig. 1.

Nectary less than  $\frac{1}{3}$  the length of tepals, flowers campanulate to narrowly campanulate, style divided less than  $\frac{1}{2}$  its length, style branches not strongly recurving.

Tepals 20–25 mm long, red with yellow tessellation, recurving at their tips . . . . . 1. *F. recurva*

Tepals 10–15 mm long, red, orange, or pale green, rarely showing tessellation, straight to flaring at their tips . . . . . 2. *F. eastwoodiae*

Nectary greater than  $\frac{1}{3}$  the length of tepals, flowers open-campanulate, style divided more than  $\frac{1}{2}$  its length, style branches strongly recurving.

Flowers inconspicuously tessellated, sepals narrower than petals . . . . . 3. *F. micrantha*

Flowers conspicuously tessellated, sepals broader or approximately equal to petals . . . . . 4. *F. lanceolata* var. *gracilis*

The tepal color in both *F. micrantha* and *F. lanceolata* var. *gracilis* is purple-brown or rarely greenish, but the nectary of *F. lanceolata* var. *gracilis* is longer and generally more conspicuous.

We return now to the question of the hybrid origin of *F. eastwoodiae*. Its geographical distribution lies at the intersection of those of *F. recurva* and *F. micrantha* (see the distribution map in Fig. 2). It should be stressed that in this region it occurs as a series of stable populations, not as sporadic individuals of recent hybrid origin. Pollination experiments in the field show that the plants are self-sterile but produce normal capsules when unprotected from visits by pollinators. This is the case in all other N. American species studied, viz. *F. atropurpurea*, *F. lanceolata*, *F. micrantha*, *F. pluriflora*, and *F. recurva*. It was also noted by Rix (1976) in E. Mediterranean species, and it is believed that in general *Fritillaria* are obligate outcrossers. The regular production of seed capsules in populations of *F. eastwoodiae* containing diploids therefore suggests that these are normal outbreeding populations.

Typical *F. eastwoodiae* is found on serpentine and it is therefore plausible that the mode of speciation involved stabilization of the hybrid, via apomixis, in a habitat not occupied by either of the alleged parents. Not all regions of overlap provide such a habitat, e.g., near Nevada City, Nevada Co., *F. recurva* and *F. micrantha* are found, but not *F. eastwoodiae*.

There are several other characteristics which strongly suggest hybrid origin. First, the floral characters, which are the main points of distinction in this group of species, place *F. eastwoodiae* intermediate between *F. recurva* and *F. micrantha*—e.g., the flower and tepal shape and color, and the style division (see Fig. 1). *Fritillaria eastwoodiae* shows a rather

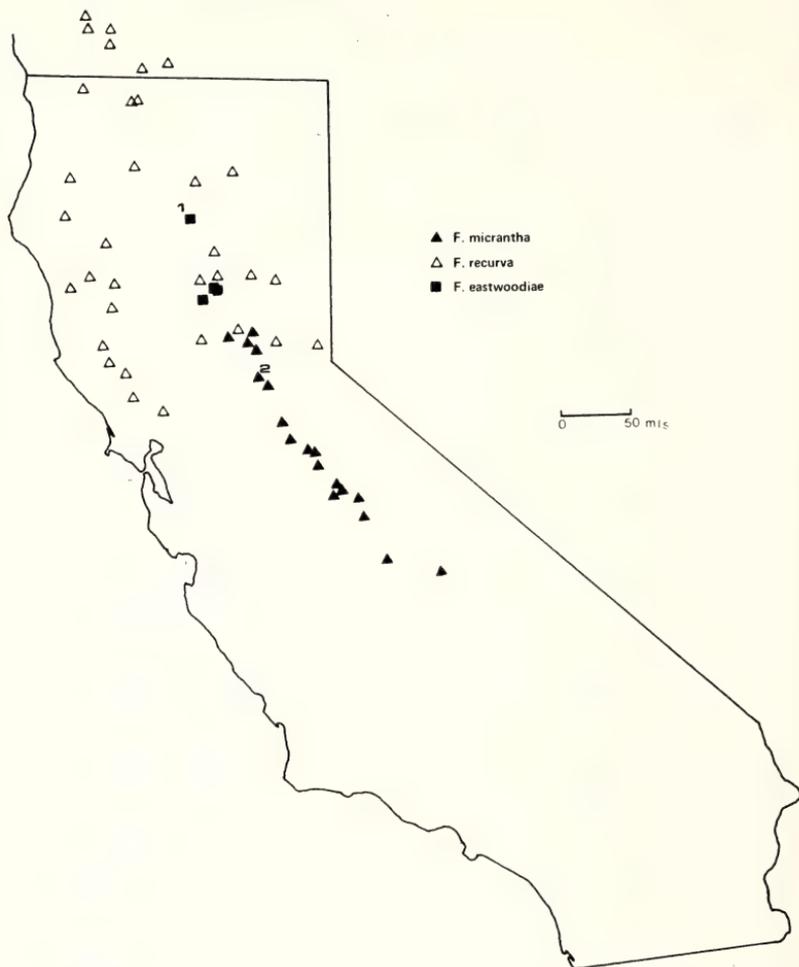


FIG. 2. Distribution map showing the occurrence of *F. eastwoodiae* in California, at the intersection of the distributions of *F. micrantha* and *F. recurva*. 1 denotes a location with possible backcrosses between *F. eastwoodiae* and *F. recurva*; and 2, between *F. eastwoodiae* and *F. micrantha*.

large variation in flower color and shape even in one population, but the flowers are smaller than in *F. recurva* and do not have strongly recurving tepals or prominent yellow tessellation. Second, *F. eastwoodiae* shows irregularities in chromosome pairing at meiosis (Cave, 1970) and frequent cases of female sterility (ovary and style absent). Many individuals which have been studied cytologically are triploids. Somatic cell counts give  $2n = 36$  and pollen grains in a given individual show variable chromosome numbers distributed around  $n = 18$  (Cave, 1970). This behavior is expected as a result of meiosis in the triploids. As noted

earlier, diploid plants also occur and seed capsules are regularly produced. Finally, controlled pollination of *F. recurva* (♀) by *F. micrantha* (♂), and also the reverse cross, yielded capsules about 80% of the seeds of which had normally developed embryos. Seeds from a single capsule of *F. recurva* (♀) × *F. micrantha* (♂) showed better than 50% germination, suggesting that interspecific sterility barriers do not exist between these species. In particular, the endosperm of the hybrid seed does not appear to contain embryo growth inhibitors such as have been found in *Lilium* (Emsweller *et al*, 1962) and suspected in the case of E. Mediterranean *Fritillaria* (Rix, 1971).

The diversity of flower form found in *F. eastwoodiae* is probably due in part to the frequent occurrence of triploids with their associated sexual sterility, and to a stabilization of the diversity by vegetative propagation which exists via the rice-grain bulblets produced in great abundance. The mechanism for producing triploids is not clear. No tetraploid individuals of *F. recurva* or *F. micrantha* which potentially could be parents in a triploid-diploid hybrid are known. Indeed, tetraploidy is rare in N. American *Fritillaria*, only one case having been reported (in *F. lanceolata* by Beetle, 1944). This is true of the genus as a whole, and is probably due to the large size of the chromosomes, which might inhibit cell division in the tetraploid condition (Darlington, 1932; Grant, 1971). If it were not for this, allotetraploidy would provide a convenient route to bypass hybrid sterility. A more likely hypothesis is that triploids have been formed many times from unreduced gametes, and these individuals, because of their well-developed habit of vegetative apomixis, have survived as clones. The triploid character apparently confers some constitutional advantage, since the triploids have competed successfully with diploid parents and siblings, which have both sexual and vegetative channels available to them. The possibility of agamospermy is being investigated. Chromosome counts have been done on only a few individuals of the *F. eastwoodiae* complex (Cave, 1970), but it is interesting that the only diploids reported (from Magalia, Butte Co., Cave, 1970; Marchant, pers. comm.) are also the most intermediate morphologically and geographically between *F. micrantha* and *F. recurva*. Individuals closer to *F. recurva* (e.g., *R. Bacigalupi* 7019, JEPS 25404 from Shasta Co.) are triploid, and possibly represent backcrosses to *F. recurva*. Similarly, triploid plants have been found in El Dorado Co. (*W. Roderick s.n.*, JEPS 55692) which are close morphologically and geographically to *F. micrantha* and perhaps represent backcrosses to the latter (see Fig. 2). Whether unreduced gametes function more effectively in the backcrosses remains, however, a matter of speculation, since populations of typical *F. eastwoodiae* contain both diploid and triploid individuals. The origin of *F. eastwoodiae* needs further investigation, e.g., by a study of the degree of heterozygosity using chromosome banding patterns (La Cour, 1951; Dyer, 1963).

Finally, the probable hybrid origin of *F. eastwoodiae* raises an interesting question regarding pollinators, since one of the supposed parents, *F. recurva*, is hummingbird pollinated (Grant and Grant, 1968; D. Santana, pers. comm.) whereas the other, *F. micrantha*, with its open brownish-green flowers and much less abundant nectar, almost certainly is not. This suggests that hummingbirds are not the exclusive pollinators of *F. recurva*.

## ACKNOWLEDGMENTS

I thank Dr. Peter Raven and Dr. John Thomas for helpful discussions on nomenclature and for their critical reading of the manuscript; Dr. Chris Marchant for providing a chromosome count of *F. eastwoodiae*; and Mrs. Margaret Campbell, archivist at the California Academy of Sciences, for help in locating correspondence between Alice Eastwood and Carl Purdy.

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## A NEW SPECIES OF DRABA (CRUCIFERAE) FROM WYOMING AND UTAH

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In 1953 Rollins described *Draba pectinipila* with the type from Clay Butte, Park County, Wyoming, at an elevation of 3050 meters. Two other specimens from Daggett County, Utah, were cited. Rollins noted that these plants are similar to *Draba oligosperma* but the petals are white instead of yellow, the fruits are more elongate and bear doubly pectinate hairs rather than simple hairs, and the pedicels and scapes are pubescent instead of glabrous and are longer. He further noted that the Utah specimens are very similar to the type material but differed in having a slightly coarser pubescence and siliques that are tapered both above and below rather than just below. He commented that the northeastern Utah-northwestern Wyoming disjunct distribution may seem unusual but cites the parallel distributions of *Draba apiculata* and *Parrya nudicaulis*.

Two points were apparently overlooked by Rollins (1953). First, the type of *Draba pectinipila* is from an alpine habitat while the Utah specimens are from the juniper-pinyon zone. Populations of *Parrya nudicaulis* and *Draba apiculata* are from alpine or subalpine habitats in both localities. Second, one of the Utah collections, *Williams 476*, is labeled "Fls. yellow." I have since confirmed the yellow petal color in populations in Sweetwater County, Wyoming, near the Utah border.

The Utah and southern Wyoming populations grow among *Pinus edulis* Engelm. and *Juniperus osteosperma* (Torrey) Little or just with the juniper when the pine drops out to the north. Some plants occur in sagebrush (*Artemisia* spp.) which is adjacent to or among the juniper. In contrast, *Draba oligosperma* grows on exposed rocky slopes and ridges.

The juniper-pinyon populations are sufficiently different from the alpine population and from *Draba oligosperma* to warrant specific status. Differences between the taxa are summarized in Table 1.

***Draba juniperina*** Dorn, sp. nov. Herba perennis caespitosa, caulibus erectis pubescentibus 3–15 cm longis; foliis linearibus vel lineari-oblongeolatis dense pubescentibus 2–14 mm longis, 0.5–1.5(2) mm latis; pedicellis tenuibus divaricatis pubescentibus 3–10 mm longis; petalis luteis spatulatis 4–5 mm longis; siliquis ovatis vel ellipticis pubescentibus 4–7 mm longis, 2–3 mm latis; stylis 0.7–1.5 mm longis.

Caespitose, perennial herb; caudex much branched; leaves all near base, linear to linear-oblongeolate, 2–14 mm long, 0.5–1.5(2) mm wide, pubescent with appressed doubly pectinate hairs, opposite pairs of leaves connate to form a sheath; scapes erect, 3–15 cm long, pubescent with doubly pectinate hairs; pedicels divaricately ascending, straight to slight-

Table 1. DIFFERENCES BETWEEN THREE SPECIES OF *Draba*.

Character	<i>D. oligosperma</i>	<i>D. pectinipila</i>	<i>D. juniperina</i>
Habitat	Exposed rocky slopes and ridges	Alpine slopes	Juniper-pinyon and sagebrush
Habit	Compactly caespitose	Loosely caespitose	Compactly caespitose
Scape	Glabrous	Pubescent	Pubescent
Petal length	3-5 mm	Mostly 3-4 mm	Mostly 4-5 mm
Petal color	Yellow	White	Yellow
Silique tip	Tapered or rounded	Rounded	
Valve surface	With simple, rarely forked hairs	With doubly pectinate hairs	With doubly pectinate hairs
Style length	0.1-1 mm	0.3-0.7 mm	0.7-1.5 mm

ly curved upward, usually pubescent, 3-10 mm long; sepals broadly oblong to elliptic, hyaline-margined, 2-3.5 mm long, pubescent; petals yellow, spatulate, mostly 4-5 mm long; siliques elliptic to ovate, tapered to tip, 4-7 mm long, 2-3 mm wide, flattened parallel to replum, pubescent on valve surfaces with appressed doubly pectinate hairs; styles 0.7-1.5 mm long; stigma slightly greater in diameter than style; seeds 2-5 in each locule, wingless, ca. 1.5 mm long,  $\frac{1}{2}$  to  $\frac{2}{3}$  as wide.

Type: Wyoming, Sweetwater Co., T12N R107W Sec 4, ca. 2135 meters, juniper forest, June 18, 1973, *Dorn 1837* (holotype RM, isotype UTC).

Additional Collections: UTAH: Daggett Co.: vicinity of Flaming Gorge ca. 1675 meters, dry hillsides, June 1, 1932, *Williams 476* (GH, RM); same location, 24 km SE of Manila, June 3, 1938, *Rollins 2275* (GH). WYOMING: Sweetwater Co.: T12N R107W Sec 9, ca. 2135 meters, juniper-pinyon forest, May 29, 1977, *Dorn 2895* (RM); T12N R106W SE $\frac{1}{4}$  Sec 12, ca. 2350 meters, sagebrush, May 29, 1977, *Dorn 2898* (RM); Richards Gap, ca. 1950 meters, sagebrush at edge of juniper forest, May 29, 1977, *Dorn 2902* (RM); T15N R102W Sec 18, ca. 2135 meters, juniper forest, May 29, 1977, *Dorn 2903* (RM).

Specimens will be distributed to additional herbaria.

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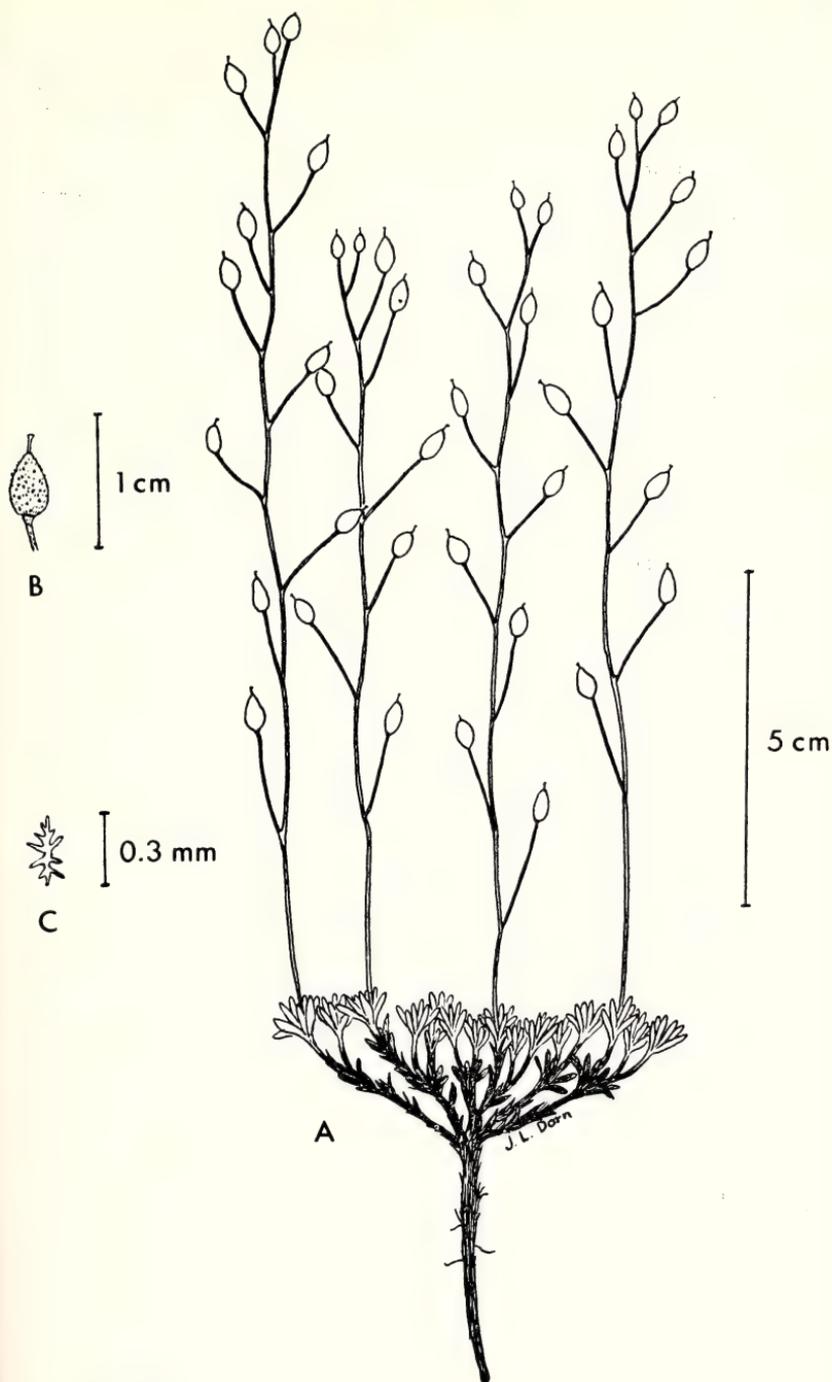


Fig. 1. *Draba juniperina*. A, habit. B, silique. C, doubly pectinate hair. From Dorn 1837.

## NOTES AND NEWS

VALIDATION OF THE NAME *Juncus bufonius* var. *occidentalis*. — In the publication of *Juncus bufonius* var. *occidentalis* as "nom. et stat. nov." for *J. sphaerocarpus* auct. Amer., non Nees, (USDA Forest Service General Technical Report RM-18, page 14. Oct. 1975) the mistaken assumption was made that reference to a previously published description was adequate for validation. Dr. Edward G. Voss reminds me, however, that even in this instance Article 36 of the International Code requires accompaniment by a Latin description or previously published Latin description, and Article 37 requires the indication of a nomenclatorial type. The omission, therefore, is remedied herewith.

***Juncus bufonius* var. *occidentalis*** F. J. Hermann, var. nov. *Plantae plerumque minus quam 15 cm altae; tepala 2–4 mm longa; fructus subglobus usque late ovoideus, 2–3 mm longus.* Type: near Camp by Grizzly Butte, Crook Co., Oregon, *J. B. Leiberger* 256, June 16, 1894 (US; isotype MICH). — F. J. HERMANN, Forest Service Herbarium, Rocky Mountain Forest and Range Experiment Station, 240 W. Prospect St., Fort Collins, Colorado 80521.

PLANT ABUNDANCE AND DISTRIBUTION IN RELATION TO TYPES OF SEED DISPERSAL IN CHAPARRAL. — Recent attempts to relate the structuring of local communities to dispersal mechanisms warrant examination of diverse vegetation types, and casual explanation. Tree species diversity in the Great Smokey Mountains decreases significantly with increases in the proportion of trees that are wind-dispersed (Beyer, Amer. Natur. 109:103–104. 1975). The relationship does not hold for Ohio woodlands (Tramer et al., Amer. Natur. 110:500–501. 1976). The California chaparral provides a strong contrast to the eastern forests in both physiognomy and dynamics. Adaptation for wind dispersal is rare in chaparral, but a major division may be made between dry- and fleshy-fruited species. The former have no obvious means of dispersal as far as three diameters of the parent shrub; the latter are presumably dispersed in animals and to relatively large distances. Then, is species diversity in chaparral inversely related to the proportion of individuals that have dry fruits?

Chaparral in the San Gabriel Mountains was extensively sampled by Hanes (Ecol. Monogr. 41:27–52. 1971) using 10m transects on which each individual plant was noted by species and length of intercept. Hanes has kindly allowed me to analyze 287 of the transects. H. G. Baker kindly provided much of the data on fruits and seeds. Sixty species occurred in the sample, of which 40% have fleshy fruits.

The correlation coefficient between species diversity  $-\sum p_i \ln p_i$ , and the proportion of individuals on a transect that have dry fruits is only  $-.268$ , although this is significant ( $p < .01$ ). In fact, both species and individuals with fleshy fruits are sparsely distributed. Over 80% of the transects had only 0 or 1 fleshy-fruited species, while 90% had 2–4 dry-fruited species. Also, given that a species occurs on a transect, the mean number of individuals is 1.6 for fleshy-fruited species, but 2.8 for dry-fruited species (considering only species occurring on at least 10 transects;  $p < .01$ , Mann-Whitney U-test). The fleshy-fruited species may be regarded as interstitial, persisting in small cracks in the general matrix of dry-fruited shrubs.

I suggest the following two hypotheses as explanations of the above observations. 1) Seeds dispersed by frugivorous animals tend to be deposited in compact groups, and therefore have a very low dispersion within an area of the magnitude of 10m diameter, even though the groups may be deposited at considerable distances from the mother plant. 2) For any of a variety of reasons, seeds of fleshy-fruited species cannot remain dormant beyond the first winter, yet only occasionally (in space) does the moment of germination correspond with the moment when the site is suitable for establishment. Reasons for the lack of dormancy may include the following: a) The seeds may be susceptible to fungal/bacterial attack in fecal material; b) Other seeds of the group might germinate first and preempt the site; c) Seeds of

these species tend to be heavier than those of dry-fruited species (mean weight of 23.49mg compared to 6.45mg,  $p < .01$ , excluding three species of each fruit type with seeds  $> 100$  mg), making these seeds more favorable targets for seed predators. — STEPHEN H. BULLOCK, Biology Department, University of California, Los Angeles 90024.

GREAT BASIN VEGETATION IN CARBON COUNTY, MONTANA. — Great Basin vegetation is well represented in only two counties in Montana, Beaverhead and Carbon. Both counties are along the southern edge of Montana, the former bordering Idaho and the latter bordering Wyoming. This vegetation is best represented in Carbon County where it covers about 1800 sq. km. The greatest diversity of species occurs in an area of less than 260 sq. km. in the south foothills of the Pryor Mountains and along the Big Horn Canyon.

The Pryor Mountains and Big Horn Canyon have a predominant substrate of limestone, sandstone, shale, and some gypsum. Several formations with red soils are also well represented. These form extensive areas of nearly barren hills. The conspicuous vegetation of the area contains extensive stands of Utah juniper, *Juniperus osteosperma* (Torrey) Little, and black sagebrush, *Artemisia nova* A. Nels. Several species of *Atriplex* are also common.

Field work by the author in 1976 turned up several interesting plants from this area including some first records for the state. The most interesting collections are listed below. A few are not strictly Great Basin plants but are significant for other reasons. Apparent first state records are indicated by an asterisk (\*). Specimens are deposited in MONT with some duplicates in RM and my personal herbarium.

BORAGINACEAE — *Cryptantha ambigua* (Gray) Greene, *Dorn* 2633; *C. cana* (A. Nels.) Payson, *Dorn* 2546\*, 2627; *C. flavoculata* (A. Nels.) Payson, *Dorn* 2543\*, 2626.

CAPPARACEAE — *Cleome lutea* Hook., *Dorn* 2630.

COMPOSITAE — *Artemisia pedatifida* Nutt., *Dorn* 2534; *A. spinescens* Eaton, *Dorn* 2552; *Erigeron allocotus* Blake, *Dorn* 2625\* (This species is endemic to the area and was known previously from only Big Horn Co., Wyoming.); *Hymenopappus filifolius* Hook. var. *luteus* (Nutt.) B. L. Turner, *Dorn* 2660\* (These plants were growing with *Hymenopappus polycephalus* Osterh. with no evidence of intergrading.); *Hymenoxys torreyana* (Nutt.) Parker, *Dorn* 2549\*; *Malacothrix torreyi* Gray, *Dorn* 2677; *Platyschkuhria integrifolia* (Gray) Rydb., *Dorn* 2638, 2670; *Sphaeromeria capitata* Nutt., *Dorn* 2564; *Tetradymia spinosa* Hook. & Arn., *Dorn* 2684; *Townsendia incana* Nutt., *Dorn* 2628\*, 2658; *Wyethia scabra* Hook., *Dorn* 2629; *Xylorhiza glabriuscula* Nutt., *Dorn* 2535, 2686.

CRUCIFERAE — *Malcolmia africana* (L.) R. Br., *Dorn* 2540\*; *Physaria australis* (Payson) Rollins, *Dorn* 2547, 2559; *Stanleya tomentosa* Parry, *Dorn* 2652; *Streptanthella longirostris* (Wats.) Rydb., *Dorn* 2570\*, 2653.

HYDROPHYLLACEAE — *Phacelia ivesiana* Torrey, *Dorn* 2567\*, 2632.

LEGUMINOSAE — *Astragalus grayi* Parry ex Wats., *Dorn* 2642; *A. hyalinus* Jones, *Dorn* 2774.

LOASACEAE — *Mentzelia pumila* Nutt. ex T. & G., *Dorn* 2775\*.

ONAGRACEAE — *Cammissonia andina* (Nutt.) Raven, *Dorn* 2568; *C. minor* (A. Nels.) Raven, *Dorn* 2654\*; *C. scapoidea* (T. & G.) Raven, *Dorn* 2662.

POLEMONIACEAE — *Gilia leptomeria* Gray, *Dorn* 2631\*; *Gilia tweedyi* Rydb., *Dorn* 2566\*; *Ipomopsis pumila* (Nutt.) Grant, *Dorn* 2639.

POLYGONACEAE — *Erigonum brevicaule* Nutt. [*E. pauciflorum* Pursh var. *canum* (Stokes) Reveal], *Dorn* 2690, 2773.

ROSACEAE — *Physocarpus monogynus* (Torrey) Coult., *Dorn* 2778.

SAXIFRAGACEAE — *Sullivantia hapemanii* (Coult. & Fish.) Coult., *Dorn* 2674\* (This species is otherwise known from only a few localities in Wyoming. It was found on dripping limestone.).

SCROPHULARIACEAE — *Penstemon caryi* Pennell, *Dorn* 2669\*, 2777 (This species is endemic to the area and was known previously only from Big Horn Co., Wyoming.); *P. laricifolius* Hook. & Arn., *Dorn* 2651.

TAMARICACEAE — *Tamarix chinensis* Loureiro, *Dorn* 2673.

UMBELLIFERAE — *Musineon vaginatum* Rydb., *Dorn* 2683 (This record from the Pryor Mountains adds to the previous known range of the Big Horn and Bridger mountains.). — ROBERT D. DORN, Box 1471, Cheyenne, Wyoming 82001.

KNOBCONE PINE SOUTHWARD RANGE EXTENSION IN THE SIERRA NEVADA. — *Pinus attenuata* Lemm. has previously been reported as reaching its southern Sierra Nevada limit in Yosemite National Park (Griffin, J. R., and W. B. Critchfield, The distribution of forest trees in California, 1972; specifically, along the fire road to Deer Camp, Arno, S. F., Discovering Sierra trees, 1973). We report here the existence of a population near Bass Lake, for a range extension of ca. 35km south, out of Yosemite Park and into Madera County. The population is distributed west of the Beasore Rd. 2.0–2.5 km north of Malum Ridge Rd. T7S, R22E, 10 (J. Keeley 7014, Occidental College, Los Angeles). At this site it occurs in close association with *Arctostaphylos viscida* and, on the periphery, mixes with *Pinus ponderosa*, *Pinus lambertiana*, *Libocedrus decurrens* and *Quercus chrysolepis*. The population is an uneven-aged stand of several hundred trees centered on a knoll at ca. 1200 m elevation. Several smaller populations occur 1.5–2.5 km further north on the Beasore Rd.

*Pinus attenuata* has previously been reported south of Yosemite Park (Munz, P. A., Supplement to a California flora, 1968), but Munz's report was apparently based on knobcone pine planted along the Mineral King Rd. (Griffin and Critchfield, op. cit.). The Beasore Rd. population is apparently indigenous. This is suggested by the large size of the population and confirmation by a Sierra Nevada Forest spokesperson (J. F. Underwood, Timber Management Officer, pers. comm. 14 Sept. 77) that knobcone pine has *not* been planted in this area. — JON E. KEELEY, Department of Biology, Occidental College, Los Angeles, Ca. 90041, STERLING C. KEELEY, Department of Biology, California State University, Northridge, Ca. 91330, and JANET LEE, Department of Botany, University of Kansas, Lawrence 66044.

SCROPHULARIA LAEVIS (SCROPHULARIACEAE), A LEGITIMATE SPECIES — Wootton and Standley (Contr. U. S. Nat Herb. 16: 173. 1913) described *S. laevis* based on collections from the Organ Mountains without flowers. The key in their "Flora of New Mexico" (Contr. U. S. Nat Herb. 19, 578. 1915) states the flowers to be dull-greenish, apparently without basis.

Shaw, having seen only the type specimen in the National Herbarium, indicated in his monograph (Aliso 5(2): 172. 1962) that *S. laevis* was synonymous with *S. montana*. In the same monograph, (Ibid., 173) he listed the type specimen under *S. parviflora*. His distribution map (Ibid., 173) showing both *S. montana* and *S. parviflora* locations does not show the Organ Mountain location at all. That it was probably omitted unintentionally is indicated since there are more New Mexico voucher specimens cited than there are locations plotted. Later, based on his observation of plants grown from Organ Mountain seed, Shaw (private communication with R. Roy Johnson) stated the plants resembled his hybrid, *S. macrantha* x *S. parviflora*.

All confirmed locations of *S. parviflora* are west of the Continental Divide, while all those of *S. montana* are east of the Divide. The location of *S. laevis* in the Organ Mountains is about 80 km from the nearest station of *S. montana* and over 200 km from the nearest station of *S. parviflora*.

Plants of *S. laevis* collected at several sites in the Organ Mountains over the past 15 years show little variation, indicating the stability and homogeneity of the population. They differ from both *S. montana* and *S. parviflora* in their smaller stature,

carmine corolla, orbicular sterile filament, longer relative length of petiole to leaf blade, non-fasciate inflorescence, and possible obligate substrate. The plants further differ from *S. montana* in their slender habit, single type of pubescence, and doubly serrate leaf margins and from *S. parviflora* in distribution, larger corolla, completely deflexed lip, and limited pubescence.

Based on the above, *S. laevis* should be recognized as a valid species. The description of Wootton and Standley should be supplemented to include the following:

Glabrescent perennial, 4-10(12) dm tall, stems simple or sometimes with several weak branches after cropping; leaf blades lanceolate to ovate, acute, proximally doubly and distally simply serrate with acute teeth, obtuse to cordate at base, glabrous except sparsely glandular-puberulent along the main veins; larger leaves with blades 5-7 cm long, 2-3.5 cm wide, on slender petioles 2-3 cm long; panicle sparse, short, consisting of 2-5 pairs of few-flowered open corymbs; peduncles and pedicels slender, glandular-puberulent at anthesis; sepals 3-4 mm long, triangular to lanceolate; corolla 7-12 mm long, pale carmine below, bright carmine above, the upper lobes dark carmine, the reflexed lower midlobe white to pink, the throat glabrous; sterile filament orbicular above, green, 1 mm broad; capsule narrowly ovoid, 8-11 mm long.

Distribution: Canyons, northern part of the Organ Mountains, Dona Ana County, New Mexico, on quartz monzonite substrate at 2250-2600 m elevation. — THOMAS K. TODSEN, Biology, New Mexico State University, Las Cruces, NM 88003.

*CORDYLANTHUS MOLLIS* SPP. *MOLLIS* (SCROPHULARIACEAE), REDISCOVERY OF EXTINCT RECORD WITHIN NAPA COUNTY, CALIFORNIA. — On 5 August 1976, Craig Thomson and the author, during an examination of the salt marsh plant community along Fagan Slough due west of the Napa County Airport about 1.5 km east of the Napa River (USGS Cuttings Wharf quadrangle: UTM 10/05610/42300, 10/05611/42300; SE¼ SW¼ Sec. 3 and NE¼ NW¼ Sec. 10 T4N R4W M.D.B. & M.), observed a vigorous population of *Cordylanthus mollis* Gray ssp. *mollis* (soft bird's beak) encompassing 250-300 individuals in a 30 x 70 m area in association with *Salicornia virginica*, *Jaumea carnosa*, *Limonium californicum*, and *Cuscuta salina*. *Cordylanthus mollis* ssp. *mollis* is officially listed as *Endangered* by the U. S. Fish and Wildlife Service in 1976 (40 FR 24566). This taxon, identified by the Code COMOM, is also listed by the California Native Plant Society as "Possibly Extinct" (Powell, W. W. 1974. *Inventory of Rare and Endangered Vascular Plants of California*, C. N. P. S. Spec. Pub. 1, p. 18), and was last reported in 1966 although previously collected in Marin, Merced, Napa, Solano and Sonoma Counties. Voucher specimens have been deposited by the author at the California Academy of Sciences. — STEPHEN P. RAE, Box 66, Napa, California 94558.

*TRAGUS RACEMOSUS* IN ARIZONA. — The genus *Tragus* comprises six or seven species of annual grasses native to warmer regions of the Old World. Two of these, *T. berteronianus* Schult. and *T. racemosus* (L.) All., have been introduced into the Americas, where the former species is often a common weed, being found from the southern United States to Argentina. *Tragus racemosus* seems to be encountered less frequently.

Hitchcock's Manual (U. S. Dept. Agric. Misc. Publ. 200, 2nd. ed. revised by Agnes Chase, 1951) gives the range of *Tragus racemosus* as: "Waste ground and on ballast at a few places from Maine to North Carolina; Texas to Arizona; introduced from the Old World." Swallen, in his treatment of the grasses for Kearney & Peebles' Arizona Flora (Univ. of Calif. Press, 1951), indicates for this species; "Campus of the University of Arizona (Pima County), probably only cultivated." In the supplement to this work (1960) there is no further note regarding *T. racemosus*. Gould (Grasses of Southwestern U. S., Univ. of Arizona Press, 1951) also states that this

species is known in Arizona only from collections made on the University of Arizona campus, but elaborates further: "This species was grown in the early grass garden of the University as stated on the label of a Toumey collection made in 1892. Collections by Griffiths and Thorner made in 1901, 1902, and 1903, are labeled 'Campus, U. of A., Tucson.'" He also comments: "If this species actually did become established in Tucson outside of the grass garden it is highly improbable that it has persisted for nearly fifty years without detection."

Examination of the *Tragus racemosus* folder at ARIZ in the summer of 1977 revealed that the only specimens from Arizona were those mentioned above by Gould. However, while botanizing in the Chiricahua Mountains (Cochise County) in September of that year, we encountered *T. racemosus* in abundance in Rucker Canyon. In this area it grows thickly as a weed in the sandy soil of the roadside from the top of the pass (ca. 1750 m) for a distance of some ten miles as one descends toward the east where the elevation is ca. 1525 m. *Tragus berteronianus* occurs here also, but appears to be rather rare. In fact, we were able to find only two or three small colonies in the entire ten mile stretch. Curiously, the two species did not appear to form mixed stands.

As an additional check of our determinations, we collected young inflorescences of plants considered to represent the two different species. These were preserved in the standard 3:1 absolute alcohol-acetic acid solution for cytological study. Subsequent examination of acetocarmine squashes revealed a chromosome number of  $2n = 20$  for *T. berteronianus*, and  $2n = 40$  for *T. racemosus*. This is in accord with information in the literature which indicates that the former species is a diploid, whereas *T. racemosus* is tetraploid. Voucher specimens, as cited below, are deposited in ARIZ, with duplicates at US. Collection numbers are those of the authors.

*Tragus racemosus* (L.) All., 6875,  $2n = 40$ ; *T. berteronianus* Schult., 6880 & 6882,  $2n = 20$ .

That *Tragus racemosus* is not a recent invader of Rucker Canyon is attested to by a specimen collected there more than 30 years ago, incorrectly identified as *T. berteronianus*, and placed in that folder at ARIZ where we found it in 1977. The collectors are F. W. Gould & H. S. Haskell 4514. The label reads: "In sand along broad wash, *Juglans-Cupressus-Platanus* woodlands; altitude 5700 feet; entrance to Rucker Canyon recreational area. Chiricahua Mountains. Oct. 5, 1946." — JOHN R. REEDER & CHARLOTTE REEDER, Herbarium, University of Arizona, Tucson 85721.

## REVIEW

*A Survival Handbook to Sierra Flora*. By NORMAN WEEDEN. 1975. iv. + 406, illus. Interface California Corporation. \$5.95. ISBN 0-915580-03-9.

In the past few years there has been a veritable explosion in the number of 'popular' wildflower guides at the disposal of the interested amateur botanist. Most professionals would view this book as part of the exploitation of this market. Weedén's flora (W), however, is potentially of interest to the practicing botanist.

Essentially W is a series of keys to montane, subalpine and alpine Sierran plants, supposedly including all species listed by Munz and Keck (M&K) from above 1066 m and 2438 m on the western and eastern slopes of the range respectively. *Erigeron*, *Carex*, *Cryptantha* and *Plagiobothrys* are not treated by W at the specific level, and the keys presented are not all entirely new, being mostly in the Abrams-M&K mold. Illustrations are provided for most of the genera, and are useful although a few border on primitive-art (i.e., Poaceae) and are not at all helpful. A glossary of 350 terms is provided. Brief habitat and morphological descriptions are also given for most of the taxa. Numerous infraspecific taxa are omitted.

The pretension of survival in the wilderness by consuming wild plants is one unfortunate intimation of the book's title. Weedén does present information on the edibility of many taxa, but many are cast aside with an "edibility unknown".

I have carried W along with M&K in the field for the past two seasons to test the usefulness of the former, and I have generally found W's keys useful, but at times ambiguous. The most frequent problem with W's keys is the improper simplification of morphological terminology. There are few errors, and only one glaring misspelling.

From this field comparison, and making the calculations below, I would say that W deserves a place in the botanist's backpack if weight is costly. One is most likely to go astray with W's keys when botanizing near the lower boundaries of his stated elevational ranges: numerous species common within his limits are not keyed. If we take P to be the probability of keying an unknown,  $P_r$  being a correct determination and  $P_w$  an incorrect determination, and if we assume  $P = .95$  for M&K and  $P = .65$  for W (my estimate !), then  $P_r \text{ gram}^{-1}$  for M&K is .0006, and  $P_r \text{ gram}^{-1}$  for W is .0023. Clearly, then, W wins on a weight basis if determination error is tolerable. However,  $P_w \text{ gram}^{-1}$  for W is .0012, compared to  $P_w \text{ gram}^{-1}$  for M&K of .0003, so that M&K is more exactly accurate on a weight basis.

Botanists do tire from lugging around heavy books in the field, and we do need accurate field guides to introduce the objects of field botany to the people. Weber's *Rocky Mountain Flora* is exemplary in this regard ( $P_r \text{ gram}^{-1} = .0016$ ;  $P_w \text{ gram}^{-1} = .0001$  !). Weeden's book does not quite approach this ideal, but it does serve a distinct need. — DEAN WM. TAYLOR, Department of Botany, University of California, Davis 95616.

*Vascular Plants of the Nevada Test Site and Central-Southern Nevada: ecological and geographical distributions.* By JANICE C. BEATLEY. 1976. vii + 308, 28 figs. Technical Information Center, U. S. Energy Research and Development Administration, Springfield, Virginia 22161. \$9.75. ISBN 0-87079-033-1.

Inaccessible botany is often the product of the distance which botanists are able to travel in their mostly random wanderings during vacations. In the case of the area covered by this floristic volume, long distances from major botanical centers and governmental access restrictions have conspired to make the flora of the 5100 km<sup>2</sup> of the Nevada Test Site and vicinity poorly known. Janice Beatley, assisted in the field at times by several other botanists, has amassed a significant number of collections (25000) in the past fifteen years, and has produced several previous plant checklists for the area. Culminating this effort is the release of this much-needed and reasonably priced book.

The area covered lies on the phytogeographically important transition zone between the Sonoran and Great Basin floristic regions. An introduction presents the background on the previous lack of floristic work in the area. Maps giving the physiographic and political features of the area comprise the first 3 figs., and the fourth gives a generalized vegetation map. Unfortunately, several of the categories in the legend to the latter map are nearly indistinguishable due to poor reproduction. Figs. 5-28 are well chosen photographs of plant habitats.

The bulk of the book is divided into 2 parts: 1) Desert Environment and Vegetation (66 pp.); and 2) Vascular Plants (190 pp.). The first part presents a detailed description of the habitat types in southern Nevada, and is perhaps our most comprehensive description of such to date. Numerous site data are reviewed, including climatic and soil parameters. Kinds of vegetation of the area are discussed in a semi-hierarchical classification: Mojave, Transition and Great Basin deserts subdivided into kinds of sites (bajadas, mountains, arroyos, springs) or plant associations, the latter being typified by phytosociologically uninformative 'genus-genus' or 'genus-common name' epithets. The second part is a catalogue of the flora arranged alphabetically, listing 1093 taxa, describing habitat, local range, and phenology. Keys and descriptions of the taxa are not given. The author justifies this omission by stating that these identification tools "are (or will be) available for nearly all of the taxa in the various floras of adjacent areas." This omission is unfortunate. Keys in

local floras can be more useful than those of the regional manuals in that they simply involve fewer choices, and are often the product of extensive field experiences with the plants in hand.

Following are additional statistics on the flora which might be needed by users of this book. The largest 10 families are (native taxa only): Asteraceae (17.4%), Poaceae (6.8), Polygonaceae (5.8), Fabaceae (5.5), Brassicaceae (4.9), Polemoniaceae (4.8), Scrophulariaceae (4.2), Boraginaceae (3.8), Onagraceae (3.5), Chenopodiaceae (3.4). Of the 125 introductions, 28.8% are Poaceae, and the remainder: Asteraceae (14.4%), Brassicaceae (10.4), Farabaeae and Chenopodiaceae (5.6), Tamaricaceae and Polygonaceae (3.2). A Life Form Spectrum for native taxa is: Phanerophytes (2.9%), Chamaephytes (16.7), Hemicryptophytes (34.4), Geophytes (11.8), Therophytes (31.4), Eiphytes (0.4), Succulents (2.1). Half of the introductions are therophytes, and a fourth are hemicryptophytes.

The layout of the book is of adequate utility, and is mostly free of printing error. However, taxa are not numbered in the catalogue of plants.

All factors considered, the book appears to this reviewer to be a good contestant in the scramble competition for personal and university library dollars. — DEAN WM. TAYLOR, Department of Botany, University of California, Davis 95616.

*The Story of Pines.* By NICHOLAS T. MIROV and JEAN HASBROUCK. xi + 148 pp., including colored frontispiece, forty halftones, five line drawings and one map. Indiana University Press, Bloomington, Indiana. 1976. \$7.95.

If one chose to write a book for the layman about a single group of plants, what could be more appropriate than a genus containing the oldest known living "higher" plant, the bristlecone pine? But not only are some pine individuals long-lived, the group also has a long geological history. The chapter, "The First 200 Million Years" discusses pines from the Jurassic to the present.

Dr. Mirov has worked with and loved pines for more than fifty years. Readers may imagine themselves chatting with the Mirovs in the study or in front of their fireplace, and hearing, in simple language, about fragrance of pines (one of Dr. Mirov's favorite subjects) — why one species exudes a different fragrance than another; or the legend of how the Black Sea *Pinus pityusa* was named for the Greek wood nymph Pitys; or reminiscences on how geneticists developed the science of breeding pines, a science which had its beginning in 1925 at the Eddy Tree Breeding Station in Placerville, California (now the Institute of Forest Genetics). The chapter on the Pine Forest includes discussion of the ecosystem of which the forest is a part, and also takes up the importance of fire to pines, "Fire never exterminated a pine forest; only climate can do that." [that is if man's activities are excluded].

There is all this "and much much more" — structure, physiology, economic importance, natural distribution of pines in the northern hemisphere and their successful introduction into parts of the southern — all in a welcome, readable style. Aspects of pines that still require research are touched upon and these may intrigue the scientists who pick up this volume.

Anyone who feels the exhilaration of being among pines, whether they be on a coastal plain, on a mountain peak, or in the foothills between, will enjoy this book and will undoubtedly look upon pines with a deepened understanding. — ANNETTA CARTER, Herbarium, Department of Botany, University of California, Berkeley 94720.

*Daleae Imagines, an illustrated revision of Errazurizia Philippi, Psorothamus Rydberg, Marina Liebmann, and Dalea Lucanus emend. Barneby, including all species of Leguminosae tribe Amorphaeae ever referred to Dalea.* By RUPERT C. BARNEBY. 891 pp., including 142 plates drawn by the author. Memoirs of the New York Botanical Garden, vol. 27. 1977. \$50.00 (paperbound!).

Sage BARNEBY, who's had his share of fame,  
 With this new work may greener laurels claim;  
 We've seen some monographs of equal length,  
 But few that mix such elegance with strength;  
 So often merit's antonym to size  
 That epic length we're tempted to despise  
 (Thus STANDLEY wrote, with great facility,  
 Long works of flawed reliability,  
 And RYDBERG, who penned much with firm decision,  
 Was cursed, like SMALL, with brash pedantic vision).  
 So now we're grateful for this splendid book  
 Which justifies the decade Rupert took;  
 Amorpheae, as Barneby defines,  
 Includes eight genera in its confines;  
 We're startled that the *Dalea* we knew  
 Was not erected by A. L. JUSSIEU  
 (But after all, we got into this bind  
 Because the great LINNAEUS changed his mind);  
 From *Dalea* two taxa are set free:  
 To *Psorothamnus* goes the fair Smoke Tree,  
*Marina* comes back from obscurity;  
 The prairie clovers (*Petalostemon*)  
 Regain their petals — but their rank has gone.  
 The species groups are many and compound  
 But their new circumscriptions look quite sound;  
 We find that the descriptions and the keys  
 Are well designed, and can be used with ease.  
 The many illustrations set this book apart  
 Through exquisite detail of patient art:  
 The author's pencil draws each plant's Gestalt  
 As BAUER might have done, without a fault;  
 These species portraits, polished and unique  
 (Though one regrettably is forced to seek  
 Each picture far removed from its own text),  
 Have captions discursive and multiplex.  
 Although it would have made the book more weighty,  
 We miss the maps and indexed exsiccatae;  
 Still, these are but inconsequential flaws  
 Which need not damp our chorus of applause:  
 For Barneby, with flair and art precise,  
 Has wrought a masterpiece of awesome price;  
 This noble guidebook to the Daleae  
 Will find botanic immortality.

— GRADY L. WEBSTER, Department of Botany, University of California, Davis 95616.

#### SCIENTIFIC COLLECTING IN MEXICO

In a recent interview with Lic. Juan Soto Fierro of the Departamento de la Consultoría Jurídica del Consejo Nacional de Ciencias y Tecnología, on the matter of collectors, the following rules are presented that should be observed in collecting plants, animals, and geological specimens. This message is directed especially to the Members of the Society who reside outside of Mexico. — Signed:

Biol. Magdalena Peña de Sousa, Presidente,  
 Sociedad Botánica de Mexico.

As an aid to foreign scientists and the Mexican scientific community, the Consejo can help in their applications to the appropriate authorities when it is proposed to make scientific collections in Mexico. In all cases investigators should apply to the Mexican Consulate [nearest them] for entry as "No-immigrante visitante".

#### COLLECTING OF PLANTS, ANIMALS, AND GEOLOGICAL SPECIMENS

Application should be made three months in advance of the proposed collecting trip to Consejo Nacional de Ciencia y Tecnología (CONACYT) (Consultoría Jurídica, Lic. Margarita Peimbert) [Insurgentes Sur 1677, Apdo. Postal 20-033, Mexico 20, D.F., Mexico, telephone 5-34-80-80, Ext. 164]. CONACYT processes applications and issues permits. Applications should give the following information:

1. Name, nationality, and special interest.
2. Letter from their institution stating approval of the proposed investigation; thus an authority of the institution accepts the responsibility of sending a follow-up report.
3. Curriculum vitae.
4. General program of the work, specifying the scientific boundaries to be pursued in the project.
5. Proposed itinerary for the investigation, noting the places and routes to be followed.
6. Intended dates of the investigation.
7. Number and scientific names of the species to be collected.

#### *Animals, Including Insects*

Those collecting animals, including insects, should send in addition:

8. Two photographs of passport size.
9. A check for \$30.00 (U. S.) to "Dirección General de la Fauna Silvestre" for permission, which will be valid only for the year of the expedition.
10. The place and approximate date that they will leave Mexico in order to advise the Delegado Forestal y de Fauna in order to issue a certificate of compliance.

After completing the expedition, the investigator should do the following:

1. Send a report of the field work to CONACYT [see above] and to the Secretaría de Agricultura y Recursos Hidráulicos [Ave. Insurgentes Sur 476, Mexico 7, D.F.].
2. Send a representative series of the collections obtained.

#### *Plants*

Those collecting plants should send a specimen of each species or variety collected, with labels including scientific name, vernacular name, locality, habitat, altitude, and date of collection, plus an ecological description of the locality, to each of the following institutions:

1. Herbario Nacional del Instituto de Biología, U.N.A.M., Apdo. Postal 70-367, México 20, D.F., México.
2. Instituto Nacional de Investigaciones Forestales, Progreso No. 5, Coyoacán, México, D.F., México.

Also send to both of the above institutions a copy of the final report as well as any publications that result.

\*\*\* Massive collection of plants is prohibited. \*\*\*

#### *Both Plants and Animals*

Check at point of departure from Mexico with Delegado Forestal y de la Fauna and obtain certificate of having complied with the stipulations of the permit.

The Secretaría de Agricultura y Ganadería stipulates that failure to comply with any of the mentioned requisites will be sufficient to prevent granting of further permission either to the person in question or to the institution who recommended the investigator.

[Above translated from Macpalxichitl, the Boletín Bimestral de la Sociedad Botánica de México, Sep-Oct 1977, by Annetta Carter.]

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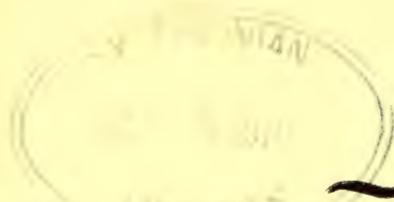
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Editorship of Madroño. — Terms of current editors of Madroño end 31 June 1978. The Board of Directors of the California Botanical Society have appointed James Hickman to serve as Editor. After 15 June 1978, manuscripts intended for publication in Madroño should be sent to Dr. James C. Hickman, Department of Botany, University of California, Berkeley 94720.



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# MADROÑO

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# SYSTEMATICS OF MIRABILIS SUBGENUS QUAMOCLIDION (NYCTAGINACEAE)

GEORGE E. PILZ

Department of Biology, The Polytechnic, Ibadan, Nigeria

Monographs and revisions by Standley (1909, 1911, 1918) and Heimerl (1889, 1897, 1934) form the basis of the present taxonomic knowledge of a predominantly North American family. After having studied the family for over two decades, Standley (1931a) stated that he knew few groups of plants in which specific differences were more unstable or baffling. After studying South American material, Standley (1931b) transferred to *Mirabilis* all those plants he had previously placed in *Oxybaphus*, *Hesperonia*, *Quamoclidion*, and *Allioniella*. Heimerl (1934) followed Standley's circumscription of *Mirabilis* but retained *Quamoclidion* with the single species of *Q. triflorum*. Subsequent treatments of *Mirabilis* (sensu Standley, 1931b) have dealt only with small parts of the genus as they are represented in regional floras.

Plants referable to *Mirabilis* subgenus *Quamoclidion* are characterized by a gamophyllous involucre that is only slightly accrescent after anthesis and surrounds three or more flowers. An initial purpose of this study was to compare the broad, ovate, distinct bract subtending each individual flower of *Hermidium alipes* with the gamophyllous involucre of *Quamoclidion*. As a taxonomic result of this study I am transferring *Hermidium alipes* to *Mirabilis* subgenus *Quamoclidion*.

*Mirabilis* subgenus *Quamoclidion* comprises six species that grow predominantly in western North America between 20°–45° N. Open habitats at the lowermost edge of juniper woodland are where most populations and the greatest number of plants per population are found. *Quamoclidion* is not restricted, however, to areas where *Juniperus* occurs. *Mirabilis triflora* inhabits a scrub vegetation dominated by *Acacia*, *Opuntia*, and an occasional *Ficus* in Baja California del Sur and in Jalisco. At the other geographic extreme *M. marfarlanei* shares dry sand bars with *Celtis* on the floors of the Snake and Salmon River canyons.

## MORPHOLOGY

My circumscription of *Quamoclidion* is based on characters that are stable and rather uniform within the subgenus but which differ widely in other members of Nyctaginaceae. These include inflorescence and pollen morphologies as well as chromosome number and habitat preference. Floral and fruit morphologies possess the most diagnostic characters for circumscription of species within *Quamoclidion* because they are stable at the population level but may vary considerably within a species. Leaf

shape and vestiture vary considerably even within populations. Unfortunately, characters used by other authors (Heimerl, 1934; Standley, 1918) to delimit species of *Mirabilis* are those which I have found to vary widely within populations due to extreme seasonally and environmentally induced morphological variation.

**INFLORESCENCE.** Flowers of *Quamoclidion* are arranged in solitary, determinate, involucrate heads at ends of branches and in axils of upper cauline leaves. As in *Bougainvillea*, each flower is intimately associated with a subtending bract. Most taxa of *Quamoclidion* have a six-flowered head consisting of a naked, solitary, central flower surrounded by five flowers borne on the bases of gamophyllous involucre bracts. Occasionally the central flower is not naked. In all taxa of *Quamoclidion*, I have observed heads that possess central flowers subtended by a distinct bract similar to one of the involucre bracts. Barneby (1942) stated that this occasional occurrence suggests that heads of "advanced" members of *Quamoclidion* may have evolved rather recently from the "primitive bougainvilleoid" flower head of *Mirabilis alipes*, in which every flower has its own independent, subtending floral bract. Although distinct bracts are usual in this species, heads with the five outermost bracts united by their margins to one-half their length are common. These involucre are campanulate and have the aspect of the gamophyllous involucre of other taxa within *Quamoclidion*.

Exceptions to the six-flowered head of most taxa of *Quamoclidion* occur in the consistently three-flowered *Mirabilis triflora* and in *M. greenii* with as many as 16 flowers in some involucre. When a second or third whorl of flowers is present, each member of the whorl is borne on the midvein of one of the five bracts, each one distal to the flower of the first whorl. Flowers on the second and third whorls often abort before anthesis but many others may produce fruit.

**POLLEN.** Nowicke (1970), utilizing light microscope and scanning electron microscope techniques, found that pollen of Nyctaginaceae is structurally variable; however, features within genera are remarkably uniform. This is certainly true for the uniformly very large, spheroidal, and pantoporate pollen grains, with a spinulose sexine pattern, of *Quamoclidion*. Pollen-grain diameters form a continuum (100–160  $\mu\text{m}$ ) and are not taxonomically useful for separating taxa within the subgenus. The range, standard deviation, and mean of pollen-grain diameters from 54 collections of *Quamoclidion* may be found elsewhere (Pilz, 1974).

Pollen viability is typically very high. If immature flowers or flowers from plants that are obviously under water stress are observed, the pollen viability sometimes drops below 90%. The relatively small pollen-grain diameter reported by Nowicke (1970) for *Mirabilis alipes* is probably due to the selection of an immature flower. A notable exception, *M. pudica*, often has 30–50% of its grains ill-formed and noticeably

smaller than the mean grain size of other species. These smaller grains also fail to stain in aniline blue-lactophenol. Only one collection of *M. pudica* (Beatley 8211, RSA) has nearly 100% viable pollen, and this is coupled with a significantly smaller grain diameter than is typical of the species. This aspect of the reproductive biology of *M. pudica* requires further study because other collections made by Beatley in the same area have the low viability typically found in the species throughout its geographic range.

**FRUITS.** The basal portion of the perianth begins to enlarge rapidly soon after fertilization, reaching a size slightly larger than that of the mature fruit. It is initially bright green and contains an ovary that is about one-fifth that of the ultimate size of the fruit. The developing embryo enlarges and fills the cavity of the persistent perianth, and the mature fruit is termed an anthocarp: "a fruit formed by the union of floral organs or part of them, with the fruit itself" (Jackson, 1928). A thin pericarp envelops the single uncinat embryo and the mealy perisperm. The endosperm is completely absorbed during growth and maturation of the embryo, except for a small amount forming a cap or collar around the apex of the radicle. Cells of the nucellus become packed with starch and form a mealy perisperm, which constitutes the storage tissue of the mature seed (Cooper, 1949).

Anthocarps are generally ellipsoidal, although they range from narrowly ovoid to subglobose (Fig. 1). The proximal end is constricted and the distal end may be so to a lesser extent. Anthocarps are brown to nearly black except in *Mirabilis alipes*, which has olive-green fruits that turn brown only if they are wetted after maturity and allowed to dry again. Ten slender, tan, longitudinal ribs are evident on anthocarps of most species, particularly those of *M. multiflora*. These are remnants of vascular traces that earlier extended to the upper portion of the perianth.

The surface of mature anthocarps is sparsely pubescent in *Mirabilis triflora* and in some individuals of *M. multiflora* var. *glandulosa*. Other members of *Quamoclidion* have glabrous anthocarps. The anthocarp surface is smooth or rugulose, a difference that is correlated with production of mucilage by the fruit when wetted. The rugulose anthocarps of *M. triflora*, *M. alipes*, *M. greenei*, *M. macfarlanei*, and *M. multiflora* var. *glandulosa* produce mucilage in variable amounts. *Mirabilis triflora* produces a light mucilage that surrounds the fruit and is two or three times the volume of the anthocarp. Other mucilage-formers produce a thick heavy substance that is usually less than 1 mm thick. Plants of those taxa that have smooth anthocarps, on the other hand, produce no mucilage when wetted. *Mirabilis pudica*, *M. multiflora* var. *multiflora* and *M. multiflora* var. *pubescens* are included in this second group.

#### CHROMOSOME NUMBERS AND REPRODUCTIVE BIOLOGY

Chromosome numbers have been reported for only 19 of the more than

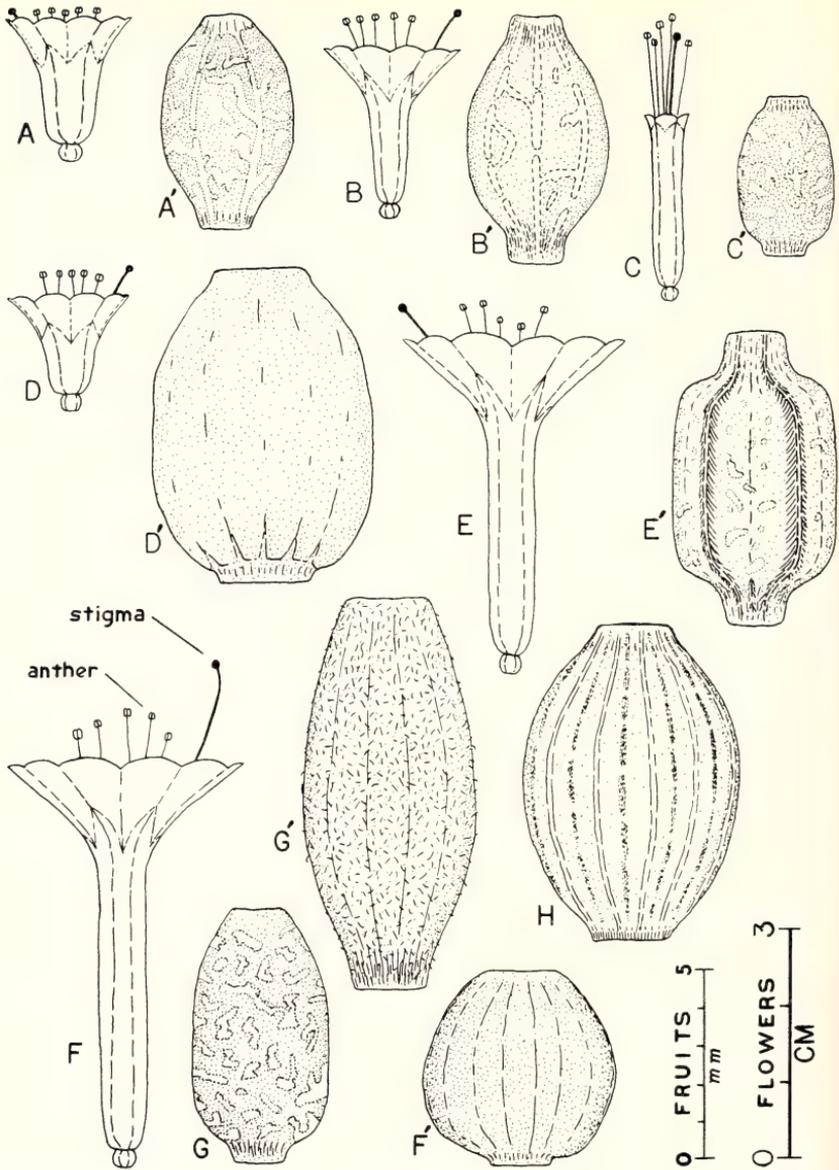


FIG. 1. Representative flowers and anthocarps of *Mirabilis* subg. *Quamoclidion*. Collection numbers are mine unless otherwise indicated. Voucher specimens are in UC. A. *M. alipes* 788, A'. 1125; B. *M. macfarlanei* Constance et al. 1579. B'. 1282; C. *M. triflora* 1270, C'. 949; D. *M. pudica* Ripley & Barneby 4403, D'. 1132; E. *M. greenii* 998, E'. 990; F. *M. multiflora* var. *multiflora* 1235, F'. 869; G. *M. multiflora* var. *glandulosa* 1151, G'. Osterhout 6559; H. *M. multiflora* var. *pubescens* 831.

250 taxa of Nyctaginaceae (Pilz, 1974). Many counts were determined from serial sections of paraffin-embedded material, a technique that can easily lead to errors in interpretation (Epling et al., 1962). Showalter (1935), using paraffin-embedded material reported  $n = 29$  for *Mirabilis multiflora*. This report is probably due to incorrect interpretation of sectioned material. Using slightly modified aceto-carmin squash techniques (Beeks, 1955; Pilz, 1974) for anthers and root tips I have consistently found the gametic chromosome number  $n = 33$  in the taxa under consideration throughout their geographical ranges (Table 1). This consistency is significant in view of the variation existing within the family as a whole. Species of the same genus within the family tend to have identical chromosome numbers although considerable variation occurs within both *Boerhavia* and *Bougainvillea* that have both aneuploid and polyploid series (Pilz, 1974).

Except for *Mirabilis triflora* all species of *Quamoclidion* are night-blooming. The ephemeral flowers usually open about three hours before dusk and close about mid-morning. Cloudy days may extend the hours that flowers remain open in the morning; however, once closed, the thin delicate perianth lobes become flaccid and do not reopen.

Visitations to flowers by several kinds of animals have been observed, but only hummingbirds and hawkmoths are effective pollinators. Ants, bees, butterflies, and even flies commonly visit the flowers and collect pollen (Cruden, 1970), but the exerted style, 2–30 mm beyond the perianth tube, and its position at one side of the flower make the transfer of pollen to the stigma by these organisms rare.

I have observed *Hylocharis xanthusii*, the Black-Fronted Hummingbird, a species restricted to the southern half of Baja California, to be the principal pollinator of *Mirabilis triflora* in that region. While hovering before the long red tubular flower and taking nectar, the birds brush the exerted stamens and stigma with the tops of their heads, which become yellow with pollen. Hummingbirds show very low species consistency.

TABLE 1. CHROMOSOME NUMBERS IN *Mirabilis* SUBG. *Quamoclidion*. Collection numbers are mine. Voucher specimens are in UC.

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<i>M. pudica</i> Barneby. Nevada, Lincoln Co., 4 mi W of Crystal Spring, 975	$2n = 33$ II.
<i>M. greenei</i> S. Wats. California, Glenn Co., 7 mi N of Stonyford, 1274,	$2n = 33$ II.
<i>M. multiflora</i> (Torr.) Gray var. <i>multiflora</i> . New Mexico, Grant Co., 3 mi. W of San Lorenzo, 724,	$2n = 33$ II.
New Mexico, Catron Co., 10 mi S of Luna, 726,	$2n = 33$ II.
Arizona, Coconino Co., 6 mi SE of Desert View, 1236,	$2n = 66$ .
New Mexico, Rio Arriba Co., 8 mi W of Abiquiu Dam, 1245,	$2n = 66$ .
<i>M. multiflora</i> (Torr.) Gray var. <i>pubescens</i> S. Wats. California, Kern Co., Caliente, 081,	$2n = 66$ .
Arizona, Mohave Co., 23 mi E of Kingman, 910,	$2n = 33$ II.
California, Kern Co., Caliente, 961,	$2n = 33$ II.
Nevada, Lincoln Co., 13 mi S of Caliente, 1143,	$2n = 33$ II.
<i>M. multiflora</i> (Torr.) Gray var. <i>glandulosa</i> (Standley) Macbr. Nevada, White Pine Co., 1 mi E of Connor's Pass, 1144,	$2n = 33$ II.
<i>M. triflora</i> Benth. Baja California del Sur, 2 mi N of La Burrera, 947,	$2n = 33$ II.

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cy when visiting flowers unless a single nectar-producing species markedly predominates (Baker, 1961). *Mirabilis triflora* often grows in large, dense populations in the Laguna Mountains of Baja California del Sur, and this, along with the abundance of hummingbirds observed visiting the flowers, may account for the very high percentage of seed set (see further discussion below).

Pollinators of taxa other than *Mirabilis triflora* are less certainly known. Baker (1961) reported that *M. multiflora* var. *pubescens* (*M. froebelii*) is visited by hawkmoths, *Celerio lineata*, at the University of California Botanical Garden in Berkeley, but this site is outside the natural range of the species. He also noted that hummingbirds make their visits in the morning and evening when the flowers are open, and he hypothesized that the sharing of flowers by both hawkmoths and hummingbirds may be a widespread phenomenon (Baker, 1961). Cruden (1973) stated that flower opening and anther dehiscence occurs too late in the day in *M. multiflora* for visits by hummingbirds and bees "prior to visitation by hawkmoths, the coevolved pollinators". In contrast, I have observed hummingbirds and hawkmoths sharing flowers of *M. multiflora* with dehisced anthers at dusk in Grant County, New Mexico. Thus at least some sharing of floral resources by these two pollinators is occurring late in the day soon after the flowers open. No pollinators of other taxa have been reported, and I have not observed any.

The amount of seed set on a plant is often extremely low. Plants isolated from others by more than 100 m rarely produce fruit. This probably is due to their self-incompatible breeding system, known in at least three taxa (Pilz, 1974), coupled with the lack of compatible pollen transfer to these isolated plants. Many populations fail to produce fruit in a given year. I have recorded abortion, presumably due to lack of available water, of all flower buds on all plants of some populations of *Mirabilis alipes*, *M. macfarlanei*, *M. greenei*, and *M. multiflora*. Absence of pollinator visits during periods of strong winds also contributes to low seed set recorded for populations of *M. alipes*.

Establishment of new plants within a population is presumably infrequent in this group of long-lived perennials. In three years of field work I have seen only two first-year seedlings. After the first-year stage it is difficult if not impossible to estimate the age of plants, so I have little idea of the age-distribution of plants within populations.

#### TAXONOMIC TREATMENT

MIRABILIS L. subg. QUAMOCLIDION (Choisy) Jepson, Flora Calif. 1(4):457. 1974. — *Quamoclidion* Choisy in DC. Prodr. 13(2):429. 1849. — *Mirabilis* sect. *Quamoclidion* (Choisy) Gray, in Torr. Bot. Mex. Bound. Surv. 173. 1859 [This combination has been erroneously attributed to Heimerl, Nat. Pflanzenfam. 3(1b):24. 1889]. Type: *Mirabilis triflora* Benth.

*Hermidium* S. Wats., Bot. King's Exped. 5:286. 1871. Type: *Hermidium alipes* S. Wats.

*Mirabilis* sect. *Paramirabilis* Heimerl, Notizbl. Bot. Gart. Berlin-Dahlem 11(106):453. 1932. Type: Heimerl (1932) included two species in this section; I here designate as lectotype, *Mirabilis multiflora* (Torr.) Gray.

Herbaceous perennials from a long spongy cylindrical taproot, the stems branching alternately or subdichotomously from an expanded multicipital caudex; branches erect or ascending to nearly decumbent, the primary branches stout, more slender above, swollen at nodes; herb-age green, occasionally purplish-red on surfaces exposed to direct sunlight, densely pubescent to glabrous; leaf opposite, petiolate, thin to succulent, decurrent at base onto petiole, margins entire to repand; lowermost leaves orbicular to widely ovate; middle cauline leaves very widely ovate to ovate; uppermost leaves ovate to lanceolate, highly reduced near involucre; leaf stomata anomocytic; peduncles axillary and in terminal cymes, erect to abruptly reflexed; flowers involucrate, heads 3-16-flowered; involucre bracts connate to distinct, slightly accrescent in age; perianth tubular, campanulate, or funnellform-salverform, magenta to creamy white, constricted above the ovary, the limb 5-lobed; stamens 5, circinate before anthesis, filaments unequal, capillary, pubescent to glabrous, connate at base into a cup enveloping the ovary; anther of paired locules, yellow, versatile, loculicidal; pollen grains spheroidal, pantoporate, sexine spinulose, spinules 1  $\mu$ m long; ovary ellipsoidal, green, style filiform, glabrous, stigma capitate, papillose, magenta; anthocarp ovoid to ellipsoidal, smooth to rugulose, glabrous to sparsely pubescent; seed with light brown testa, adherent to pericarp; embryo uncinat, perisperm enclosed on three sides by cotyledons and bounded by hypocotyl and descending radicle on the other. Chromosome number  $n = 33$ .

Involucre heads 5-16-flowered; involucre bracts 12-35 mm long; fruit 5-11 mm long.

Free portion of perianth campanulate.

Head erect on peduncle; leaves horizontally oriented; fruit 5-7 mm long, olive-green, rugulose . . . . . 1. *M. alipes*.

Head pendent upon recurved peduncle; leaves conspicuously ascending; fruit 7-8 mm long, dark brown, smooth . . . . . 2. *M. pudica*.

Free portion of perianth funnellform-salverform.

Perianth 15-25 mm long; involucre bracts 15-20 mm long . . . . . 3. *M. macfarlanei*.

Perianth 35-60 mm long; involucre bracts 20-35 mm long.

Fruit 5-angled . . . . . 4. *M. greenii*.

Fruit ovoid to subglobose, not angled . . . . . 5. *M. multiflora*.

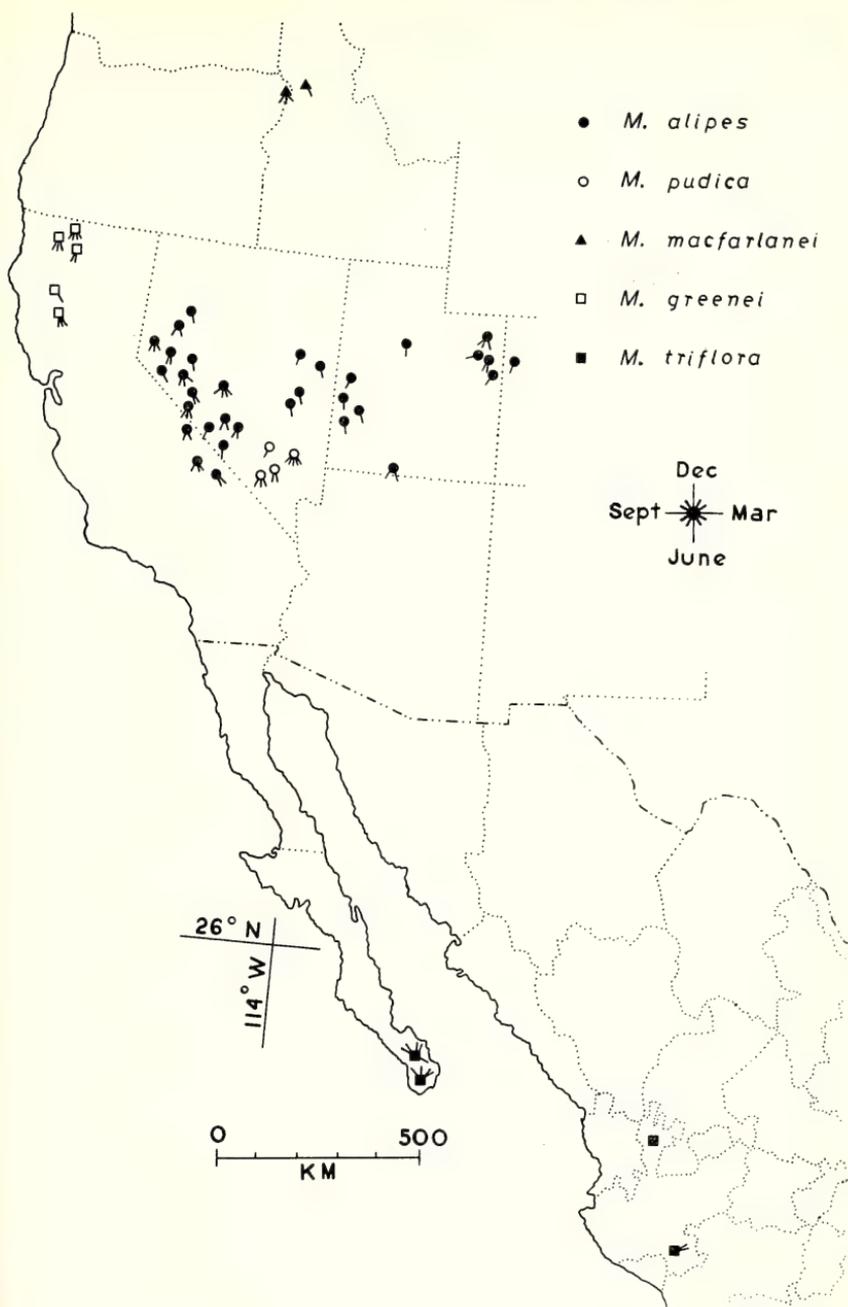
Involucre heads 3-flowered; involucre bracts 7-10 mm long; fruit 4-5 mm long . . . . . 6. *M. triflora*.

1. **MIRABILIS ALIPES** (S. Wats.) Pilz, comb. nov.—*Hermidium alipes* S. Wats., Bot. King's Exped. 5:268. 1871. Type: Nevada, Humboldt Valley, May 1868, *S. Watson 968* (erroneously cited as "1860" and "960" by Standley, 1909). Holotype: US! isotypes; GH!, NY!

*Hermidium alipes* S. Wats. var. *pallidum* Porter, Rhodora 54:158. 1952. Type: Utah, Uintah Co., "on the Wasatch formation, 5 miles south of Vernal", 3 June 1950, *C. L. Porter 5308*. Holotype: RM!; isotypes: CAS!, MO!, RSA!, SMU!, TEX!, UC!

Plants from taproot 1–2 m long, 3–5 cm in diameter; branches erect or ascending to nearly decumbent, 2–4 dm high, forming hemispheric clumps 6–8 dm in diameter, the primary branches stout, 4–6 mm thick, more slender above; herbage pale green, glabrous to very sparsely puberulent; leaves horizontally spreading, succulent, glaucescent; lowermost leaves suborbicular to widely ovate and occasionally asymmetrical, 4–7 cm long, 3.5–6.5 cm wide, base rounded, apex obtuse to rounded and occasionally apiculate; middle cauline leaves ovate to widely ovate and often asymmetrical, 4.5–5.0(–9) cm long, 3.5–4.0(–5) cm wide, base rounded, apex obtuse (rarely acute) and occasionally apiculate; uppermost leaves narrowly ovate and symmetrical, 2.5–4.0 cm long, 1–2 cm wide, base obtuse to rounded, apex acute; petioles often narrowly winged, 5–7 mm long on lower leaves, the uppermost leaves sessile; leaf stomata 30–36  $\mu\text{m}$  long, 18–24  $\mu\text{m}$  wide; peduncles 3–10 mm long, 1 mm in diameter, erect to ascending; involucre consisting of distinct bracts, or bracts united by their margins to one-half their length, the tube to 15 mm long or lacking and the free portions 15–30 mm long, 10–25 mm wide, ovate, apex acute to obtuse (rarely rounded), often apiculate; involucre 6–8(–9)-flowered, the individual flowers borne on pedicels 0.2–1.0 mm long on midvein of involucral bract, 1 flower on each midvein; perianth campanulate, 15–16 mm long, magenta, occasionally creamy white, glabrous, tube 6–7 mm long, 5–6 mm broad, throat gradually widening, 5–6 mm long, the 5 lobes very widely ovate, 1–2 mm long, 7–10 mm broad, apex emarginate, longitudinal nerves 5, extending to the sinus, apex of nerve pubescent; stamens equalling perianth, filaments pubescent to middle, glabrous above, pollen grains 106–133  $\mu\text{m}$  in diameter; style exerted 2–10 mm; anthocarp ellipsoidal with 10 slender tan longitudinal ribs, slightly constricted at both proximal and distal ends, 5.5–7.0 mm long, 3.0–4.5 mm wide, mottled olive-green, rugulose, glabrous, producing a thick heavy mucilage when wetted.

**DISTRIBUTION** (Fig. 2). Scattered throughout much of Great Basin; transmontane California (Inyo and Mono counties) across Nevada and Utah to Rio Blanco Co., Colorado. On gravelly-sandy soil of mesas, washes, and alluvial fans between 1200 and 2000 m in Shadscale Scrub and Sagebrush Scrub, or, rarely, Pinyon-Juniper Woodland. Flowers early May through mid-June.

FIG. 2. Distribution and date of collection of *Mirabilis*.

The status of *Mirabilis alipes* as a monotypic representative of a distinct genus, *Hermidium*, has always been based on the possession of discrete involucre bracts (Heimerl, 1934; Standley, 1918). Although perfectly distinct bracts are typical, heads with the five outermost bracts united by their margins to one-half their length are common. These involucre bracts are campanulate and have the aspect of the gamophyllous involucre bracts of other taxa within *Quamoclidion*. Flowers, leaves, and fruits of *M. alipes* closely resemble those of other taxa within *Quamoclidion*. Much more morphological variation occurs within *Mirabilis* (sensu Standley, 1931b) than exists between *Quamoclidion* and *Hermidium*. Thus the inclusion of *M. alipes* within subgenus *Quamoclidion* places it with its closest relatives and represents the most "natural" classification for these species.

I have observed several populations of plants in Pershing, Washoe, and Nye counties, Nevada (*Pilz* 1113, 1127, 1128, 1276-79; all in UC), which possess creamy white perianths and are referable to Porter's (1952) var. *pallidum* from northeastern Utah. These occur, in this region, in populations with plants possessing purple perianths and a wide range of intermediate colors. They do not appear distinct enough to warrant varietal status.

2. *MIRABILIS PUDICA* Barneby, *Leafl. W. Bot.* 3:175. 1942. Type: Barneby (1942) designated two cotypes; I here designate as lectotype (CAS!): Nevada, Lincoln Co., "3 miles W. of Crystal Springs", 10 May 1942, *Ripley and Barneby* 4403. Isotypes: GH!, K!, NY!, RSA!, UC!

Plants from a taproot 1-2 m long, 3-5 cm in diameter; branches erect or ascending, 3-5(-6) dm high, forming upright columnar clumps 3-5 dm in diameter, the primary branches 3-5 mm thick, more slender above; herbage pale green to whitish, glabrous to densely pubescent; leaves conspicuously ascending, very often vertically oriented, succulent, glaucescent; lowermost leaves ovate to widely ovate and symmetrical, 1.5-3.0 cm long, 1.0-2.5 cm wide, base obtuse to acute, apex acute to rounded and apiculate; middle cauline leaves ovate to narrowly ovate and symmetrical, 3.5-5.0 cm long, 2.0-2.5 cm wide, base acute to rounded (rarely cordate), apex acute; uppermost leaves narrowly ovate to lanceolate and symmetrical, 1.4-3.7 cm long, 0.5-1.8 cm wide, base rounded to acute, apex acute; petioles short, often narrowly winged, 3-5 mm long on lowermost leaves, the uppermost leaves sessile; leaf stomata 27-36  $\mu\text{m}$  long, 24-30  $\mu\text{m}$  wide; peduncles 6-10 mm long, 1 mm in diameter, abruptly reflexed to produce a pendent involucre; involucre campanulate to nearly rotate in fruit, 12-21 mm long, the bracts united by their margins, the tube 5-10 mm long, unequally 5-lobed, free portion of bract 6-12 mm long, 9-17 mm wide at base, triangular to widely ovate, apex acute, apiculate; involucre 6-flowered, the flowers borne on pedicels 0.2-1.0 mm long, on midvein of involucre bracts, 1 flower on each mid-

vein, the central flower solitary and naked (rarely subtended by a distinct bract); perianth campanulate, 12–14 mm long, creamy white, glabrous to densely pubescent, the tube 5–6 mm long, 6–7 mm broad, the throat gradually widening, 5–6 mm long, the five lobes very widely ovate, 2–3 mm long, 6–9 mm broad, apex emarginate, the five longitudinal nerves extending to the sinus, apex of nerve densely pubescent; stamens exerted 2–4 mm, filaments villous to middle, glabrous above, pollen grains 110–145  $\mu\text{m}$  in diameter; style exerted 3–5 mm; anthocarp ellipsoidal to widely ellipsoidal with 10 slender tan ribs occasionally evident at base, occasionally constricted at both proximal and distal ends, 7–8 mm long, 4.5–5.0 mm wide, dark brown, smooth, glabrous, not producing mucilage when wetted.

DISTRIBUTION (Fig. 2). On calcareous alkaline hills and sandy playas of Lincoln and Nye counties, Nevada, in Shadscale Scrub and Creosote Bush Scrub between 1000 and 1500 m. Flowers early May to mid-June.

This is a distinctive species within *Quamoclidion* because of its heads, which are pendent upon recurved peduncles, and its conspicuously ascending, often vertically oriented, leaves.

3. *MIRABILIS MACFARLANEI* Constance & Rollins, Proc. Biol. Soc. Wash. 49:148. 1936. Type: Oregon, Wallowa Co., "Lower Cottonwood Landing, between mouth of Somer's Creek and Pittsburg Landing, Snake River Canyon", 15 May 1936, *Constance, Rollins, Clements and Dillon 1579*. Holotype: WS!; isotypes: CAS!, DS-2 sheets!, GH!, JEPS!, K!, MO!, NY!, POM-2 sheets!, RM!, UC-2 sheets!, US-2 sheets!, WIS!, WS!

Plants from taproot 1–2 m long, 3–5 cm in diameter; branches erect or ascending to nearly decumbent, 6–8(–10) dm high, forming hemispheric clumps 8–10(–12) dm in diameter, the primary branches stout, 6–8 mm thick, more slender above; herbage green, glabrous to sparsely puberulent; leaves horizontally spreading, succulent, glaucescent on lower surface; lowermost leaves orbicular to very widely ovate, 2.0–5.5 cm long, 2.5–6.5 cm wide, base obtuse to cordate and often asymmetrical, apex rounded to broadly obtuse (rarely short apiculate); middle cauline leaves suborbicular to widely ovate, 3.5–4.5 cm long, 3.0–4.5 cm wide, base obtuse to cordate and symmetrical, apex obtuse to rounded (rarely acute) and often short apiculate; uppermost leaves ovate and symmetrical, 1.5–3.0 cm long, 1.0–2.5 cm wide, base rounded to obtuse (rarely cordate), apex acute; petioles stout, 17–25 mm long on lowermost leaves, the uppermost leaves sessile; leaf stomata 27–30  $\mu\text{m}$  long, 21–24  $\mu\text{m}$  wide, peduncles 4–8(–25) mm long, 1 mm in diameter, erect to ascending; involucre campanulate to nearly rotate in fruit, 13–20 mm long, the bracts united by their margins, the tube 6–12 mm long, unequally 5-lobed, the free portion of bract 6–12 mm long, 11–14 mm wide at base, triangular to very widely ovate, the apex acute to acuminate; involucre 6-flowered, the flowers borne on pedicels 1–3 mm long, on midvein of

involucral bracts, 1 flower on each midvein, the central flower solitary and naked (rarely subtended by a distinct bract); perianth funnellform-salverform, 15–25 mm long, magenta, glabrous, the tube 7–12 mm long, 3–4 mm broad, the throat gradually widening, 5–7 mm long, the five lobes very widely ovate, 2–3 mm long, 6–9 mm broad, the apex emarginate, the five longitudinal nerves extending to the sinus, apex of nerve densely pubescent; stamens exerted 3–4 mm, filaments glabrous, pollen grains 115–122  $\mu\text{m}$  in diameter; style exerted 4–5 mm; anthocarp ellipsoidal with 10 slender tan ribs, constricted at the proximal and often the distal end, 6–7 mm long, 3–4 mm wide, brown to dark brown, slightly tuberculate, glabrous, mucilaginous when wetted.

DISTRIBUTION (Fig. 2). On dry exposed slopes bordering the Snake and Salmon rivers of Oregon and Idaho, between 450 and 500 m. Flowers throughout May.

*Mirabilis macfarlanei* is most notable for its geographic isolation in the Snake and Salmon river canyons. These are much more arid than the surrounding canyon walls and mountain slopes, which support Yellow Pine Forest. The closest relative of this species is probably *Mirabilis multiflora* var. *glandulosa* with which it shares a funnellform-salverform perianth, general anthocarp characteristics, and a similar though more depauperate flavonoid profile (Pilz, 1974).

This taxon is named for E. B. MacFarlane, for 30 years a pilot of boats on the Snake River, who pointed out the location of the plant to the authors. It has been said that Harold St. John had pointed out the plant to MacFarlane on an earlier trip up the river, but St. John did not publish his find (Constance, pers. comm.).

4. MIRABILIS GREENEI S. Wats., Proc. Amer. Acad. Arts 12:253. 1876 (1877). — *Quamoclidion greenei* (S. Wats.) Standley, Contr. U. S. Natl. Herb. 12:358. 1909. Type: California, Siskiyou Co., "mountain sides about Yreka", 20 June 1876, *E. L. Greene* 876. Holotype: GH! mounted with *V. Rattan* 56, June 1884; isotype: NY! mounted with *T. Howell* 1389, July 1889.

Plants from taproot 2–4 m long, 3–5(–12) cm in diameter; branches erect or ascending to nearly decumbent, 4–8 dm high, forming hemispheric clumps 6–10 dm in diameter, the primary branches stout, 5–13 mm thick, more slender above; herbage green, glabrous to very sparsely puberulent; leaves horizontally spreading, succulent, glaucescent; lowermost leaves orbicular to suborbicular, 3.0–5.5 cm long, 2.5–5.0 cm wide, base obtuse to cordate and often asymmetrical, apex rounded to obtuse; middle cauline leaves widely elliptic to ovate, 4.0–7.5 cm long, 3.0–4.5 cm wide, base obtuse and often asymmetrical, apex acute or acuminate; uppermost leaves narrowly ovate to elliptic and symmetrical, 2.7–4.5 cm long, 1.0–2.5 cm wide, acute at base and apex; petioles stout, 10–27 mm long on lowermost leaves, the uppermost leaves sessile; leaf stomata 30–36  $\mu\text{m}$  long, 24–30  $\mu\text{m}$  wide; peduncles 25–85 mm long, 1.5–2.0 mm

in diameter, erect or ascending; involucre campanulate, 26–36 mm long, the bracts united by their margins, the tube 13–20 mm long, unequally 5-lobed, the free portion of bract 10–17 mm long, 10–13 mm wide at base, triangular to widely ovate, the apex acute to acuminate; involucre 6(–16)-flowered, the flowers borne on pedicels 1–4 mm long, on midvein of involucral bract, as many as 3 flowers borne along a single bract, the central flower solitary and naked (rarely subtended by a distinct bract); perianth funnellform-salverform, 40–50 mm long, magenta, glabrous, the tube 25–30 mm long, 5–7 mm broad, the throat gradually widening, 12–15 mm long, the five lobes very widely ovate, 3–5 mm long, 10–14 mm broad, the apex emarginate, the five longitudinal nerves extending to and 1 mm beyond the sinus, apex of nerve densely pubescent; stamens exerted 1–5 mm, filaments glabrous, pollen grains 130–150  $\mu\text{m}$  in diameter; style exerted 3–5 mm; anthocarp widely obovoid to widely ellipsoidal, 5-angulate, constricted at both proximal and distal ends, 7.0–7.5 mm long, 4.0–4.5 mm wide, light brown, tuberculate, very sparsely puberulent to glabrous, mucilaginous when wetted, the mucilage most abundant on ribs (10 visible when wet).

DISTRIBUTION (Fig. 2). Scattered on eastern flank of North Coast and Klamath ranges from Colusa Co. to Siskiyou Co., California. Growing on steep talus slopes and gravelly flats with junipers from 400 to 1000 m. Flowers early May to mid-June.

*Mirabilis greenei* is easily recognizable within *Quamoclidion* because of its distinctive 5-angled fruit, an involucre that often surrounds more than six flowers, and a novel flavonoid profile (Pilz, 1974).

5. MIRABILIS MULTIFLORA (Torr.) Gray, in Torr. Bot. Mex. Bound. Surv. 173. 1859.

Plants from taproot 1–2 m long, 2–5 cm in diameter; branches erect or ascending to nearly decumbent, forming hemispheric clumps 6–8 dm in diameter, the primary branches stout, 5–12 mm thick, more slender above; herbage green, densely pubescent to glabrous; leaves horizontally spreading, succulent, glaucescent; lowermost leaves orbicular to very widely ovate and often asymmetrical, (3–)5–12 cm long, (4–)5–15 cm wide, base rounded to cordate, apex rounded to obtuse, occasionally mucronate; middle cauline leaves ovate to very widely ovate and often asymmetrical, 5–10 cm long, 4–8 cm wide, base cordate to rounded, apex obtuse to acuminate and often apiculate; uppermost leaves widely ovate to narrowly ovate and only slightly asymmetrical, 2–7 cm long, 1–5 cm wide, base cordate to obtuse, apex acute to acuminate and often apiculate; petioles slender to stout, 20–40 mm long on lowermost leaves, the uppermost leaves subsessile; leaf stomata 24–36  $\mu\text{m}$  long, the bracts peduncles 4–75 mm long, 1–2 mm in diameter, erect to ascending; involucre campanulate to broadly campanulate, 22–35 mm long, the bracts united by their margins, the tube 11–25 mm long, unequally 5-lobed, the free portion of bract 6–14 mm long, 8–17 mm wide at base, triangular to

very widely ovate, apex acute to rarely obtuse in fruit, apiculate; involucre 6-flowered, the flowers borne on pedicels up to 2 mm long on midvein of involucre bracts, one flower on each midvein, the central flower solitary and naked (rarely subtended by a distinct bract); perianth funnelform-salverform, 40–60 mm long, magenta, occasionally the tube green, puberulent to glabrous, the tube 27–40 mm long, 5–10 mm broad, the throat gradually widening, 10–20 mm long, the five lobes very widely ovate, 2–7 mm long, 10–20 mm broad, apex emarginate, the five longitudinal nerves extending to the sinus, apex of nerve densely pubescent; stamens exerted 1–10 mm, filaments glabrous to pubescent, pollen grains 118–150  $\mu\text{m}$  in diameter; style exerted 3–13 mm; anthocarp ellipsoidal to widely ellipsoidal, often constricted at both proximal and distal ends, 6–11 mm long, 4.0–5.5 mm wide, brown with 10 slender tan longitudinal ribs alternating with 10 raised dark brown (often interrupted) ribs to nearly solid black, rugulose to smooth, glabrous to pubescent, the mucilage production diverse.

*Mirabilis multiflora* may be divided into three varieties as follows:

Fruit smooth to only slightly tuberculate, producing no mucilage when wetted; involucre bracts acute.

Fruit dark brown to black, the ribs inconspicuous . . . . .  
 . . . . . 5a. *M. multiflora* var. *multiflora*.

Fruit light brown with 10 slender tan longitudinal ribs alternating with  
 10 brown (often interrupted) ribs . . . . .  
 . . . . . 5b. *M. multiflora* var. *pubescens*.

Fruit definitely tuberculate, producing mucilage when wetted; involucre bracts obtuse . . . . . 5c. *M. multiflora* var. *glandulosa*.

The nature of the mature fruit is the most consistent character for distinguishing the varieties of *Mirabilis multiflora*. There are many recognizable anthocarp types that have discrete geographic limits, but these fall into three major groups as indicated by the key to varieties. In some areas where the varieties of *M. multiflora* occur together they are quite distinct morphologically, as in Colorado National Monument, Mesa County, Colorado. In this region var. *glandulosa* has obtuse bracts and the apices of most leaves are obtuse to rounded, while var. *multiflora* has narrowly acute bracts and leaf apices. In addition var. *glandulosa* flowers in May and June while var. *multiflora* usually flowers in July and August. In contrast the plants of southwestern Utah and northwestern Arizona show a collage of characteristics normally typical of the different varieties.

5a. MIRABILIS MULTIFLORA (Torr.) Gray var. MULTIFLORA—*Oxybaphus multiflorus* Torr., Ann. Lyceum Nat. Hist. New York 2:237. 1827. — *Allionia multiflora* (Torr.) Eaton, Man. Bot. ed. 5 Addenda:2. 1829. — *Nyctaginia? torreyana* Choisy, in DC. Prodr. 13(2):430. 1849, illegitimate superfluous name. — *Quamoclidion multiflorum* (Torr.) Torr. ex Gray, Amer. J. Sci. Arts II. 15:321. 1853. Type:

"Forks of the Platte" (label), "About the Forks of the Platte" (protologue), 1820, *Dr. E. James s.n.* Holotype:NY!; isotype:K!

DISTRIBUTION (Fig. 3). Occasional in Chihuahua, Coahuila, Nuevo Leon, and San Luis Potosi, Mexico. More often collected in western Texas, through New Mexico, Arizona, and Colorado, United States of America. On gravelly-sandy or loose soils of mesas, washes, and open hillsides between 300 and 2300 m in Pinyon-Juniper Woodland and Yellow Pine Forest. Flowers mid-May through mid-October.

Among the plants collected by Edwin James, M.D., Assistant Surgeon in the United States Army, in the summer of 1820, was a member of Nyctaginaceae collected "About the Forks of the Platte" (Torrey, 1827). The specimen is incomplete and Torrey (1827) stated that the "country was traversed with great rapidity, . . . and little opportunity was afforded of making observations, or even of recording all the stations of the plants." This collection was published as *Oxybaphus multiflorus* by Torrey. After crossing the Platte River at Forks (now Lincoln County, Nebraska, fide McKelvey, 1955) the party, commanded by Major Stephen H. Long, continued up the South Platte River to the base of the Rocky Mountains. I have not seen plants belonging to Torrey's *O. multiflorus* from Nebraska. The closest locality lies over 400 km southwest in Pueblo County, Colorado. Given Torrey's remark that James' records were not always complete, it seems probable that the collection of *O. multiflorus* was made later in James' journey, perhaps somewhere on the eastern flank of the Rocky Mountains where the plants are known to occur.

5b. *MIRABILIS MULTIFLORA* (Torr.) Gray var. *PUBESCENS* S. Wats., Bot. Calif. 2:2. 1880. Type: In the protologue Watson stated, "The variety is peculiar to S. California, from near Fort Tejon (*Wallace, Kennedy*) to San Diego County, *Palmer*." Of the three collections cited by Watson only Wallace's is at the Gray Herbarium (GH), and it consists solely of two detached involucre and flowers. This specimen says simply "California, *Wallace*". On the same sheet there are two other collections of *Mirabilis multiflora* var. *pubescens*. The label of one of these, *W. Matthews*, 1877, from Owen's Valley, is in Watson's handwriting, and he has determined the specimen to be *M. multiflora* var. *pubescens*. The only specimen of the Kennedy collection I have seen is at Field Museum (F), and there is no indication on the sheet that Watson saw this specimen. The label of the Palmer specimen at New York Botanical Garden (NY) is inscribed in Watson's handwriting "*Mirabilis multiflora*" but it is not designated var. *pubescens*. In addition the specimen is glabrate. I therefore designate as lectotype (GH!): California, *Wallace s.n.*

*Oxybaphus froebelii* Behr, Proc. Calif. Acad. Sci. 1:69. 1855. — *Mirabilis froebelii* (Behr) Greene, Bull. Calif. Acad. Sci. 1:124. 1885. — *Mirabilis multiflora* (Torr.) Gray var. *froebelii* (Behr) Jones, Contr. W. Bot. 10:49. 1902 (illegitimate superfluous name, since Jones cited

"var. *pubescens* Wats." as a synonym). — *Quamoclidion froebelii* (Behr) Standley, Contr. U. S. Natl. Herb. 12:359. 1909. Type: California, San Diego Co., "Warner's Ranch" (protologue), 1855, J. Froebel, not seen, perhaps destroyed at CAS in the fire of 1906.

*Quamoclidion froebelii* (Behr) Standley ssp. *glabratum* Standley, Contr. U. S. Natl. Herb. 12:360. 1909. — *Mirabilis froebelii* (Behr) Greene var. *glabratum* [sic] (Standley) Jepson, Flora Calif. 1(4):458. 1914. Type: California, San Bernardino Co., "Providence Mts.", 25 May 1902, T. Brandegee s.n. Holotype: UC!; isotype: NY!

DISTRIBUTION (Fig. 3). Northern Baja California, Mexico, through southern California, southeastern Nevada, southwestern Utah, and western Arizona, United States of America. On dry gravelly-sandy soil of mesas, washes, and open hillsides between 50 and 2100 m in Oak Woodland, Pinyon-Juniper Woodland, Chaparral, Sagebrush Scrub, Creosote Bush Scrub, and Shadscale Scrub. Flowers late April through July.

5c. *MIRABILIS MULTIFLORA* (Torr.) Gray var. *GLANDULOSA* (Standley) Macbr., Contr. Gray Herb. 49:49. 1917. — *Quamoclidion multiflorum* (Torr.) Torr. ex Gray ssp. *glandulosum* Standley, Contr. U. S. Natl. Herb. 12:359. 1909. Type: Colorado, "Grand Junction, dry mesa", 12 May 1894, C. Crandall 423. Holotype: US!; isotypes: MO!, NY!, RM!

*Quamoclidion multiflorum* (Torr.) Torr. ex Gray ssp. *obtusum* Standley, Contr. U. S. Natl. Herb. 12:359. 1909.—*Mirabilis multiflora* (Torr.) Gray var. *obtusa* (Standley) Macbr., Contr. Gray Herb. 49:49. 1917. Type: Nevada, "Kernan, rocky ledges", 29 April 1902, L. Goodding 653. Holotype: RM!; isotypes: F!, GH!, MO!, NY!, POM!, UC!, US!

*Quamoclidion cordifolium* Osterh., Bull. Torrey Bot. Club 55:75. 1928. Type: Colorado, Mesa Co., "six miles from Grand Junction, in the hills across the Colorado River" (protologue), "Hills across the Colorado River from Grand Junction" (label), 18 June 1926, G. Osterhout 6559. Holotype: RM!; isotypes: GH!, NY!, POM!, RM-3 sheets!

Note: two varietal names are available for this taxon, var. *obtusa* and var. *glandulosa*. The latter name has been chosen because Crandall 423 is a more representative collection for my circumspection of the taxon, since it possesses mature fruits on some sheets while Goodding 653 has only immature fruits.

DISTRIBUTION (Fig. 3). Scattered from Inyo Co., California, across southern Nevada and Utah to western Colorado. On gravelly-sandy soil of mesas, washes, and open hillsides between 900 and 2500 m in Sagebrush Scrub, Shadscale Scrub, and Pinyon-Juniper Woodland. Flowers May through July.

6. *MIRABILIS TRIFLORA* Benth., Pl. Hartw. 23. 1839. — *Quamoclidion nyctagineum* Choisy, in DC. Prodr. 13(2):429. 1849 (superfluous

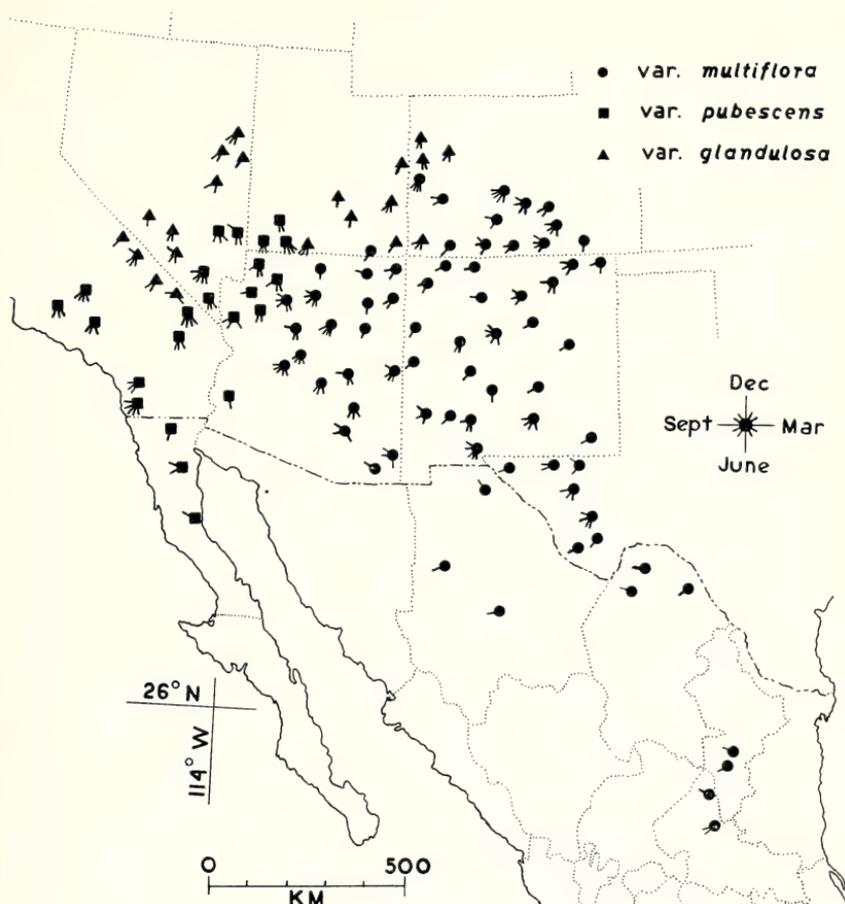


FIG. 3. Distribution and date of collection of *Mirabilis multiflora*.

name). — *Quamoclidion triflorum* (Benth.) Standley, Contr. U. S. Natl. Herb. 12:358. 1909. Type: Jalisco, "Bolaños", 1837, *T. Hartweg* 197. Holotype: K!; isotypes: G-2 sheets!, GH!, P!; photographs of holotype: DS!, MICH!

Plants from taproot 1–2 m long, 2–5(–8) cm in diameter; branches ascending to nearly decumbent, 1–5 m long, forming loose trailing clumps 1–6 m in diameter, the primary branches 5–7 mm thick; herbage green, sparsely to densely glandular-pubescent, occasionally glabrate; leaves horizontally spreading, thin; lowermost leaves ovate and often asymmetrical, 3–9 cm long, 2–6 cm wide, base cordate, apex acute to attenuate; middle cauline leaves similar to lowermost leaves in all respects; uppermost leaves narrowly ovate to ovate and only slightly asymmetrical, 1–3 cm long, 0.5–1.5 cm wide, base rounded to cordate, apex acute

to attenuate; petioles slender, 20–30 mm long on lowermost leaves, 5–10 mm long on uppermost leaves; leaf stomata 21–27  $\mu\text{m}$  long, 15–21  $\mu\text{m}$  wide; peduncles 2–15 mm long, 1 mm in diameter, erect or ascending; involucre campanulate, laterally compressed, 7–10 mm long, the bracts united by their margins, the tube 3–5 mm long, very unequally 5-lobed, the free portion of bract 3–7 mm long, 3–5 mm wide at base, triangular to very widely ovate, apex acute to attenuate; involucre 3-flowered, the flowers borne on pedicels up to 1 mm long on midvein of the two largest involucral bracts only, one flower on each midvein, the central flower solitary and naked; perianth tubular, 20–25 mm long, deep cardinal red, puberulent on both surfaces, the tube 20–25 mm long, 4–5 mm wide, a throat lacking, the five lobes very widely ovate, 1 mm long, 2.0–2.5 mm broad, apex rounded, the five longitudinal nerves extending to the sinus, apex of nerve densely pubescent; stamens exerted 7–14 mm, filaments densely pubescent, pollen grains 115–135  $\mu\text{m}$  in diameter; style exerted 7–14 mm; anthocarp ellipsoidal, slightly constricted at proximal end, occasionally constricted at distal end, 4–5 mm long, 2.0–2.5 mm wide, dark brown, tuberculate, sparsely pubescent, producing copious amounts of clear mucilage when wetted.

**DISTRIBUTION** (Fig. 2). Scattered in scrub vegetation of Baja California del Sur and Jalisco, Mexico, occurring at 300 to 1200 m. Flowers October through April.

This is certainly the most remote taxon, both geographically and taxonomically, of subgenus *Quamoclidion*. Heimerl (1934) proposed that *Quamoclidion* be resurrected as a genus composed solely of *Mirabilis triflora*. He separated *Quamoclidion* from *Mirabilis*, as a genus, on the following basis: 4-lobed versus 5-lobed involucre and filaments with spreading hairs versus glabrous filaments. He further stated that only *Hermidium* in subtribe Mirabileae-Boerhaaviinae had similarly pubescent filaments. In fact, many taxa of *Mirabilis* have pubescent filaments and one of the four involucral bracts of *M. triflora* is deeply bifid and supplied by two vascular traces rather than the usual single midvein. Although *M. triflora* is quite distinctive within *Quamoclidion*, I prefer to keep it here until the other members of *Mirabilis* are better known, since I have not seen any *Mirabilis* that resembles *M. triflora* more than do plants of subgenus *Quamoclidion*.

#### EXCLUDED NAMES

*Quamoclidion angulatum* Choisy, in DC. Prodr., 13(2):429. 1849 (*Nyctago angulata* DC.; Choisy, in DC. Prodr. 13(2):429, as synonym. 1849.) Choisy doubtfully referred this species to the genus. Choisy's specimens for this taxon were collected in Mexico by Mociño and Sessé. Standley (1911) remarks that Choisy's description does not agree with the collectors' drawing of the specimen in all particulars, and Standley (1918) later concluded that "the identity of the plant is

problematical." I have not been able to locate the collection made by Mociño and Sessé, but I have seen a copy of the collectors' drawing (MO). The plant represented may belong to *Mirabilis* section *Allionia*, but it is definitely not a *Quamoclidion*.

*Quamoclidion laeve* (Benth.) Rydberg, Bull. Torrey Bot. Club 29:687. 1902. ≡ MIRABILIS LAEVIS (Benth.) Curran, Proc. Calif. Acad. II. 1:235. 1888.

*Quamoclidion oxybaphoides* Gray, Amer. J. Sci. Arts II. 15:320. 1853. ≡ MIRABILIS OXYBAPHOIDES (Gray) Gray, in Torr. Bot. Mex. Bound. Surv. 173. 1859.

#### ACKNOWLEDGEMENTS

I am grateful to Lincoln Constance for his advice and numerous valid criticisms during all phases of this study. I also thank Robert Ornduff and William Libby for criticizing portions of this study. Special thanks go to John L. Strother for his help as well as his companionship in the field. Thanks are due to the curators of the following herbaria for loans of specimens: A, ARIZ, BM, CAS, COLO, DS, ENCB, F, G, GH, IA, JEPS, K, MEXU, MICH, MO, NY, OKLA, P, POM, RM, RSA, SMU, TEX, UC, US, WIS, and WS. This research was supported in part by NSF grant GB 36647.

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#### NOTES AND NEWS

*RANUNCULUS CALIFORNICUS*, A NEW RECORD FOR THE STATE OF WASHINGTON. — Known as an indicator species for coastal prairies, *Ranunculus californicus* is typically found on the islands in southern California and along the coast in northern California and southern Oregon. Until now, there were apparently only two locality records north of Lincoln County, Oregon: one disjunction from Sauvie Island, near Portland, Oregon (ORE), and one from the Trial Islands, near Victoria, British Columbia (V). Recent exploration has resulted in documentation of seven sites in the Puget Trough of Washington where *Ranunculus californicus* Benth. var. *cuneatus* Greene is locally common to abundant. All sites are open, south to southwest facing grassy bluffs or rocky slopes just above the seacoast, at elevations up to 150 feet.

Although *R. californicus* intergrades with *R. occidentalis* (L. Benson, Amer. Midl. Naturalist 40:1-261, 1948), the features demonstrated by the coastal collections from the Puget Trough are most similar to *R. californicus* in these diagnostic features: petals 5-14, 2-2.5 times longer than wide; nectary glands 0.5-0.8 mm long; and beaks of the achenes 0.5-1 mm long, strongly curved or hooked at the apex. *Ranunculus occidentalis* does occur in nearby areas but not sympatrically with *R. californicus*. The populations show differences in the number of petals per flower and in the proportion of petal length to width. In the populations from Fidalgo and Lopez Islands, the petals number (5-) 8-14 per flower and are typically 2-2.5 times longer than wide. On San Juan Island, the petals usually number 5-8 (-11) and are about two times longer than wide. The San Juan Island populations show greater similarity to *R. occidentalis* than do other populations. Further study of this complex is needed to explain the interpopulational variation.

Specimens of *R. californicus* var. *cuneatus* from Washington, all at WTU: SAN JUAN Co. Lopez Island: Iceberg Point, 8 May 1974, *Denton* 3420, 17 Apr 1976, *Denton* 3975; Point Colville, 17 Apr 1976, *Denton* 3802. San Juan Island: west slope of Mt. Dallas, 5 May 1974, *Denton* 3407, 1 May 1976, *Elvander* 602; San Juan County Park, west side of island, 6 May 1976, *Lerner* 152; English Camp, north-west side of island, 6 May 1976, *Lerner* 151. SKAGIT Co. Fidalgo Island: Deception Pass, 17 Apr 1976, *Denton* 3814; Fidalgo Head, 17 Apr 1976, *Denton* 3813.

I am grateful to R. E. Norris who informed me of an "unusual" buttercup on Iceberg Point of Lopez Island, to C. L. Hitchcock for verifying my identifications, and to R. L. Taylor at UBC and the curators at ORE, OSC, UBC, WS, and V for information about their collections of *R. californicus*. — MELINDA F. DENTON, Department of Botany, University of Washington, Seattle 98195.

LEAF ANGLE AND LIGHT ABSORPTANCE OF  
ARCTOSTAPHYLOS SPECIES (ERICACEAE)  
ALONG ENVIRONMENTAL GRADIENTS

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The purpose of this research was to test the hypothesis that changes in leaf energy balance characteristics are correlated with the distribution of *Arctostaphylos* Adans. species along environmental gradients. It was expected that species from low light, low temperature environments should hold their leaves more horizontally and absorb more light than leaves of species from warmer, high insolation areas. Similar results have been reported by Billings and Morris (1951) for leaf reflectance and by Mooney *et al.* (1971) for leaf angle distributions of groups of shrubs from different habitats. The present research differed from these studies in that it involved a more detailed comparison within a single genus.

There are over fifty recognized taxa of *Arctostaphylos*, nearly all of them confined to the west coast of North America. All are woody evergreen shrubs with flat leaves (Munz 1959, Adams 1949). About half of the species are highly localized endemics (Stebbins and Major 1965). Seven species of *Arctostaphylos* were studied in the field at 54 sites in California, Oregon, and Washington. The sites and species were chosen for their distribution along two macroclimatic gradients of air temperature and insolation. These climatic gradients were associated with elevational changes in the Sierra Nevada of California, and with latitude and distance from the seacoast in northern California, Oregon, and Washington. Climatic information was obtained from the *Climatic Atlas of the United States* (U. S. Environmental Sciences Administration, 1968), the *U. S. National Atlas*, and *Climates of the States* (U. S. NOAA, Dept. of Commerce, 1973).

METHODS

Leaf angles were measured using a protractor to which a plumb line was attached at the origin (Kvet and Marshall 1971). The protractor was held up to the leaf and the angle between the leaf and the horizontal was measured to the nearest 5°. For these flat leaves, angle to the horizontal was considered to be the steepest angle that could be measured and did not take into consideration the azimuth angle, leaf-branch angle, etc. This method was found to give rapid, highly repeatable results. Angle measurements were made throughout the canopy of the shrubs examined,

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usually 10–20 leaves from each of several branches per shrub, 3–10 shrubs per site.

Reflectance and transmission of *Arctostaphylos* leaves were measured using a Zeiss PMQII spectrophotometer with reflecting sphere attachment. Absorptance was then calculated as: Absorptance =  $1 - (\text{Reflectance} + \text{Transmittance})$ . All values were calculated as percentages, either of reflectance from a standard  $\text{MgCO}_3$  block (reflectance) or of transmittance measurements taken with no obstructions between light source and sensor (transmittance). Measurements between 325 and 800 nm were taken using a photomultiplier tube as a sensor, while a PbS photocell was used between 700 and 2500 nm, with a 100 nm overlap between sensors. Variation among leaves at a single wavelength was rarely greater than 5%, and repeated measurements of the same leaf varied by less than 1%. In most cases, reflectance and transmittance were measured for at least six leaves of each species at each wavelength.

#### RESULTS AND DISCUSSION

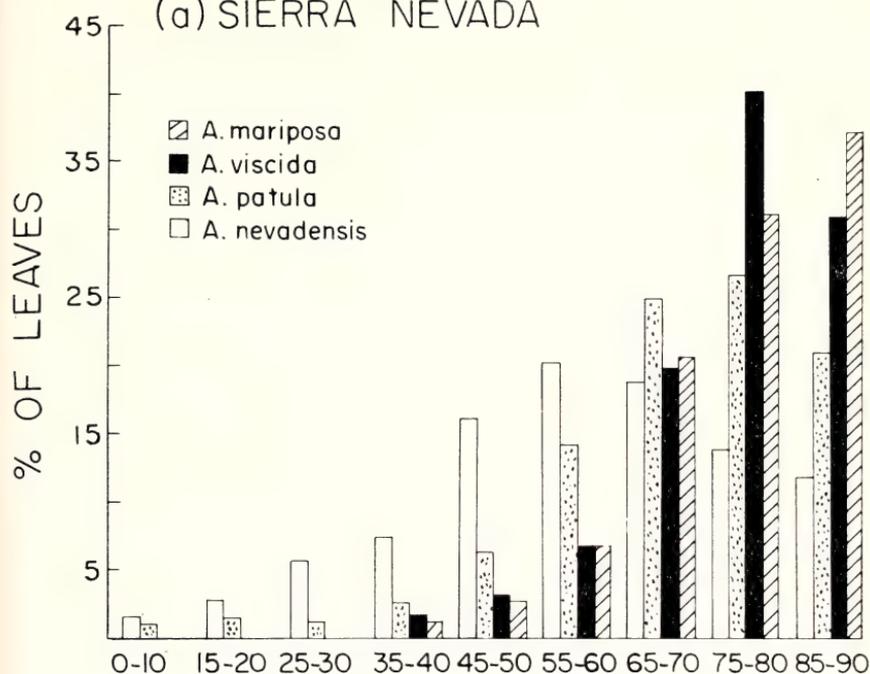
Figure 1a and Table 1 summarize the results of leaf angle observations at 29 sites between Yosemite National Park and Truckee, California. The data show that *A. nevadensis*, the species from the highest elevation sites, has many fewer vertical or near vertical leaves than *A. viscidula* or *A. mariposa*, the two lowest elevation species. *Arctostaphylos patula*, the species from middle elevations in the Sierra Nevada, is intermediate in its leaf angle distribution.

Similar results are recorded in Figure 1b. *Arctostaphylos uva-ursi*, which is circumboreal in its distribution, was measured at three sites in Mason and Kitsap counties, Washington, and Curry County, Oregon. On these sites, *A. uva-ursi* grows between 10 and 100 m elevation, rarely more than 1 km from the ocean. *Arctostaphylos columbiana*, which was sampled at the same three sites plus another in Humboldt County, California, grows above *A. uva-ursi* to 800 m in the Pacific coast ranges. *Arctostaphylos manzanita* grows mainly in the interior coast ranges and was sampled in Humboldt and Mendocino Counties, California, at two sites about 50 km from the coastline. The data of Figure 1b show that *A. uva-ursi*, the species from the cool, foggy, coastal habitat, holds its leaves most nearly horizontal, and that leaf inclination tends to increase with distance from the ocean. Leaf inclination of *A. manzanita* is not as steep as in *A. mariposa* (Fig. 1a, Table 1), but growing season temperatures and insolation are much lower in the northern California coast ranges than in the Southern Sierran foothills (*Climatic Atlas of the United States*, U. S. Environmental Sciences Administration, 1968).

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Fig. 1. Relative frequency of leaves in various leaf angle classes in the Sierra Nevada and Coast gradients.  $\alpha$  = mean of all measurements.

## (a) SIERRA NEVADA



## (b) NORTH COAST

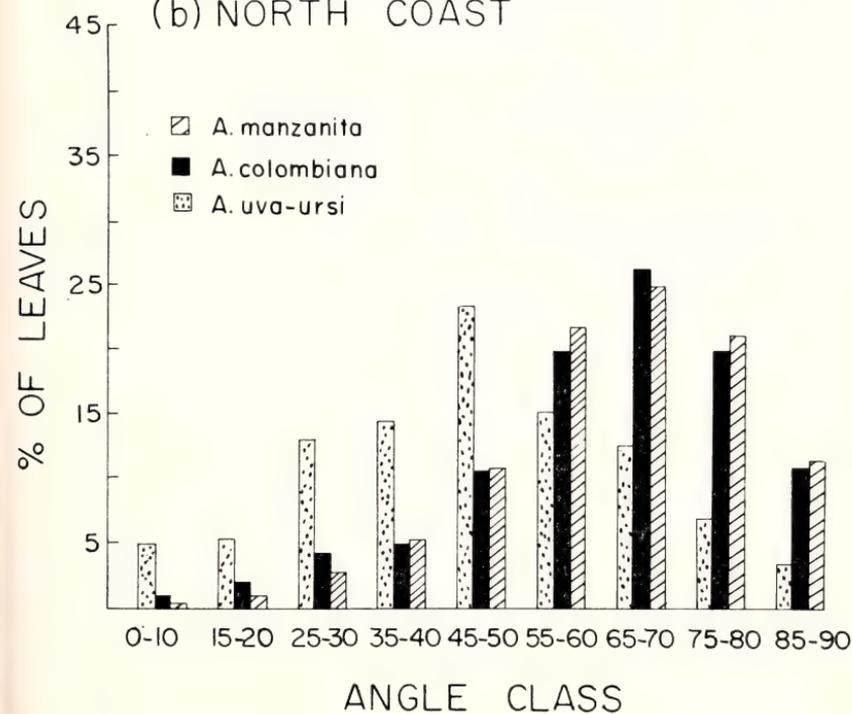


TABLE 1. ELEVATIONAL RANGES, MEAN LEAF ANGLES FROM THE HORIZONTAL ( $\alpha$ ), COS  $\alpha$ , AND MEAN LIGHT ABSORPTANCE IN THE VISIBLE AND NEAR-INFRARED REGIONS FOR THE SPECIES USED IN THE PRESENT STUDY. Values in parentheses indicate sample size.

	Elevation, m	$\alpha$	cos $\alpha$	Mean absorptance, %	
				400-675 nm	800-1100 nm
Sierra Nevada					
A. mariposa	150-1500	77.35 (420)	.22	—	—
A. viscida	150-1500	76.24 (460)	.24	78.96	4.01
A. patula	1000-2800	69.72 (1260)	.35	86.58	4.35
A. nevadensis	1700-3500	50.97 (1030)	.63	83.83	4.89
North Coast					
A. manzanita	200-1500	62.83 (320)	.46	—	—
A. columbiana	50- 800	62.01 (720)	.47	87.97	8.01
A. uva-ursi	10- 100	47.51 (410)	.68	91.87	8.67

In addition to the differences in leaf orientation, there are also differences among species of *Arctostaphylos* in light absorptance, particularly in the visible region (Fig. 2, Table 1). *Arctostaphylos viscida*, the species from the warmest, highest insolation environment, absorbs much less visible radiation than any of the other species. *Arctostaphylos uva-ursi*, from the foggy coastline, clearly absorbs the most light between 25,000 and 15,000 wave numbers (400-675 nm). The intermediate species, *A. patula* and *A. columbiana*, are intermediate in their visible light absorptance characteristics. *Arctostaphylos nevadensis* is the only species that contradicts the predictions of the original hypothesis. This anomaly may be related to the frequently very high radiation intensities during the growing season at the high elevations where *A. nevadensis* is found. In the near infrared region, all three of the Sierran species absorb about half as much radiation as the Coastal species.

Differences among species in light absorption are much smaller than those for leaf orientation (Fig. 1, 2), suggesting that leaf orientation is much more important than absorptance in regulating the energy balance of *Arctostaphylos* leaves. Lack of precise correspondence with the predictions for absorptance of the original hypothesis therefore may not be critical. In general, however, the predictions of the hypothesis are validated for leaf angle and for light absorptance of at least the two extreme species, *A. viscida* and *A. uva-ursi*.

Several other factors also might tend to counteract the predicted trends. For example, leaves of both *A. uva-ursi* and *A. nevadensis* are the smallest among all species studied, usually less than 2.5 cm long by 1.5 cm wide. Leaves of *A. viscida* may be over 4.0 cm long and 4.0 cm wide. If large leaves tend to have greater leaf-air temperature differences, the advantages of near vertical leaves and low absorptance may be counteracted. Field measurements of leaf temperature and photosynthesis are

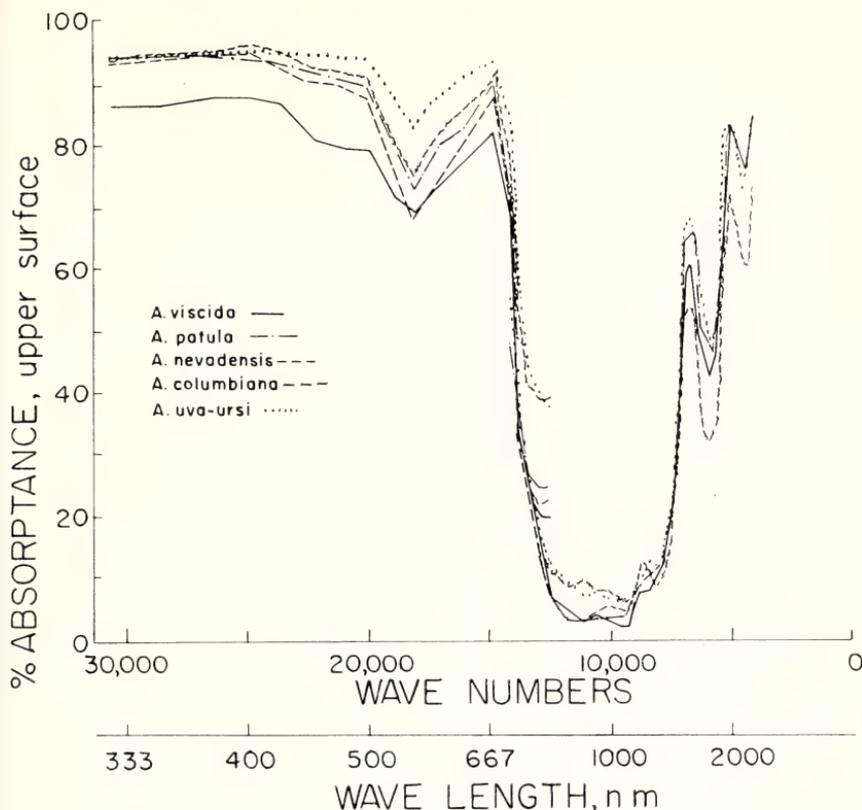


Fig. 2. Percent of incident light absorbed by leaves of *Arctostaphylos* spp. Wave numbers are used in the abscissa of this plot in order to emphasize the shorter, high energy wavelengths.

needed. This research also has not considered the importance of canopy structure on light absorptance and leaf temperature. *Arctostaphylos* appears to be a genus of plants very well suited to future studies of adaptation to radiation and temperature in the environment.

#### ACKNOWLEDGMENTS

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## NOTES AND NEWS

NOTES ON TWO RARE, ENDEMIC SPECIES FROM THE KLAMATH REGION OF NORTHERN CALIFORNIA, *PHACELIA DALESIANA* (HYDROPHYLLACEAE) AND *RAILLARDELLA PRINGLEI* (COMPOSITAE). — *Phacelia dalesiana* J. T. Howell was originally described from a population in the Scott Mountains at what is now Scott Mountain Summit on Highway 3 in Trinity County (Howell, J. T., 1937. Leafl. W. Bot. 2:51-52). The second known locality for this species was found 31 km to the south in the Trinity Alps (7 July 1975; *J. M. Di Tomaso 109*, DAV). The population consists of 700-1,000 individuals and is scattered in open Red Fir Forest at 2,011 m along the trail from Deer Flat to Shimmy Lake, 9.6 km WNW of Trinity Center; T36N, R8W, Section 5, NW-¼ (41°0'50"N, 122°48'40"W). Additional specimens have been deposited at CAS, HSC, and JEPS (8 July 1976; *Ferlatte and Di Tomaso 1776*).

*Raillardella pringlei* Greene was first collected by Pringle in 1881 from the "mountains about the head waters of the Sacramento River" in Siskiyou County and described by E. L. Greene (Bull. Torrey Bot. Club 9:15-17, 1882; isotype: CAS!). It has also been collected in the same general area near Gumboot Lake 12 km south of Mt. Eddy (*D. Barbe 538*, CAS, JEPS). Ferlatte (*A Flora of the Trinity Alps of Northern California*, Univ. Calif. Press, Berkeley, pp. 50-51, 1974) reported this species from Union Creek and Landers Creek in Trinity County at elevations from 6,500-7,200 ft. (1980-2195 m). Further field work in the Trinity Alps has shown *Raillardella pringlei* to be relatively common in the Swift Creek drainage and to occur as low as 1,295 m (*J. Di Tomaso 640*, CAS, DAV, and HSC). J. L. Strother obtained chromosome counts of  $2n = 17$  II from populations on Union Creek (*Ferlatte 1805, 1806*) and Landers Creek (*Ferlatte 1812*). Vouchers have been deposited at HSC, JEPS, RSA, and UC. In all cases where *Raillardella pringlei* has been observed in the field it occurs in wet places such as stream banks or boggy areas, usually among serpentine rocks or in soils derived from serpentine or related ultramafics. Associated genera include the following: *Darlingtonia*, *Caltha*, *Schoenolirion*, *Carex*, *Adiantum*, and *Dodecatheon*. I thank Joseph M. Di Tomaso and John L. Strother for their contributions to the data presented here. — WILLIAM J. FERLATTE, California Dept. of Agriculture, 3288 Meadowview Rd., Sacramento, CA 95832.

FLORA AND CHOROLOGY OF THE  
PINUS ALBICAULIS—VACCINIUM SCOPARIUM  
ASSOCIATION

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Floristic variation within a plant association may indicate that the habitat of the association is not uniform throughout, and that two or more plant associations are being considered as one, the extreme case being that each community is an individual, an association unto itself. Other interpretations exist; summaries can be found in several texts dealing with vegetation. In this report I shall describe the compositional variation of the *Pinus albicaulis*–*Vaccinium scoparium* association, and relate some of the variation to one factor of vegetation formation (Major, 1951), i.e., the flora from which the vegetation may have originated.

The suggestion that a single plant association varies according to the flora available to it suggests that this association may exist in more than one floristic region. If regional climate and events during evolutionary time determine floristic regions, one might conclude that these factors could act differentially within the association and thereby affect its variation. Alternatively, if one assumes that a recurring mixture of plant species indicates a particular set of environmental conditions, and that the probability of two or more of these species concurrently evolving the same degree of ecotypic variation is low (at least lower than with a single taxon), then it follows that the habitat within which this association of plant species exists is more or less equivalent throughout (if it is integrated over ecologic time). Thus, if this be the case, floristic differences of communities with “identical” habitats must be a result of either the availability of their flora at the time of their establishment (Egler, 1953) and/or through the remainder of their existence. Major and Pyott (1965) give an interesting review and discussion of this topic. More recently, Westhoff and van der Maarel (1973) and Mueller-Dombois and Ellenberg (1974) have included this aspect of vegetation in their writings.

METHODS

Stands in Wyoming, Idaho and Montana with overstories dominated by *Pinus albicaulis*, understories dominated by *Vaccinium scoparium*, and lacking conspicuous populations of *Abies lasiocarpa* seedlings and/or layered shoots (i.e., *Abies* reproduction less than that of *P. albicaulis*), and soils not stony or rocky (Soil Survey Staff, 1976) enough to obviously affect the growth and distribution of plants, were sampled. Within a 600 m<sup>2</sup> area the coverage of each vascular plant taxon was estimated. Foliose boreal lichens were also collected, but not systematically. No-

menclature follows that of Hitchcock and Cronquist (1973) for the Pacific Northwest vascular plants, Munz and Keck (1968) for other vascular plants, and Hale (1969) for lichens. Taxonomic authorities not in the text are listed in Table 1.

### RESULTS

Four species other than *Pinus albicaulis* and *Vaccinium scoparium* were nearly ubiquitous in the sampled stands: the widespread *Carex rossii*, *Abies lasiocarpa* and *Poa nervosa* with constancies of 80, 90 and 70% respectively, and *Arnica latifolia* (80% constancy, though absent from most Wyoming stands). The presence of these taxa lends some support (or degrees of freedom in a statistical sense) to the initial assumption of the improbability of two or more species concurrently evolving associated ecotypes.

In Table 1, the flora and some other stand characteristics are provided in relevé form. This table lists the stands in a latitudinal sequence, with adjustments to accommodate latitudinally-similar stands with widely separated longitudinal ordinates (cf. Fig. 1). Stands have not been sorted according to their floristic similarities as is usually done in relevé analyses (Mueller-Dombois and Ellenberg, 1974). However, taxa have been arranged to give the maximum impression of latitudinal change to demonstrate that the flora of the association changes clinally with latitude, and that the flora of any stand is at least a *partial* consequence of the floristic region in which the stand exists (certainly other factors are also involved).

Table 1a consists of those taxa with constancies  $> 15\%$ , and whose presence appears to be nonrandomly distributed within the association. When the within-association distributions of these taxa are compared to their general distributions listed in standard Floras for the Pacific Northwest (Hitchcock and Cronquist, 1973; Davis, 1952; Booth and Wright, 1966; Shaw, 1976; Despain, 1975), approximately 15% are found to be distributionally restricted from attaining 100% constancy in the *P. albicaulis*-*V. scoparium* association. Similarly, of those taxa with between 5 and 15% constancies, and those with  $< 5\%$  constancy (Tables 1b and 1c), about  $\frac{1}{2}$  of the former and  $\frac{1}{3}$  of the latter are distributionally restricted from ubiquity in the association. Taxa which exhibit no latitudinal affinities (Table 1c) are characteristically widespread in their general distributions. In total, about 25% of the association flora shows limited general distributions within the area encompassed by the association.

A few taxa in Table 1 deserve special mention. The low glandular shrub, *Leptodactylon pungens*, and the similar but more cushion-like *Arenaria aculeata* both have stiff spinulose leaves often found in desert-region plants, as indeed both are. In *P. albicaulis* forests these species are found in the southern Bitterroot Mountains and the Salmon River Moun-





TABLE 16. FLORA OF THE *PINUS ALBERTAULIS* - *VACCINIUM SCOPARIUM* ASSOCIATION; THE TAXA OF THE ASSOCIATION EXHIBITING NO LATITUDINAL AFFINITIES 1/.  
Table specifications follow those in Table 1a.

	16	17	18	19	20	09	10	01	02	28	27	29	13	14	15	11	12	06	07	08	04	05	03	30	26	25	24	23	22
<i>Abies lasiocarpa</i> (Hook.) Nutt.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Carex rostris</i> Boott	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Poa nemosa</i> (Hook.) Vasey	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Hieracium gracile</i> Hook.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Pteridium angustifolium</i> L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Junciperus communis montana</i> Ait.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Antennaria umbrosella</i> Rydb.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Ficosa engelmannii</i> Parry	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Pyrola secunda obtusata</i> Turcz.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Festuca rydbergii</i> A. Nels.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Oryzopsis eriquia</i> Thurb.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Avenaria songesia cephaloidea</i> (Rydb.) Naquire	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Erigeron peregrinus</i> (Pursh) Greene	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Polygonum bistortoides</i> Pursh	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Fraxina virginiana platypetala</i> (Rydb.) Hall	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Ribes lanatum</i> (Pers.) Poir.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

1/ Thirty-two taxa have only single occurrences in the stands (constancy 5%). In the latitudinal sequence shown above, the stands with their respective taxa are: 17 *Erigeron peregrinus* Nutt.; 19 *Mertensia alberta* (Torr.) G. Don., *Gentiana mesovilla* L.; 20 *Arenaria albertica* (Rydb.) Fern., *Colobella leuca scopulorum* (Maxon) Tryon, *Sarcocolla lyonsii* L.; 10 *Penstemon fruticosus* (Pursh) Greene; 2 *Trifolium haydenii* Porter; 28 *Stipa occidentalis* Thurb., *Hippopappus suffruticosus* (Nutt.) Gray; 27 *Stelene repens* Pers.; 15 *Goodenia oblongifolia* Raf.; 7 *Poa alpina* L.; 5 *Vaccinium membranaceum* Dougl.; 3 *Valeriana edulis* Nutt., *Lloydia serotina* (L.) Sweet; 30 *Hippopitys montana* Grantz; 2f *Aster stenomerus* Gray, *Phlox arbutus* H. & A.; 25 *Leptodactylon purpureum* (Torr.) Nutt.; 24 *Carex paniculata* Nutt., *Salix phylicifolia* L., *Veronica susstakii* Gray, *Léontastrum nuttallii* (Gray) Ewan., *Penstemon flavescentis* Pennell, *Hesperium albidiflorum* Hook., *Dianthus intermedia* Vasey, *Hesperium formosum* hortoniae (Jones) Hitchc., *Agoseris glauca albertiana* (Hook.) Greene, *Spiraea densifolia* Pall., *Anaphalis margaritacea* (L.) B. & H.; 23 *Carex paysonis* Clokey, *Poa snodgrassii* Vasey, *Festuca ovina brevifolia* (R. Br.) Wats.; 22 *Comanula parryi* Gray.

tains of east and central Idaho. The dry finger-like intermountain valleys (Lemhi, Pahsimaroi and Lost River Valleys) which extend from the northern edge of the Great Basin and abut these mountain ranges probably supplied the migratory path for these species from the deserts to *P. albicaulis* forests. To find either taxon in a mesic subalpine forest is surprising, but would have been much more so if that forest had been in central Montana, rather than east-central Idaho with its direct connection to the Great Basin.

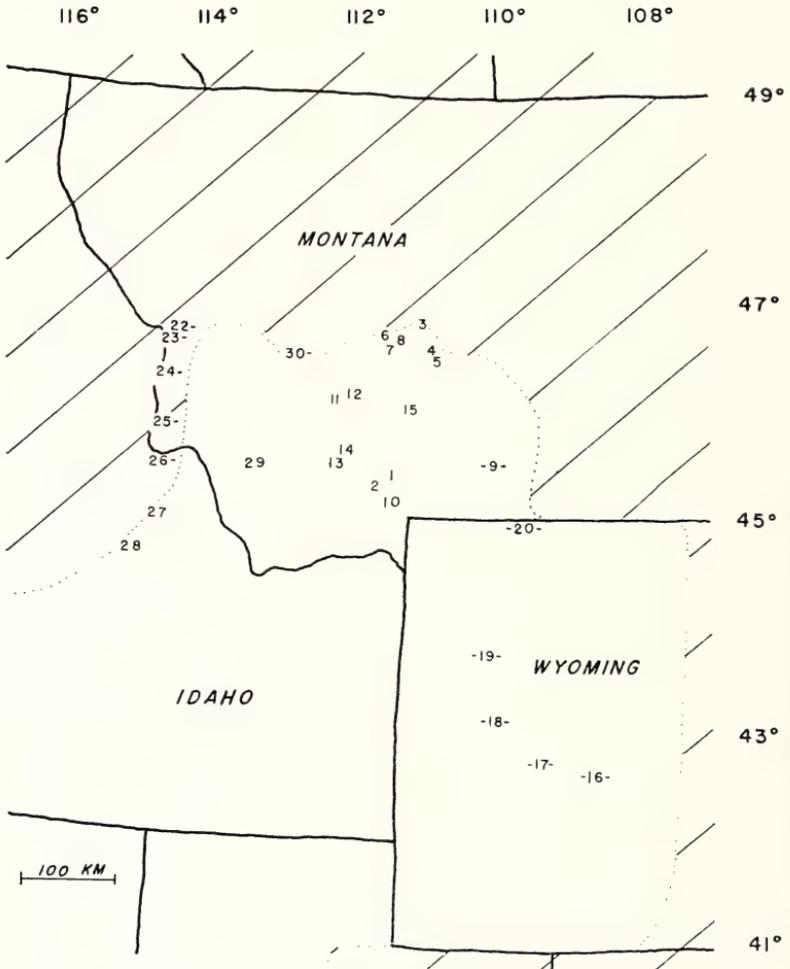


FIG. 1. Distribution of the *Pinus albicaulis-Vaccinium scoparium* association. The numbers and their associated characters (e.g., n-, -n-) represent stand numbers and the three geographic/floristic regions referred to in the text. The geographic extent of the stands is thought to depict the range of the association. The unhatched area inside the dotted line represents the gap in the distribution of *Pinus ponderosa* (from Little, 1971). (There is no Stand 21).

Three species of the *P. albicaulis*-*V. scoparium* association are relatively narrow endemics: *Penstemon flavescens* (Idaho Co., Idaho and Ravalli Co., Montana), *Chionophila tweedyi* (central Idaho and adjacent Montana), and *Aster stenomerus* (central Idaho and adjacent Montana to northeastern Washington and southeastern British Columbia). These taxa would not be expected to occur in whitebark pine stands outside their restricted ranges. Similarly, the typically alpine *Trifolium haydenii* extends only as far north as southern Montana. It occurs in a whitebark pine stand immediately adjacent to alpine meadows and scree in the Madison Range (Gallatin Co., Montana) and would not be expected in *P. albicaulis* forests farther north.

Though the general regional occurrences of the above taxa are easily obtained from standard Floras, their equally important intraregional distributions are not so readily available. For example, *Arnica latifolia* and *Carex geeyeri*, which are prominent in many Montana whitebark pine stands, are absent from the stands in the Wind River Mts. This mountain range does support both taxa but their populations are not as extensive as elsewhere. In such cases the chance of limited taxa reaching *Pinus albicaulis* forests is low. King (1977) has noted this same phenomenon but on a much smaller scale; the ability of a plant to colonize ant mounds in British pastures is determined by its relative abundance and distance from the mounds.

*Lichens.* Both *Letharia vulpina* (L.) Hue and *Hypogymnia vittata* (Ach.) Gas. were widespread throughout the association, the former being much more prominent. *Alectoria oregana* Tuck. and *A. americana* Mot. were confined to the northern-most stands. Both alectorias have limited distributions in the Rocky Mts. which correlate with their presence in the whitebark pine forests.

*Ecological Factors.* Ecological factors (s. strictu) do, of course, differ somewhat between stands, and plants respond accordingly. For instance, whitebark pine forests in the Wind River Mts. of Wyoming are more stoney than most. A very sandy soil develops about the stones that lie on the general soil surface; these small patches of "open" sandy soils are preferred sites for *Sedum lanceolatum* (cf. Table 1a).

Superficially at least, in some regions of *P. albicaulis* forests there appears to be taxonomic replacement within "life forms". *Arnica cordifolia* is generally prominent in those stands in which *A. latifolia* is not, and *Luzula hiichcockii* is relatively important in the Bitterroot Mts. where *Carex geeyeri* is not.

*Disjunctions.* Daubenmire (1975) has applied the term "oceanic element" to taxa with distributions largely restricted to maritime-influenced climates of the Pacific Northwest (NW Montana, N Idaho, W Oregon, W and NE Washington and the adjacent parts of Alberta and British

Columbia). I had considered both *Xerophyllum tenax* and *Luzula hitchcockii* to be strict oceanic elements, but their actual distributions are, in fact, more extensive. Widely disjunct populations of both species occur as far south as Teton Co., Wyoming (Shaw, 1976; Pfister et al., 1974; Maule, 1959). *Menziesia ferruginea* Smith and *Pinus monticola* Dougl. (not in whitebark pine forests) are other oceanic elements often found close to or associated with *X. tenax* and *L. hitchcockii*. They also have disjunct distributions nearly identical to the others (Hickman and Johnson, 1969; and personal observations). Perhaps in past times, the paleoclimate was sufficiently different to support an "oceanic" vegetation throughout the northern Rocky Mountains, as presently exists in NW Montana and N Idaho. Additional evidence for such a maritime paleoclimate is the discovery of *Taxus brevifolia* Nutt. (an unquestionably oceanic species) wood remnants during archaeological excavations in the Yellowstone Valley, SW Montana (Arthur, 1966; the same valley presently supports very localized populations of *X. tenax* and *M. ferruginea*). Radiocarbon dates for the *Taxus* materials were 5000 years BP (Such an age predates the well-known use of *Taxus* wood for archer's bows, thus long distance transport of the wood to this site is not likely.) The early Holocene epoch in the Rocky Mountains is thought to have been cool and wet (Hansen, 1947); the Xero- or Altithermal interval began about 7500 BP and lasted until the onset of Neoglaciation, ca. 4000 BP (Richmond, 1970). Wells (1970) has suggested that the "Xerothermal" interval in the Laramie Basin of Wyoming was wetter, not dryer, than present. Unless these plant disjunctions and excavations represent relict vegetation from pre-Pinedale Glacial times, with the recession of Cordilleran ice (12,000 BP; Richmond, 1970), a Pacific maritime climate and vegetation may have pervaded the entire northern Rocky Mountains. A subsequent cooling and drying trend in W Wyoming and SW Montana could not support a maritime vegetation, and extinctions and disjunctions resulted. High elevation bog pollen profiles in Yellowstone National Park (Waddington and Wright, 1974) are dominated by *Pinus contorta* from ca. 11,600 BP to present; an increase of *Picea engelmannii* pollen at 5000BP implies climatic cooling. That the W Wyoming-SW Montana area is still subjected to a relatively cold climate can be seen by the present gap in the distribution of *Pinus ponderosa* Laws. (Fig. 1), a typically "warm" pine (Mirov, 1967). Curiously, the absence of *P. ponderosa* from this area correlates generally with the occurrence of the *P. albicaulis*-*V. scoparium* association. If those whitebark pine stands with oceanic elements are omitted the correlation is nearly perfect.

*Species Number.* The number of species in the whitebark pine stands ranged from 6 in the oldest (640 years) to 33 in one of the youngest (33 years). There was a general trend in decreasing species number with stand age but stands that were proximal tended to have similar species numbers despite age differences.

*Management Implications.* Although whitebark pine forests receive relatively little resource management attention at present, this can be expected to increase rapidly. *P. albicaulis* produces exceptionally large mast crops (Forcella, 1977) and such production may significantly affect the habits of wildlife (Craighead, 1976; Forcella, 1977). Total net primary productivity in these forests may exceed 900 g/m<sup>2</sup>/yr. and standing crops may approach 60 kg/m<sup>2</sup> (Forcella and Weaver, 1977); economically these figures are substantial.

There are also some practical aspects involved with the floristic distributional anomalies of whitebark pine forests. The three dominant herbaceous species of the association are *Carex geyeri*, *Arnica latifolia* and *A. cordifolia*. These taxa all have known forage value for both domestic and wild ungulates. The biomass and energy (kcal) per unit area of each species can be readily predicted from their canopy coverages (measured separately; Forcella, 1977). Further, as can be seen in Table 1, the species have distributional limits within the association. If the 29 stands are split into three geographic/floristic regions (Fig. 1; separations based on plant distributions and agglomerative cluster analysis), the mean energy value per m<sup>2</sup> for each species differs significantly between at least two regions (t-test,  $p = 0.01$ ). In vegetation mapping, the *P. albicaulis*-*V. scoparium* association as a whole would probably comprise a single cartographic unit. Knowledge of regional differences in forage availability within associations might prove valuable to resource managers.

*Chorology.* The stands shown in Fig. 1 essentially outline the distribution of the *P. albicaulis*-*V. scoparium* association. To the north and northwest, *Abies lasiocarpa*, *Larix lyallii* and *Vaccinium membranaceum* gain importance in whitebark pine forests. In Alberta, Canada (on acidic substrates), *P. albicaulis* occurs with equal amounts of *Picea engelmannii* and *A. lasiocarpa* in the overstory. Understory components always contain *V. scoparium*, but it may be accompanied or dominated by *Vaccinium caespitosum* Michx., *Empetrum nigrum* L., *Dryas octopetala* L., *Salix arctica* Pall., or *Spiraea* ssp. In Banff National Park, I found one stand on dolostone totally dominated by *P. albicaulis*; its understory, in order of importance, consisted of *Betula glandulosa* Michx., *Potentilla fruticosa* L., *Linnaea borealis* L., *Shepherdia canadensis* (L.) Nutt., *Juniperus communis* and *Dryas octopetala*. There were no vacciniums in this stand, probably due to its basic substrate.

The eastern limit of the *P. albicaulis*-*V. scoparium* association is correlated with the eastern extent of acid-rock mountain ranges in Alberta and Montana. Limestone ranges such as the Big Snowy Mountains (Montana) do not contain this association. The eastern limit in Wyoming is the Absaroka and Wind River Mountains; the granitic Big Horn Mountains, 170 km eastward, have only scattered populations of *P. albicaulis* (Hoffman and Alexander, 1976; D. Despain *pers. comm.*)

To the south, the Medicine Bow Mountains (Wyoming), the Colorado

Rockies, and the Uinta Mountains of Utah all lack whitebark pine. That the southern limit of *P. albicaulis* coincides with the northern boundary of other edible large-seeded, grove-forming pines (*P. edulis* Engelm., S Wyoming; *P. monophylla* Torr. & Frem., S Idaho to California) may be more than coincidental. Forcella and Rumley (in prep.) hypothesize that prehistoric man carried seed of *P. sibirica* L. (= *P. albicaulis*) across Beringia. His dispersal of the energy-rich seed ceased when contact was made with native large-seeded pines.

In far western Wyoming (the Wyoming Range), *P. albicaulis* forests contain an understory of *Ribes montigenum* McClatchie (which forms conspicuous closed circles under the canopies of the rather widely spaced trees) and *Bromus carinatus*. To the northwest, in the White Cloud Peaks and Sawtooth Mountains of central Idaho, *P. albicaulis* stands often support an understory of *Artemisia tridentata* Nutt. and/or a carpet of forbs, *Lupinus argenteus* being the most prominent.

Within the distributional limits of the *P. albicaulis*-*V. scoparium* association, there may be other associations which contain *P. albicaulis*. On limestone outcrops, Weaver and Dale (1974) mention a stand in which *P. flexilis* James and various forbs associate with whitebark pine. I have seen such stands and others similar, but always including *Arctostaphylos uva-ursi* (L.) Spreng. This type of community, with a distinctly different habitat (limestone), appears to have been lumped with the *P. albicaulis*-*V. scoparium* association in the "habitat-type" classification of Pfister et al. (1974) and Reed (1976). Also, on what may be more mesic sites, *Abies lasiocarpa* shares the overstory with whitebark pine, and *V. membranaceum* is often present in the understory. It is possible that alternate plant associations (*Abies* vs. *Pinus*) may exist on the same site at different times, the occurrence of either possibly being a function of its seed crop size at the time of stand establishment. Seed production of *P. albicaulis* varies significantly from year to year (Forcella, 1977). A treeline form(s) of whitebark pine community occurs also; its distinguishing feature is, of course, the stunted growth and flagged structure of the trees (Daubenmire and Daubenmire, 1968). Clausen (1965) speculates a genetic basis for the stunted *P. albicaulis* of the Sierra Nevada krummholz.

#### CONCLUSIONS

The *Pinus albicaulis*-*Vaccinium scoparium* association is limited to subalpine sites on non-calcareous substrates in western Wyoming, southwestern Montana and east-central Idaho. Its floristic composition changes clinally with latitude, but this does not necessarily imply a change in habitat. Nearly 25% of the taxa which comprise the association are distributionally restricted from occurring in all stands of the association. This suggests that to some degree the floristic composition of a stand is a function of the local flora available to it.

## ACKNOWLEDGMENTS

In addition to J. H. Rumely and T. Weaver, I thank W. Ferlatte and J. Major, the reviewers for *Madroño*, for making valuable comments on this paper. The summer field work for this study was supported by the U.S. Forest Service under Contract No. 12-11-204-12, Suppl. No. 33.

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#### SPECIAL OFFER

In July 1969 the California Botanical Society published a large, 128-page double issue of *Madroño* (vol. 20, no. 3) to commemorate the meeting of the XI International Botanical Congress in Seattle. This issue contains four articles of general interest: *Jack A. Wolfe*: Neogene floristic and vegetational history of the Pacific Northwest. *R. Daubenmire*: Ecological plant geography of the Pacific Northwest.

*A. R. Kruckeberg*: Soil diversity and the distribution of plants, with examples from western North America.

*W. B. Schofield*: Phytogeography of northwestern North America: bryophytes and vascular plants.

We have an unusually large stock of this special issue. Consequently, to reduce our inventory, we are offering (until 1 Mar. 1979) this commemoration issue at the special price of \$2.00 postpaid instead of \$3.00.

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#### Errata, *Madroño*, volume 24

- p. 140. Seventh line from bottom should read "Cactáceas" for "Cactácea".
- p. 141. Second line should read "segmentisque" for "sementisque", "enationibus" for "enatioaibus", and "filamentis" for "fiilamentis".
- p. 145. Last line should read "synonymy" for "snyonymy".
- p. 150. Sixth line from bottom should read "Mason" for "Masin".
- p. 155. Thirteenth line should read "filamentisque" for "fiilimentisque".
- p. 156. Third paragraph, third line, should read "collections" for "collection".

# THE GENUS TRICHOSTEMA (LABIATAE) IN MEXICO

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*Trichostema* L. is a North American genus consisting of 16 species. At the time of the most recent taxonomic revision (Lewis, 1945) only 19 collections representing six species were known from Mexico. Least known of these was *T. purpusii*, the one species of this genus endemic to Mexico, which was represented only by the type specimen collected in 1907 and a second collection made in 1908.

Our present interest in the genus *Trichostema* in Mexico was generated in 1967 when one of us, at the instigation of Dr. Peter H. Raven, collected seeds of *T. purpusii* (Rzedowski 24915). Plants from these seeds were grown at UCLA in 1968 and flowered about six months after germination. To the great surprise of the senior author the flowers were bright rose-pink in color and not red or scarlet as he had thought probable from small traces of pigment in the flowers of the herbarium specimens previously known to him. Under cultivation the plants proved to be shrubs 1 m or more tall with erect herbaceous tips as much as 50 cm long rather than a suffrutescent perennial 4 to 5 dm tall as described earlier (Lewis, 1945).

Chromosomes of plants from this collection were examined using standard squash preparations of microsporocytes. Ten pairs of chromosomes were found consistently in all cells examined and no meiotic irregularities were observed. A haploid number of 10 also characterizes other species that occur in Mexico, namely *T. arizonicum* and the two shrubby species in sect. *Chromocephalum*, *T. lanatum* and *T. parishii* (Lewis, 1960). With the chromosome number of every species in the genus now known it is apparent that all of the perennial species have  $n = 10$  except for *T. suffrutescens* in southern Florida, which like other species of sect. *Trichostema* has  $n = 19$ . The strictly annual sect. *Orthopodium*, represented in Mexico by *T. lanceolatum*, *T. micranthum*, and *T. austromontanum*, has a constant haploid number of seven except for the tetraploid *T. austromontanum* with  $n = 14$  (Lewis, 1960).

With living plants available and with the chromosome number known, it became apparent that *T. purpusii* is closely related to *T. arizonicum*. The conspicuous differences in the color, size, and conformation of the flowers that earlier led to placing the two species in different monotypic sections do not, in living plants, obscure the close overall morphological

similarity of these two species. We are now convinced that they are much more closely related to each other than to other species in the genus. We have, therefore, as indicated in the listing below, included them in the same section.

*Trichostema purpusii* was known to us only from the State of Puebla when our material was grown. We have since learned from a paper by Williams (1973) that Dr. Robert Cruden collected this species in the State of Oaxaca in 1966 and in the same general area in 1971. The latter collection is the type of *Eplingia saxicola* Williams, the type species of the genus *Eplingia* Williams. We are truly sorry that a genus named in honor of a distinguished student of American Labiatae must be relegated

In the course of examining material of *Trichostema* from Mexico it became apparent that not only has the number of available collections increased significantly since the genus was revised in 1945, but among these collections are some that represent significant extensions of known range of the species concerned and the first collection of *T. austromontanum* from Mexico. We have summarized below our knowledge of the genus in Mexico with a key to the seven species known to occur there and a list of all collections from Mexico seen by us. We have not given full synonymy, descriptions, ranges of distribution in the United States, and other information available in earlier publications (Lewis, 1945; 1960).

#### KEY TO THE SPECIES OF *TRICHOSTEMA* IN MEXICO

- A. Plants annual; Baja California.
  - B. Stamens 10–20 mm long. . . . . *T. lanceolatum*
  - BB. Stamens 2–6 mm long.
    - C. Stamens 2–3 mm long, straight or slightly curved, barely exserted. . . . . *T. micranthum*
    - CC. Stamens 3–6 mm long, strongly arched and exserted. . . . . *T. austromontanum*
- AA. Plants perennial.
  - B. Leaves linear; Baja California.
    - C. Corolla tube 4–7 mm long. . . . . *T. parishii*
    - CC. Corolla tube 9–14 mm long. . . . . *T. lanatum*
  - BB. Leaves oblong to ovate.
    - C. Flowers blue; stamens strongly arched; corolla tube 3–4 mm long. . . . . *T. arizonicum*
    - CC. Flowers rose-pink; stamens nearly straight or slightly curved; corolla tube 9–10 mm long. . . . . *T. purpusii*

#### *TRICHOSTEMA* COLLECTIONS FROM MEXICO

##### Section PANICULATUM Lewis (Section *Rhodanthum* Lewis)

*T. purpusii* Brandegeë (*Eplingia saxicola* Williams). Oaxaca: Cerro del Camello, 2 km al S de Tepelmeme de Morelos, 2500 m, Cruz Cisneros 2189; Route 15 at K

376, ca 13.5 km NW of Tamazulapan, 2260 m, *Cruden 1094*; Route 190 between K 72 and 73, ca 5.5 km NW of Yanhuitlan, *Cruden 1950*. Puebla: Cerro de la Yerba, *Purpus 2559*; vicinity of Puebla, Cerro de Santa Maria de Zacatepec, *Bro. Arsène* in 1908; Ladera E del Cerro Tecajete, cerca de San Miguel Papaxtla, Municipio de Cholula, *Rzedowski 24915*; San Luis de los Pinos, municipio de Ajalpan, *Robert & Moreno 364*.

*T. arizonicum* Gray. Chihuahua: Colonia Juarez, Sierra Madre, *Jones* in 1903; Carretas, Municipio de Janos, *White 962*. Coahuila: Puerta de San Lazaro, Sierra de San Lazaro, Municipio de Castaños, *Muller 3055*. San Luis Potosí: 8 km al NE de Laguna seca, km 20 carretera San Luis Potosí-Antiguo Morelos, 2300 m, *Rzedowski 6352*. Sonora: San Bernardino, *Thurber* in 1852; Pinal, Sierra Charuco, *Gentry 1693*; Las Tierritas, *Phillips 656*; N of Horconcitas, *Phillips 866*; Puerto de los Aserraderos, *White 3221*; Cañon de El Temblor, *White 3373*; Valle de Teras, near La Angostura, *White 3549*; El Rancho del Roble, NE of El Tigre, *White 4212*.

#### Section CHROMOCEPHALUM Lewis

*T. lanatum* Benth. Baja California: Salada, *Orcutt 1345*; Aliso, *Brandegge* in 1893; 5 mi NE of Cerro Coronel (32°20'N 116°51'W) 560 m, *Moran 21743*; 1 mi W of Buena Vista (31°02'N 115°48'W) 750 m, *Moran 15109*; Los Alisos, 9 mi W of Valladares (30°52'N 115°51'W) 525 m, *Moran 16245*; *Moran 16253*; 4 mi W of Valladares, 700 m (growing with *T. parishii*), *Moran 16427*; Rio Santo Domingo, Hamilton Ranch, *Moran 22387*; 20 mi E of Socorro, 30 mi N of Rosario, *Humphrey 6833e*; near Rancho El Ciprés (30°23'N 115°38'W) 475 m, *Thorne 31951*; 1.5 mi E of Rancho El Ciprés, 550 m, *Moran 11046*.

*T. parishii* Vasey. Baja California: Guadalupe Mountain, *Orcutt* in 1883; San Rafael Hills, *Orcutt* in 1889; Aliso, *Brandegge* in 1893; Nachoguero Valley, *Mearns* in 1894; Tecate, *Orcutt* in 1884; *Fosberg 8396*; 8 mi SE of Tecate, *Munz 9487*; 13 mi E of Tecate, *Moran 14887*; 15 mi E of Tecate near road to Mexicali, 3000 ft, *Wiggins & Thomas 431*; near El Compadre, *Hohenthal 33*; Sierra Pinal, 3.7 mi N of El Compadre along road from Ojos Negros to Tecate, *Wiggins 21650*; 12 mi W of La Rumorosa, 4000 ft, *Hevly 2048 & Pitman 216*; Route 2, 59.3 mi W of main route to Mexicali, *McGill & Pinkava 8699*; Alaska, on road from Mexicali to Tijuana, *Cota* in 1932; 8 mi S of Machaguera on road to Hanson Lagoon, 3200 ft, *Wiggins 11254*; summit of Cerro Bola, 1275 m (32°19'N 116°40'W), *Moran 17821*; north slope of Sierra San Antonio Jenequa (Cerro Blanco) 800 m (32°05'N 116°30'W), *Moran 8415*; upper N slope of Cerro Blanco, *Moran 17603*; 1 mi S of Rosa de Castilla (32°02'N 116°08'W) 1200 m, *Moran 14945*; 15 mi E of Ensenada, *Kappler 819*; *Kappler 8820*; 20 mi E of Ensenada, *Wiggins 11870*; 20 mi S of Ensenada, *Flemming* in 1951; 1 mi E of San Antonio (31°59'N 116°36'W) 300 m, *Moran 13966*; Sierra Juarez, 7.5 mi SW of El Rayo (31°56'N 116°04'W) 1330 m, *Moran 16504*; Cañon Doña Petra (31°56'N 116°36'W) 250 m, *Moran 22803*; 1 mi N of Rancho Escondido (31°47'N 116°14'W) 800 m, *Moran 13927*; 2 mi NE of El Florido (31°32'N 116°02'W), *Moran 17691*; Pine Canyon near San Antonio Mesa, *Epling & Stewart* in 1936; *Epling & Robison* in 1940; 1.5–2.5 mi upstream from Rincon, 3 mi NE of Santa Catarina, 4250 ft, *Broder 504*; road from Valle Trinidad to Arroyo Calentura, 3400 ft, *Hohenthal 13*; ridge 10 mi SW of Valle Trinidad (31°20'N 115°53'W), *Moran 8221*; Sierra San Pedro Martir near Las Encinas, 6000 ft, *Powell* in 1958; 2 mi S of Tepi (31°08'N 115°45'W) 1000 m, *Moran 10971*; above Rancho San Pedro Martir on road to Sam's Corral (31°04'N 115°35'W) 1900 m, *Moran 14557*; 10 km W of Rancho San Jose (Melting Ranch), *Wiggins 20971*; vicinity of Rancho San Jose, 25 mi E of San Telmo, *Meling 15*; Campo Sotol (30°50'N 115°30'W) 1700 m, *Wiggins 16560*; 5 mi E of Rancho San Jose along old wagon road to old mining camp of Socorro, 3500 ft, *Wiggins 9793*; old Socorro mining camp E of Meling Ranch, 4200 ft, *Blakley 7153*; 4 mi W of Valladares (30°53'N 115°45'W)

725 m (growing with *T. lanatum*), *Moran 16426*; 2 mi W of ex-Misión San Pedro Martir (30°47.5'N 115°29'W) 1450 m, *Moran 22172*; Arroyo 3 mi S of Santa Eulalia (30°40'N 115°19'W) 1800 m, *Moran 11159*.

Section ORTHOPODIUM Benth

*T. austromontanum* Lewis. Baja California: Near 30°55'N 115°38'W, 875 m, *Moran 16320*.

*T. lanceolatum* Benth. Baja California: Near large pond 1 mi E of Tijuana Airport tower, *Moran 16106*; 24 mi N of Ensenada, *Wiggins & Gillespie 3986*.

*T. micranthum* Gray. Baja California: Hansen's Ranch, *Orcutt 1247*; Rancho La Botella (31°57'N 115°50'W) 1680 m, *Moran 16474*; Sierra Juarez, 1.5 mi S of Rancho Marcos (31°58'N 115°52'W) 1700 m, *Moran 13503*; 3 mi S of Rancho Marcos, *Moran 13598*.

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BOOKS RECEIVED AND LITERATURE OF INTEREST

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*Flora of the Black Hills.* By ROBERT D. DORN. Illustrations by JANE L. DORN. x + 377 pp. 1977. Robert D. Dorn, P. O. Box 1471, Cheyenne, Wyoming 82001. \$7.50 paperbound. Shipping extra on foreign and credit orders.

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GOSSYPIUM TURNERI (MALVACEAE),  
A NEW SPECIES FROM SONORA, MEXICO

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In spite of extensive study of the genus *Gossypium* for more than 100 years, new species continue to be discovered and described, enlarging our understanding of this economically important and evolutionary interesting genus. Fryxell (1966) estimated that new species of *Gossypium* have been discovered and described in the first half of this century at an average rate of about one species every five years, excluding the excessive number of names that have been based on variants among the cultivated species (cf. Fryxell, 1976). The number of species described in recent decades has exceeded that rate (*G. lobatum* Gentry 1956, *G. longicalyx* Hutch & Lee 1958, *G. barbosanum* Phillips & Clement 1963, *G. nandewarensense* Derera 1964, *G. laxum* Phillips 1972, *G. pilosum* Fryxell 1974, *G. nelsonii* Fryxell 1974). The discovery of yet another species, described herein, suggests that the "age of discovery" even in this much-studied genus is not yet completed.

***Gossypium turneri*** Fryxell, sp. nov. subsectionis *Caducibracteolatae*. Frutex circa 1 m altus, nigropunctatus; ramulis tomentulosis, foliis trilobis parvis 1.5–2.0 cm longis, petiolis laminis subaequantibus; pedunculis petiolos consociatos aequantibus vel excedentibus, articulatis bractea in nodo; bracteis involucellorum late rotundatis 3–7-laciniatis, per vel post anthesin caducis; calycibus subtruncatis, petalis luteis ad basem rubris, columna staminalis pallidis 16–17 mm longis, filamentis 5–6 mm longis; fructibus 3-cellularis manifeste glandularis; seminibus ignotis.

Shrub ca. 1 m tall. Twigs densely stellate-tomentulose, the radii ca. 0.1 mm long, only partially concealing the underlying gossypol glands; glands blackish, often somewhat raised, 0.1–0.2 mm diameter. Stems becoming woody, glabrate; bark red-brown with prominent lenticels 0.3–1 mm diameter. Leaf lamina cordate, shallowly trilobed, 1.5–2 cm long, slightly broader than long, the margin entire, at apex acute to obtuse, nearly glabrous above and below, palmately 5–7-veined, with prominent black gossypol glands scattered throughout lamina, these somewhat more abundant on margin. Foliar nectary single on the midrib beneath, 1–2 mm from base of lamina, ca. 1 mm long. Petiole stellate-tomentulose and glandular, 1.2–2 cm long. Stipules 1–4 mm long, linear, black-glandular, caducous. Peduncle axillary, solitary, ca. 2 cm long, equaling or exceeding subtending petiole, with pubescence like petioles, articulate at or above middle, bracteate at articulation, the bracts stipuliform, 1.5–4 mm

long, early caducous. Nectaries of involucl 3, prominent, more or less triangular, whorled at apex of pedicel. Bracts of involucl 3, inserted immediately above nectaries, prominently punctate, subglabrous, basally cuneate to truncate, broadly rounded proximally, 3-7-laciniate distally (rarely entire), in outline ovate, 9-16 mm long, 7-9 mm wide, the longest (central) tooth up to 7 mm long, the bracts caducous at or shortly after anthesis. Calyx 5-8 mm long, subtruncate with 5 inconspicuous teeth, prominently and uniformly glandular, subglabrous or with a few minute stellate hairs on margin. Petals 4-4.5 cm long, bright yellow with small red spot at base, black-glandular except toward base, ciliate on claw with hairs 1 mm long, densely and minutely stellate-pubescent externally where exposed in bud, otherwise glabrous. Staminal column glabrous, with a few black glands at base, pallid, 16-17 mm long, surmounted by 5 teeth, staminiferous in upper half; filaments pallid, 5-6 mm long; anthers one-celled, purplish, 1-2 mm long; pollen yellow-orange, spherical, echinate; anther mass ellipsoid. Style exceeding staminal column by 5-15 mm, prominently glandular, sparsely pubescent below; stigmatic surfaces densely pubescent, decurrent on style. Fruit a 3-celled capsule, 1-1.5 cm long, globose to ovoid, beaked, with long (2 mm) white hairs along suture margin after dehiscence but otherwise glabrous, with abundant and prominent black glands externally; carpel wall 0.5 mm thick. Seeds unknown.

TYPE: Mexico, Sonora, growing on windswept rocky outcrop near beach, western base of Tetas de Cabra (near San Carlos Bay), lat. 27.9°N, long. 111.1°W; elev. 5 m, 24 July 1977, R. M. Turner & D. E. Goldberg 77-49 (holotype: ARIZ; isotypes: CHAPA, MEXU, UC, pf).

*Gossypium turneri* finds a natural position in *Gossypium* subsection *Caducibracteolata* Mauer (Fryxell, 1969), which also includes *G. harknessii* Kellogg and *G. armourianum* Kearney. Phytogeographically the subsection maintains its integrity: *G. harknessii* and *G. armourianum* occur in the Baja California peninsula and on adjacent islands; the finding of *G. turneri* across the Gulf of California in Sonora constitutes only a minor extension of the range of the subsection.

*Gossypium turneri* shows its alliance with the other two species of subsection *Caducibracteolata* in the following characters: its caducous involucler bracts; its growth habit as a low shrub; its small, thick (xeromorphic) leaves; its large yellow corolla with a red center; and its small, 3-locular, prominently glanded capsule that flares widely at maturity.

It may be distinguished from the other two species of the subsection most easily by the laciniate involucler bracts (fig. 1), but differs also in several other characters, which are compared in Table 1. The color of the seed hairs distinguishes *G. armourianum* (brownish) from *G. harknessii* (whitish), but this character is as yet unknown for the new species.

The new species is named in honor of Raymond M. Turner, who first collected it.

TABLE 1. CHARACTERS DIFFERENTIATING THE THREE SPECIES OF GOSSYPIMUM SUBSECTION CADUCIBRACTEOLATA.

Character	<i>G. armourianum</i>	<i>G. harknessii</i>	<i>G. turneri</i>
Leaf form	unlobed	lobed	lobed
Leaf glands (upper surface)	obscure	obscure	evident
Peduncle length (cm)	2-7	0.5-1.5	ca. 2
Peduncle articulation	with reduced petiole leaf	bract absent (?)	with small stipuliform bracts
Involucellar bract:			
-shape	linear	lanceolate	ovate-lanceolate
-width (mm)	1-3	4-7	7-9
-stage of loss	in bud	anthesis	anthesis
Staminal column length (mm)	12-13	7-8	16-17
Filament length (mm)	3-4	2-3	5-6
Carpel wall thickness (mm)	0.6-0.8	1.5	0.5

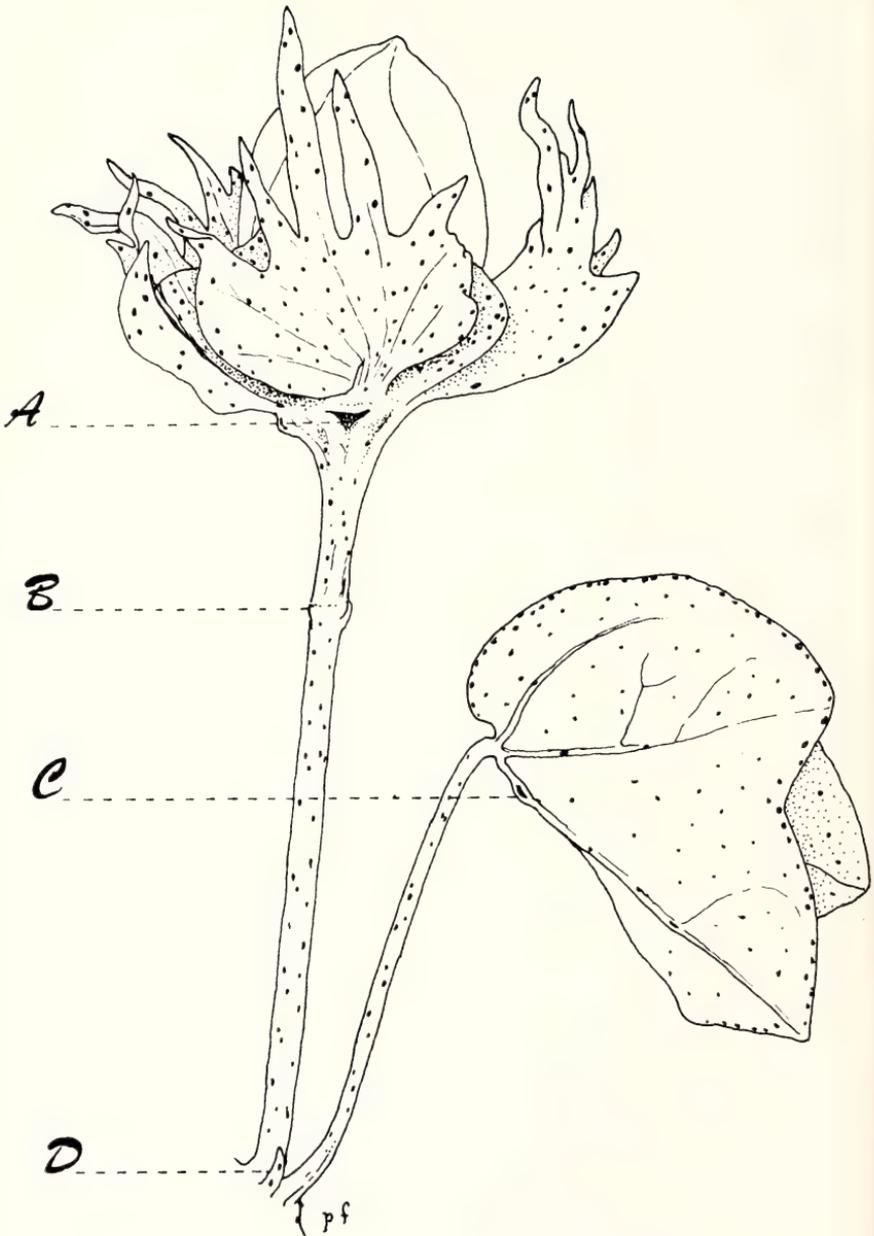


Fig. 1. Bud of *Gossypium turneri* with subtending leaf. A, involucellar nectary; B, articulation; C, foliar nectary; D, stipule.  $\times 4$ .

## LITERATURE CITED

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## NOTES AND NEWS

HEMIZONIA CONJUGENS (COMPOSITAE): DISTRIBUTION, CHROMOSOME NUMBER, AND RELATIONSHIPS — *Hemizonia conjugens* Keck (Aliso 4:101-109, 1958; type: River bottom land near Otay, San Diego County, California, *Abrams 3521*, UC!; isotypes, CAS!, POM!, NY) is a rare and poorly understood annual previously known only from southwestern San Diego County. Prior to this report this species was represented by only five other collections (*Abrams 3902*, *Stokes s.n.*, *Hall 3891*, *Hall 3916*, *Wolf 7969*) from near Otay Mesa, south of Chula Vista. Owing to the absence of this species from recent collections of the area, plus the extensive suburban and agricultural development of the area, thereby eliminating many natural habitats, it was considered possibly to be extinct. This area is fascinating as a result of its high degree of endemicity.

In May 1977, I was informed by Dr. Reid Moran of the San Diego Museum of Natural History that he had discovered a population that was apparently referable to the original description of *Hemizonia conjugens* (*Moran 24152: Tanowitz 1666*). The population was growing in mildly disturbed sandy loam, approximately 3 km SW of La Presa, Baja California (32°26'N 116°56'W). These plants were densely distributed over several acres. This represents a definite range extension for the species. Collections were made for morphological, cytological, and phytochemical studies; specimens will be distributed to various herbaria. A chromosome number,  $n = 12$ , is reported for this species for the first time.

Keck (*Munz, A California flora*, 1959; op. cit.) assigned *H. conjugens* to sect. *Deinandra* based upon its annual habit, sterile disk achenes, keeled phyllaries, and receptacular bracts of a single series surrounding the outermost series of disk florets. He considered *H. conjugens* to be most closely related to *H. fasciculata* T. & G. ( $n = 12$ ; Johansen, 1933; Tanowitz, ined.) and *H. paniculata* ssp. *paniculata* A. Gray ( $n = 12$ ; Johansen, 1933; Tanowitz, ined.). Based on morphological traits and geographical distribution, *H. conjugens* appeared to be intermediate to these species. Among the most significant of these of the former are the sterile and more or less glabrate disk achenes and among the most significant of the latter the number of ray and disk florets. They also show intermediacy in pubescence and distribution of pubescence and growth habit. Hence, Keck (op. cit.) postulated it to be an amphidiploid derivative of a hybrid between the two. This does not appear to be the case since the gametic chromosome number of *H. conjugens* is the same as the other two species: however, this evidence does suggest strongly that they are indeed related. Furthermore, preliminary flavonoid analyses of exudate aglycones display interesting patterns as well. Patuletin, quercetin, and two highly methylated flavonols are common to all three species. There is at least one flavonoid (methylated flavone) and one phenolic that is unique when compared to the other two.

The morphological, cytological, chemical, and geographical data strongly indicate that these three species are closely related and may have arisen either from the same ancestral stock or as a stabilized, diploid hybrid derivative of *Hemizonia paniculata* and *H. fasciculata*. Cytogenetical and more extensive chemical investigations are in progress to elucidate these speculations further.

I thank Dr. Reid Moran for his aid in this study and Dr. Robert Patterson for comments on the manuscript. This study was supported by a grant from the Regents of the University of California, PFG 5347. — BARRY D. TANOWITZ, Department of Biological Sciences, University of California, Santa Barbara 93106.

## CHROMOSOME NUMBERS IN ASTERACEAE

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Reports of 135 new chromosome number counts are recorded for 100 species and 54 genera of Asteraceae mostly from North America. Three genera, *Tessaria* ( $n = 10$ ), *Carramboia* ( $n = 19$ ), and *Pelucha* ( $n = 10$ ), and 15 species were previously unreported. Discussion is limited to those taxa for which chromosome numbers are previously unreported or those published counts that suggest a need for some elaboration. Many counts presented here confirm earlier reports listed in the chromosome number indexes edited by Federov (1969) and Moore (1973; 1974), or in other recent literature.

The chromosome numbers reported here were obtained through standard acetocarmine squashes of microsporocytes. Voucher specimens for most of the collections are deposited in TEX or SRSC. Vouchers for collections by Breedlove, Roe, and Raven are deposited in DS. Asterisks in Table 1 denote taxa for which chromosome numbers are previously unreported. Abbreviations of collectors preceding collection numbers in Table 1 include: B, Babcock; Br, Breedlove; I, Ittner; Pa, Patterson; P, Powell; R, Raven; S, Sikes; T, Tomb; Tu, Turner; W, Weedon.

*Astereae* — *Erigeron mimegledes* ( $2n = 27$  I) was reported earlier as  $2n = 36$  I by Turner and Flyr (1966) who discussed the species as possibly apomictic on a base of  $x = 9$  and probably related to *E. geiseri* ( $2n = 27$  I), conclusions substantiated by our count in Table 1. *Erigeron* sp. ( $n = 18$ ; Table 1) is an undescribed species. Determinations for *Machaeranthera pinnatifida* ( $n = 4, 8$ ; Table 1) follow Hartman (1976) and Turner and Hartman (1976).

*Inuleae* — The chromosome number listed in Table 1 for *Tessaria sericea* ( $n = 10$ ) is a first report for the genus and supports what appears to be a close relationship of this genus with *Pluchea* ( $x = 10$ ).

*Heliantheae* — Although the count for *Aspilia purpurea* ( $n = 12$  or 13; Table 1) is tentative and differs from previous reports of  $x = 14$  (Solbrig et al., 1972) and  $n =$  ca. 17 (Powell and Cuatrecasas, 1970) for four other species of the genus, there is reason to suspect that this large taxon of North America, South America, and Africa might be chromosomally variable and thus amenable to cytotaxonomic investigation. *Bidens ostruthioides* ( $n = 12$ ) has been reported previously as a tetraploid, but a diploid number for the taxon is recorded in Table 1. *Calea scabra* is reported to be  $n =$  ca. 27 (Table 1) evidently on a base of  $x = 9$  (Solbrig et al., 1972) although this species has been recorded previously as  $n = 16, 32$  (De Jong and Longpre, 1963; Powell and Turner, 1963). The listing in Table 1 for *Coreopsis integrifolia* ( $n = 13$ ), appar-

TABLE 1. CHROMOSOME NUMBERS IN ASTERACEAE.

Species	Gametic chromosome number	Locality and collection number
<b>EUPATORIEAE</b>		
<i>Ageratina wrightii</i> (Gray) King & Robins.	17	TEX. Hudspeth Co. Sierra Blanca Mts., <i>Wilson</i> s.n.
<i>Ageratum nelsonii</i> (Rob.) M. F. Johnson	10	MEX. Chiapas: 11 mi S of La Trinitaria, <i>Br 13269</i> .
<i>Barroetea laxiflora</i> Brandeg.	9	MEX. Sinaloa: 45 mi S of Mazatlán, <i>S</i> and <i>B 204</i> .
<i>Carphochaete bigelovii</i> Gray	11	TEX. Brewster Co. Chisos Mts., <i>Averett 240</i> .
<i>Piquieria trinervia</i> Cav.	11	MEX. San Luis Potosi: ca. 13 mi W of Ahualulco, <i>P</i> and <i>T 2589</i> .
<i>Stevia lucida</i> Lag. var. <i>lucida</i>	12	MEX. Durango: 3 mi NW of Morcillo, <i>S</i> and <i>B 374</i> .
<i>Stevia ovata</i> Willd.	ca. 33 I	MEX. Oaxaca: 3 km E of Ixtlán de Juarez, <i>Br 12244</i> .
<b>ASTEREAE</b>		
<i>Aphanostephus ramosissimus</i> DC. var. <i>humilis</i> (Bentham) Birdsong	4	MEX. Chihuahua: 25 mi S of Jiménez, <i>S</i> and <i>Pa 404</i> .
<i>Aphanostephus riddellii</i> T. & G.	5	MEX. Coahuila: 43 mi NW of Múzquiz, <i>P</i> , <i>Pa</i> , and <i>I 1576</i> .
<i>Aster subulatus</i> Michx. var. <i>ligulatus</i> Shinners	5	TEX. Maverick Co. Eagle Pass, <i>Hudson 16</i> .
<i>Astranthium purpurascens</i> (Rob.) Larsen	8	MEX. Chiapas: Cerro San Cristóbal, <i>Br 13298</i> .
<i>Erigeron mimegledes</i> Shinners	27 I	MEX. Coahuila: 43 mi NW of Múzquiz, <i>P</i> , <i>Pa</i> , and <i>I 1585</i> .
* <i>Erigeron</i> sp.	18	MEX. Coahuila: high pass E of Rancho El Jardín, <i>P</i> , <i>Pa</i> , and <i>I 1602</i> .
<i>Grindelia havardii</i> Steyerem.	12 <sup>a</sup>	TEX. Brewster Co. 13 mi S of Alpine, <i>P 2453</i> .
<i>Grindelia microcephala</i> DC. var. <i>microcephala</i>	6	TEX. Dimmit Co. 10 mi S of Catarina, <i>P 2348</i> ; Maverick Co. 13 mi E of Eagle Pass, <i>P 2349</i> .
<i>Haplopappus divaricatus</i> (Nutt.) Gray	4	TEX. Midland Co. 4 mi E of Midland, <i>R 19219</i> .
<i>Heterotheca villosa</i> (Pursh) Shinners	18	TEX. Hudspeth Co. 12 mi E of Van Horn, <i>P 2782</i> .
<i>Isocoma coronopifolia</i> Greene	6	MEX. San Luis Potosi: ca. 13 mi W of Ahualulco, <i>P</i> and <i>T 2587</i> .
<i>Machaeranthera brevilingulata</i> (Sch.-Bip. & Hemsl.) Turner & Horne	ca. 9	MEX. San Luis Potosi: ca. 13 mi W of Ahualulco, <i>P</i> and <i>T 2590</i> .
<i>Machaeranthera gracilis</i> (Nutt.) Shinners	2	TEX. Brewster Co. Alpine, <i>Hudson 1</i> ; 20 mi S of Alpine, <i>Sloan 2</i> .
<i>Machaeranthera gracilis</i> (Nutt.) Shinners	2 <sup>b</sup>	TEX. Brewster Co. Alpine, <i>Young 2</i> .
<i>Machaeranthera gymnocephala</i> (DC.) Shinners	4	MEX. Durango: 18 mi N of La Zarca, <i>S</i> and <i>B 365</i> .

- Machaeranthera pinnatifida* (Hook.) 4 MEX. Chihuahua: Sierra de Arbolitos, *P*, *Tu* and *S* 2505; TEX. Brewster Co. Big Bend Park vicinity, *Tu* s.n.
- Machaeranthera pinnatifida* (Hook.) 4<sup>b</sup> TEX. Presidio Co. Charro Canyon, *P* 2774.
- Machaeranthera pinnatifida* (Hook.) 8<sup>b</sup> MEX. Chihuahua: 25 mi S of Jiménez, *S* and *Pa* 405.
- Machaeranthera pinnatifida* (Hook.) 4 MEX. Coahuila: 43 mi NW of Múzquiz, *P*, *Pa*, and *I* 1577; TEX. Brewster Co. Alpine, *Sloan* 4; Culberson Co. 8 mi S of Van Horn, *S* and *B* 324; El Paso Co. 10 mi E of El Paso, *S* and *B* 321; Hudspeth Co. 32 mi E of El Paso, *S* and *B* 322; 37 mi E of El Paso, *S* and *B* 323; Pecos Co. 14 mi E of Ft. Stockton, *S* 438; *S* 439; Presidio Co. Marfa, *Foster* 18.
- Machaeranthera pinnatifida* (Hook.) 8 TEX. El Paso Co. 10 mi W of El Paso, *S* and *B* 318; Hudspeth Co. ca. 12 mi E of Dell City, *P*, *P*, and *W* 2837.
- INULEAE
- Pluchea odorata* (L.) Cass. 10 MEX. Sinaloa: 2 mi N of Mazatlán, *S* and *B* 198.
- \**Tessaria sericea* (Nutt.) Shinnery 10 TEX. Hudspeth Co. Quitman Mts., *P*, *P*, and *W* 2941.
- PALAFOXIINAE
- Palafoxia callosa* (Nutt.) T. & G. 10 TEX. Val Verde Co. 1 mi S of Pandale, *P*, *P*, and *W* 2965.
- Palafoxia texana* DC. var. *texana* 11 TEX. Maverick Co. Eagle Pass, *Hudson* 17.
- Palafoxia sphaelata* (Nutt. & Torr.) 12 TEX. Winkler Co. 2 mi N of Wink, *Cory* *Foster* 23.
- HELIANTHEAE
- Aspilia purpurea* Greenm. 12 or 13 MEX. Chiapas: 19 km N of Arriaga, *Roe* 853.
- Bahia pedata* Gray 12 NEW MEX. DeBaca Co. Lake Sumner, *W* and *W* 334.
- Baltimora recta* L. 15 MEX. Chiapas: 5 km N of Huixtla, *Roe* 830; Yucatán: 2 km S of Tekax, *Roe* 1333.
- Bidens ostruthioides* (DC.) Sch.-Bip. 12 MEX. Chiapas: 9 mi SE of San Cristóbal Las Casas, *Br* 13426.
- Calea scabra* (Lag.) Rob. ca. 27 MEX. Chiapas: Lagunas de Montebello, *Roe* 965.
- \**Carramboa littlei* (Cuatr.) Cuatr. 19 VENEZUELA. Merida: La Carbonera, *Lopez* and *Ruiz* 14013.
- Coreopsis integrifolia* Poir. 13 S. CAR. Colleton Co. *R* 20466.

<i>Eclipta alba</i> (L.) Hassk.	11	MEX. Baja Calif. Sur: 1 mi N of Pescadero, <i>S</i> and <i>B</i> 250.
<i>Encelia scaposa</i> (Gray) Gray	18 <sup>b</sup>	MEX. Chihuahua: 5 mi SW of Coyame, <i>P</i> , <i>Tu</i> , and <i>S</i> 2476.
<i>Engelmannia pinnatifida</i> T. & G.	9	TEX. Brewster Co. Alpine, <i>Sloan</i> 20.
<i>Helianthella quinquenervis</i> (Hook.) Gray	15	NEW MEX. Otero Co. Sierra Blanca, <i>R</i> 20348.
<i>Helianthus annuus</i> L.	17	TEX. Brewster Co. Alpine, <i>Sloan</i> 21.
* <i>Helianthus paradoxus</i> Heiser	17	TEX. Pecos Co. N of Ft. Stockton, <i>Kolle</i> 1415.
<i>Hymenopappus filifolius</i> Hook. var. <i>cinereus</i> (Rydb.) I. M. Johnston	17	COLO. San Miguel Co. 27 mi NE of Egner, <i>Tu</i> 8051; NEW MEX. Torrance Co. 8 mi E of Willard, <i>P</i> 2532.
<i>Hymenothrix wislizenii</i> Gray	12	ARIZ. Cochise Co. Benson, <i>R</i> 20341.
<i>Hymenoxys odorata</i> DC.	11	MEX. Chihuahua: 10 mi S of Ojinaga, <i>P</i> , <i>Tu</i> , <i>Magill</i> 2016; 56 mi S of Ojinaga, <i>P</i> , <i>Tu</i> , and <i>Magill</i> 2018.
<i>Iostephane trilobata</i> Hemsl.	ca. 34	MEX. Chiapas: San Cristóbal las Casas, <i>Br</i> 6742.
<i>Melampodium divaricatum</i> (Rich.) DC.	12	MEX. Mexico: 3 km S of Temascaltepec, <i>Roe</i> 1543; Oaxaca: Oaxaca, <i>Br</i> 12193; Sacatopequez: 5 km N of jct. of roads 14 and 6, <i>Roe</i> 825; Sinaloa: 70 mi S of Mazatlán, <i>S</i> and <i>B</i> 207.
<i>Melampodium gracile</i> Less.	9	MEX. Yucatán: 25 mi S of Umán, <i>Roe</i> 1317.
<i>Melampodium leucanthum</i> T. & G.	10	TEX. Jeff Davis Co. near Brack's Tunnel, <i>S</i> and <i>B</i> 312.
<i>Perymenium</i> cf. <i>asperifolium</i> Sch.-Bip. & Klatt	ca. 15	MEX. Oaxaca: 24 mi NE of Sola de Vega, <i>Br</i> 12281.
<i>Perymenium grande</i> var. <i>nelsonii</i> (Robins. & Greenm.) Fay	ca. 30	MEX. Chiapas: 11 mi S of La Trinitaria, <i>Br</i> 13267.
* <i>Perymenium klattianum</i> Fay	15	MEX. Vera Cruz: Cumbres de Acultzingo, <i>Roe</i> 1278.
<i>Perymenium mendezii</i> DC. var. <i>verbesinioides</i> (DC.) Fay	15	MEX.: 2 km N of Ixtapán, <i>Roe</i> 1917.
<i>Perymenium</i> cf. <i>purpusii</i> Brandeg.	15	MEX. Oaxaca: 3 km E of Ixtlán de Juárez, <i>Br</i> 12227.
<i>Psilostrophe tagetina</i> (Nutt.) Greene	16	TEX. Presidio Co. 2 mi NW of Marfa, <i>Foster</i> 22.
<i>Psilostrophe tagetina</i> (Nutt.) Greene	18	NEW MEX. Sandoval Co. 20 mi NE of Bernalillo, <i>Tu</i> 8027.
<i>Ruizlopezia bromelioides</i> (Cuatr.) Cuatr.	19	VENEZUELA. Mérida: Potreros de San Rafael, <i>Lopez</i> and <i>Ruiz</i> 14017.
<i>Sanvitalia ocymoides</i> DC.	8	MEX. Durango: 14 mi S of Rodeo. <i>S</i> and <i>B</i> 367.
<i>Sanvitalia procumbens</i> Lam.	8	MEX. Chiapas: 15 mi E of Cintalapa, <i>Roe</i> 878.

- Simsia amplexicaulia* (Cav.) Pers. 17 MEX. Chiapas: San Cristóbal las Casas, *Br 13283*.
- Simsia calva* (Gray & Engelm.) Gray 17 TEX. Brewster Co. Alpine, *Paul 1*.
- \**Simsia sanguinea* Gray ca. 17 MEX. Oaxaca: 24 mi NE of Sola de Vega, *Br 12254*.
- Verbesina encelioides* (Cav.) Gray 17 TEX. Presidio Co. 31 mi SE of Marfa, *Sloan 15*; Marfa, *Foster 12*.
- \**Verbesina hypoglauca* Sch.-Bip. ca. 17 MEX. Oaxaca: 3 km E of Ixtlán de Juárez, *Br 12250*.
- Viguiera stenoloba* Blake ca. 33 TEX. Presidio Co. 31 mi SE of Marfa, *Sloan 13*.
- Zinnia elegans* Jacq. 12 MEX. Mexico: 56 km S of Temascaltepec, *Roe 1652*.
- Zinnia littoralis* Robins. & Greenm. ca. 10 MEX. Sinaloa: 2 mi N of Mazatlán, S and B 196.
- TAGETEAE
- Dyssodia pentachaeta* (DC.) Robins. 8 TEX. Garza Co. 2.5 mi E of Post, R 19300.
- PERITYLINAЕ
- \**Perityle ajoensis* Todsén 17 ARIZ. Pima Co. Organ Pipe Cactus National Monument, *Todsén 2292* (seed progeny).
- Perityle angustifolia* (Gray) Shinnér ca. 68 TEX. Val Verde Co. ca. 25 mi N of Langtry, *P, P, and W 2953*.
- \**Perityle carmenensis* Powell 17 MEX. Coahuila: Maderas del Carmen, *Adamcewicz and Wendt 525* (seed progeny).
- Perityle ciliata* (L. H. Dewey) Rydb. 17 ARIZ. Santa Cruz Co. 3 mi SW of Patagonia, *Watson 234*.
- Perityle emoryi* Torr. ca. 34-36 SOUTH AMERICA. Chile?, *Robres 13-XI-1973* (seed progeny).
- Perityle emoryi* Torr. ca. 36 SOUTH AMERICA. Chile: Prov. Atacama: Caldera, *Richardson 2176* (seed progeny).
- Perityle leptoglossa* Harv. & Gray 17 MEX. Sonora: ca. 17 mi SE of Magdalena. *Van Devender s.n.* (seed progeny).
- Perityle parryi* Gray 17 TEX. Presidio Co. 2-3 mi NW of Fresno Mine, *P 2201*.
- FLAVERIINAЕ
- Flaveria australasica* Hook. ca. 18 AUSTRALIA. *Demarz 5843* (seed progeny).
- Flaverina bidentis* (L.) Ktze. 18 DOMINICAN REPUBLIC. *Loigier 18314* (seed progeny).
- Flaveria bidentis* (L.) Ktze. 18 ECUADOR. *King 6925*.
- \**Flaveria* sp. 18 TEX. San Patricio Co. Port Aransas, Mustang Island, *P 2802*; Nueces Co. Padre Island, *Urbatsch 1547* (seed progeny).
- Flaveria campestris* J. R. Johnst. 18 NEW MEX. Socorro Co. E of Socorro, *P and P 3011*; San Acacia, *Valentine, s.n.* (seed progeny).

<i>Flaveria chloraeifolia</i> Gray	18	MEX. Coahuila: ca 6 mi SW of Cuatro Ciénegas, <i>Tu 6168</i> .
* <i>Flaveria</i> sp.	18	MEX. Puebla: 5 mi SW of Tehuacán, <i>Br 14189</i> .
<i>Flaveria floridana</i> J. R. Johnst.	ca. 18	FLOR. Hillsborough Co. Tampa, <i>Anderson</i> s.n. (seed progeny).
<i>Flaveria linearis</i> Lag.	18	FLOR. St. Lucie Co. 37 mi S of Ft. Pierce, <i>Luteyn 2885</i> (seed progeny).
<i>Flaveria mcdougallii</i> Theroux, Pinkava, & Keil	18	ARIZ. Mohave Co. Grand Canyon National Park, Cove Canyon, <i>Theroux 1675</i> (seed progeny).
<i>Flaveria oppositifolia</i> (DC.) Rydb.	18	MEX. Coahuila: 3 mi NW of Nadadores, <i>P</i> and <i>Tu 2710</i> .
<i>Flaveria pringlei</i> Gdgr.	18	MEX. Oaxaca: 30 mi NNW of Huajuapán de León, <i>Tu P-50</i> ; Puebla: 5 km NW of Petalaleíngo, <i>Rzedowski 28942</i> (seed progeny).
<i>Flaveria pringlei</i> Gdgr.	ca. 36	MEX. Oaxaca: 6 mi NW of Huajuapán de León, <i>Dillon 681</i> (seed progeny).
<i>Flaveria pringlei</i> Gdgr.	36	MEX. Puebla: 16 mi S of Esperanzá, <i>Hartman</i> , et al. 3834.
<i>Flaveria pubescens</i> Rydb.	18	MEX. San Luis Potosí: 1 mi SE of Río Verde, <i>Hartman</i> , et al. 3823 (seed progeny).
<i>Flaveria ramosissima</i> Klatt.	18	MEX. Puebla: 8 mi SE of Coxcatlán, <i>Anderson</i> and <i>Anderson 5340</i> (seed progeny).
* <i>Flaveria</i> sp.	18	MEX. Sonora: near San Bernardo, <i>Martin 5</i> (seed progeny).
<i>Flaveria trinervia</i> (Spreng.) Mohr	18	TEX. Culberson Co. Rustler Springs, <i>P</i> and <i>P 3037</i> .
<i>Sartwellia flaveriae</i> Gray	18	TEX. Ward Co. 5 mi S of Pyote, <i>Sloan 66</i> . Reeves Co. 1 mi N of Pecos, <i>P 2927</i> .
<i>Sartwellia mexicana</i> Gray	18	MEX. San Luis Potosí: ca. 31 mi S of Matehuala, <i>S, Olsen</i> , and <i>P 820</i> .
<i>Sartwellia puberula</i> Rydb.	18	MEX. Coahuila: ca. 22 mi N of Monclova, <i>S, Olsen</i> , and <i>P 854</i> .

## SENECIONEAE

<i>Bartlettia scapoza</i> Gray	11	TEX. Hudspeth Co. Malone Hills, E of Tommy's Town, <i>P 2418</i> .
* <i>Pelucha trifida</i> Wats.	19	MEX. Baja California: Isla San Pedro Martir, <i>Moran 21745</i> .
<i>Raillardella argentea</i> Gray	18	CALIF. San Bernardino Co. Mt. San Gorgonio, <i>R 11148</i> .
<i>Raillardella muirii</i> Gray	16	CALIF. Fresno Co. Tehipite Valley, <i>Howell 33960</i> .
* <i>Senecio</i> cf. <i>chicharrensis</i> Greenm.	ca. 30	MEX. Chiapas: 17 km NW of Ocozocoautla, <i>Roe 891</i> .

## LACTUCEAE

<i>Pinaropappus roseus</i> Less.	9	TEX. Pecos Co. 5 mi SW of Iraan, S 441; Terrell Co. ca. 15 mi W of Longfellow, P 2673; Val Verde Co. just N of Langtry, P 2680.
<i>Pinaropappus roseus</i> Less.	9-15 <sup>d</sup>	MEX. Coahuila: 104 mi NW of Múzquiz, P, Pa, and I 1596.
* <i>Pinaropappus</i> sp. nov.	9	MEX. Coahuila: ca. 92 mi NW of Múzquiz, P, Pa, and I 1593.
<i>Stephanomeria pauciflora</i> (Torr.) A. Nels.	8	TEX. El Paso Co. Hueco Mts., P and P 2991; Hudspeth Co. 15 mi W of Van Horn, S 463.

## MUTISIEAE

* <i>Acourtia nana</i> (Gray) Reveal & King	27	TEX. Hudspeth Co. 15 mi W of Van Horn, S 462.
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<sup>a</sup>Occasionally with one IH and one I.

<sup>b</sup>Consistently with one round, probably centric, fragment.

<sup>c</sup>Consistently one I or fragment; also observed in a few cells were 17 II + 3 I; 18 II + 5 small fragments.

<sup>d</sup>Meiosis irregular, suggestive of triploidy on a base of  $x = 9$ , or apomixis.

ently a rare and localized species of South Carolina and Georgia, is a correction of an earlier publication in Solbrig et al. (1972) where the taxon was erroneously reported as *C. pubescens*. Cuatrecasas (1976) recently segregated *Carramboa littlei* and *Ruizlopezia bromelioides*, both  $n = 19$  (Table 1), from *Espeletia* ( $x = 19$ ).

*Tageteae* — The count of  $n = 8$  would appear to establish a diploid base for *Dyssodia pentachaeta*, a species for which Strother (1969) lists only  $n = 13, 16$ , or  $26$ . Keil and Stuessy (1975) have reported  $n = 16$  for *D. pentachaeta* var. *belenidium*. A varietal identification has not been made for our collection. Strother (1969) records  $n = 8$  for several other species of *Dyssodia*.

*Peritylinae* — In Table 1 the subtribe Peritylinae is positioned between the Heliantheae and Senecioneae (the classical but unnatural Helenieae is no longer recognized) in deference to those who do not wish to accept the taxon into homogeneous versions of tribes (Turner and Powell, 1977). *Perityle ajoensis* ( $n = 17$ , Table 1) was described (Todsens, 1974) after a monograph (Powell, 1973) of *Perityle* sect. *Laphamia*, to which it belongs, was completed. Todsens suggested a relationship of *P. ajoensis* to *P. palmeri* (= *P. tenella*;  $n = 16$ ), *P. inyoensis* ( $n =$  ca. 18) and *P. megaloccephala* var. *megaloccephala* ( $n = 17$ ). In our view, *P. ajoensis* doubtless belongs with the "southwestern alliance" of seven species including the three above but is perhaps closest to *P. villosa* (a triploid from one previous count) and *P. inyoensis*. The  $n =$  ca. 68 for *P. angustifolia* adds a new ploidy level to a species where  $n = 17$  and  $n =$  ca. 51 are previously known (Powell, 1968; Powell, 1973). The chromosome number for the newly described *P. carmenensis* ( $n = 17$ ) is

consistent with the base number established for sect. *Laphamia* (Powell, 1973) and with the base number of its related species *P. dissecta*, *P. castillonii*, and *P. lemmonii* (Powell, 1976). The two counts for *P. emoryi* ( $n = 34-36$ ) listed in Table 1 are the first reports of this bicontinental taxon from South America. The principal distribution of *P. emoryi* is in Baja California and Sonora, Mexico, and in parts of the southwestern United States where hexaploid and tetraploid chromosome numbers of  $n = 50-56$  (the common number throughout the range) and  $n = 32-36$  (from one collection in Baja California) are known (Powell, 1974). Raven (1963) suggested that *P. emoryi* reached Chile and Peru by long-distance dispersal (in late Pliocene or Pleistocene), a subject which is discussed further by Powell (1974). The present chromosomal data suggest the possibility that South American *P. emoryi* ( $n = 34-36$ ) might have originated from Baja California *P. emoryi* ( $n = 32-36$ ) at a time when tetraploid populations were more widespread.

*Flaveriinae* — The species of *Flaveria* and its allied genera *Sartwellia* and *Haploësthes* are consistently  $n = 18$ , except for a single case of polyhaploidy ( $n = 9$ ) in *F. campestris* (Anderson, 1972), and the two tetraploid ( $n = 36$ ) collections of *F. pringlei* in Table 1. The latter species, related to *F. angustifolia* and *F. vaginata*, is also diploid (Table 1). The three taxa listed as *Flaveria* sp. are undescribed. With the data presented here and elsewhere (Turner, 1975; Turner, 1971; Powell and Powell, 1977) a base number of  $x = 18$  seems certain for the Flaveriinae. Chromosome numbers are lacking for only four of the 21 species of *Flaveria* (*F. angustifolia*, *F. intermedia*, *F. robusta*, and *F. vaginata*); chromosome numbers are known for all four species of *Sartwellia* (Table 1) and for all but one taxon of *Haploësthes* (*H. fruticosa*; Turner, 1975).

Counts for the Flaveriinae in Table 1 were accumulated in connection with a forthcoming revision of *Flaveria* by the senior author. The study has revealed in the earlier literature two chromosome number reports that were attributed erroneously to certain species, and these are corrected as follows: *F. anomala*, Graham & Johnston 4818, reported as *F. ramosissima* in Turner and Johnston (1961); *F. anomala*, Powell & Edmondson 542, reported as *F. ramosissima* in Powell and Turner (1963).

*Senecioneae* — The count in Table 1 for *Bartlettia scaposa* ( $n = 11$ ) is consistent with the only previous report for the species (from Mexico), which is distributed almost entirely in Chihuahua and Durango, Mexico (Powell, 1963). *Pelucha trifida* ( $n = 19$ ) is an anomalous genus with uncertain tribal affinity, but its chromosome number and morphology suggest that it might belong in a group with several other North American Senecioid genera with  $x = 19$ .

*Mutisieae* — The chromosome number of *Acourtia* (= *Perezia*) *nana* ( $n = 27$ ) is the same as its two geographically related species *A. wrightii* and *Perezia runcinata* and consistent with the base number of  $x = 9$  so far indicated for *Acourtia* (Powell and Sikes, 1970).

## ACKNOWLEDGMENTS

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#### NOTES AND NEWS

NEW PLANT DISTRIBUTION RECORDS FROM THE SOUTHWESTERN UNITED STATES AND NORTHERN MEXICO. — Recent collecting activities in the Southwestern United States and northern Mexico have turned up several new or otherwise significant plant distribution records. Some of these have developed significance after passage of the Endangered Species Act and the subsequent publication of state lists of threatened or endangered species.

#### FABACEAE

*Astragalus musimonum* Barneby. Arizona, Mohave Co., ca. 30.5 km S of St. George, Utah, at 1350 m on the W slope of Seegmuller Mountain above Mokiah Wash, on calcareous bank along road in piñon-juniper community, R. Spellenberg, R. Delson, J. Syvertsen 3182, 20 May 1973.

In *Arizona Flora* (T. H. Kearney and R. H. Peebles. 1951. Univ. Calif. Press) this species was listed as possibly occurring within Arizona, the record based on a collection from the same vicinity (Ripley and Barneby 4321) as our recent collection. Their collection was immature and Barneby was uncertain of the correct identity of that material. In the supplement bound with a later edition of *Arizona Flora* (1964: p. 1054) Barneby concluded their collection was misidentified, actually representing *Astragalus amphioxys* Gray var. *modestus* Barneby. He maintained this opinion in his monumental "Atlas of North American *Astragalus*" (1964. Mem. New York Bot. Gard. Vol. 13). Our collection "keyed" easily to *A. musimonum* since it had good fruit and a few flowers. The identification was confirmed by Barneby. In our correspondence regarding the collection he noted that his and Ripley's earlier collection had been lost. The species appears in the 7/1/75 Federal Register as "threatened" in Nevada.

*Petalostemum scariosum* (Wats.) Wemple. New Mexico, Socorro Co., 1.6 km S of La Joya Game Refuge exit on IH-25, R. Spellenberg, J. M. Willson 4228, 8 Jul 1976.

The species is listed as "endangered" in New Mexico in the 6/16/76 Federal Register. In a recent revision of the genus (D. K. Wemple, 1970, Iowa State Coll. J. Sci. 45:1-102) all collections cited were made about 70 years ago from only two stations near the Rio Grande in Bernalillo and Valencia counties. However, we find the species to be more widespread, occurring from the Laguna Indian Reservation in eastern Valencia Co. to the Sandia Mountains in central Bernalillo Co., southward to east of San Antonio in central Socorro Co. The species may have been orig-

inally restricted to eroded tops and slopes of sandy-clay bluffs but seems to respond positively to disturbance, occurring sporadically in loose sand near roadsides and other sandy areas now believed to have been degraded by domestic grazing. Observations made in the spring of 1977 on a population in central Socorro Co. indicate that the species is not, or but little, grazed by cattle and horses on otherwise heavily used rangeland.

#### NYCTAGINACEAE

*Selinocarpus palmeri* Hemsl. Coahuila, 4 km by winding road E of El Coyote at NW end of Sierra de Solis, 25°40'N lat., 103°10'W long., elev. ca. 1100 m, on a large, almost pure gypsum outcrop, *R. Spellenberg* and *J. Syvertsen* 3768, 16 Aug 1974.

Until this new collection the species was known from only two others (*Palmer* 1118, 1119, May 1880, from San Lorenzo de Laguna). But perhaps more important is evidence of the precise location of Palmer's "San Lorenzo de Laguna", not to be located on modern maps. McVaugh (1956. Edward Palmer: plant explorer of the American West. Univ. Okla. Press) indicated that it should be in the near vicinity of the site from which our collection was taken. That our locality is also that of Palmer is supported by the occurrence of the newly described *Euphorbia fruticulosa* Boissier var. *hirtella* M. C. Johnston (*Wrightia* 5:141) with the *Selinocarpus*, our collection providing the holotype. M. C. Johnston (pers. comm.) subsequently discovered a specimen of this variety in the Gray Herbarium collected by Palmer at "San Lorenzo de Laguna".

#### OPHIOGLOSSACEAE

*Botrychium matricariifolium* A. Br. New Mexico, Catron Co., Gila Wilderness, ca. 16 km by air ESE of Mogollon, on Crest Trail 182, 4 km SE of Sandy Point, in mature spruce-fir-aspen forest, N slope, 3033 m elev., *R. Spellenberg, J. Reitzel, D. Hill* 4528, 5 Sep 1976.

This record is the first for this species in the state and is the southernmost record for the genus in New Mexico.

#### POACEAE

*Muhlenbergia villosa* Swallen. New Mexico, Otero Co., Otero Mesa NE of Orogrande, Sec 7 or 18, T24W, R11E, elev. 1775 m, *R. Spellenberg* 4565, 24 Sep 1976.

The species is said to be endemic to Texas and to occur there only extremely locally, apparently confined to gypsum, near the SW corner of the panhandle (F. Gould. 1975. *The Grasses of Texas*. Texas A & M Press). The newly discovered population was vigorous, on soil derived from limestone, occurring in scattered but dense patches over an area of about 25 m<sup>2</sup>. The species is listed in the 6/16/76 Federal Register for Texas as "endangered".

*Urochloa panicoides* Beauv. New Mexico, Las Cruces, New Mexico State University campus, weedy lawn, *R. Spellenberg* 4480, 26 Aug 1976.

Mr. José Valls, a student of Dr. Frank Gould, kindly identified this collection. It appears to be the first U. S. record for this Asian and African grass, now introduced elsewhere in warm parts of the world. At this point it appears to be only adventive. — RICHARD SPELLENBERG, Department of Biology, New Mexico State University, Las Cruces 88003.

IRREGULARITY OF PINYON CONE PRODUCTION AND ITS RELATION TO PINYON CONE MOTH PREDATION. — *Eucosma bobana* Kearfott (Lepidoptera: Tortricidae) larvae are prey-specific predators of maturing ovulate cones of *Pinus edulis* Engelm. and *P. monophylla* Torr. & Frem. (*Powell, Hilgardia* 39:1-36. 1968). Thus the number of ovulate cones annually produced in pinyon woodlands may determine, in part, the potential population densities of cone moths. In turn, the number of pine cone

moths produced in any one year may affect the production of viable pine seeds in the next year.

Eight *P. monophylla-Juniperus osteosperma* (Torr.) Little woodlands in southern Idaho and northern Nevada (U. S. A.) were visited during the winter and spring of 1977. Because ovulate cones leave abscission scars at the annual whorls of actively growing leader shoots, I could estimate a cone production sequence for the 1968–1977 period by the following method: sample five trees within a pinyon community and count all potential cone-bearing leader shoots within those trees; then subsample five leader shoots from each tree and count the abscission scars and currently maturing cones at the annual whorls of each leader shoot. By using the total pinyon canopy coverage of a 600 m<sup>2</sup> plot that contained the five sample trees, these data can be used as a basis for estimation of a 10-year cone production sequence on a unit-area basis for the entire pinyon population (cf. Gorchakovskii, Bot. Zurn. 43:1445–1459. 1958). The sample numbers used in this method have been shown to be adequate in a previous study (Forcella, Thesis — Montana State U., Bozeman 59715, p. 53. 1977; Weaver and Forcella, in prep.).

The accuracy of this method can be checked by comparing the abscission scar estimate of the 1976 cone crop with the number of "freshly" abscised cones found on the ground within the 600 m<sup>2</sup> plot (occasionally cones fail to abscise from the leader shoots, but these can be easily counted in most cases since the trees are only 3–5 m in height). The two methods compare favorably ( $r^2 = 0.95$ ,  $n = 7$ ,  $p = 0.01$ ).

These freshly fallen cones can also be used to estimate the extent of predation upon them. Cones infested with *E. bobana* larvae or pupa cases (normally one/cone in the several tens of cones I checked) abort before maturity and possess telltale entry-exit holes. Rodent-molested cones often exhibit chewing marks and are frequently left in piles at the bases of trees directly below feeding platforms. Cones ravaged by birds, notably pinyon jays (*Gymnorhinus cyanocephalus*) and Clark's nutcrackers (*Nucifraga columbiana*) have a generally shredded appearance.

In 1976, four of the sampled stands had cone crops well above their 10-year averages. Two of these stands also had average or above average cone crops in 1975, while the other two stands had 1975 cone crops that were only about 50% of their averages. The 1976 cones in the two stands with consecutively abundant crops were heavily utilized (80% and 50%) by *E. bobana* larvae; an additional 10–20% were preyed upon by other animals. In contrast, the abundant 1976 cones of the two stands with below average 1975 crops were only mildly infested with cone moth larvae (20% and 17%) and showed insignificant utilization by other sources. A significant correlation exists between the current magnitude of cone moth depredation and the abundance of the previous year's cone crop (Fig. 1). A similar situation occurs with *Pinus rigida* and its cone predators (Mattson, Canad. Entomol. 103:617–621. 1971).

Such evidence for prey-frequency dependent predation indicates that consecutively good (above average) cone crops in pinyon are not selectively advantageous. Instead for pinyon, fewer cones, but these produced at strategic intervals, may confer fitness. The overall annual cone crops in pinyon communities are highly irregular (C. V. =  $94 \pm 32\%$  for the eight Great Basin stands). Above average cone crops occur in only two or three out of ten years in Great Basin pinyons, and these good crops appear to be randomly distributed within the 10-year sequence investigated. In the same 10-year period *P. monophylla* communities south of N 136° 20' (southern Calif., southern Nevada, and the Santa Ancho Mts., Arizona) had good cone crops only once or twice, and their C. V.'s are correspondingly somewhat higher ( $112 \pm 24\%$ ,  $n = 7$ ; unpublished data). Such irregularity in cone production may have selective advantages by keeping the predator populations small through a low average annual cone (mast) crop, thus insuring predator satiation and seed survival in years of good cone crops.

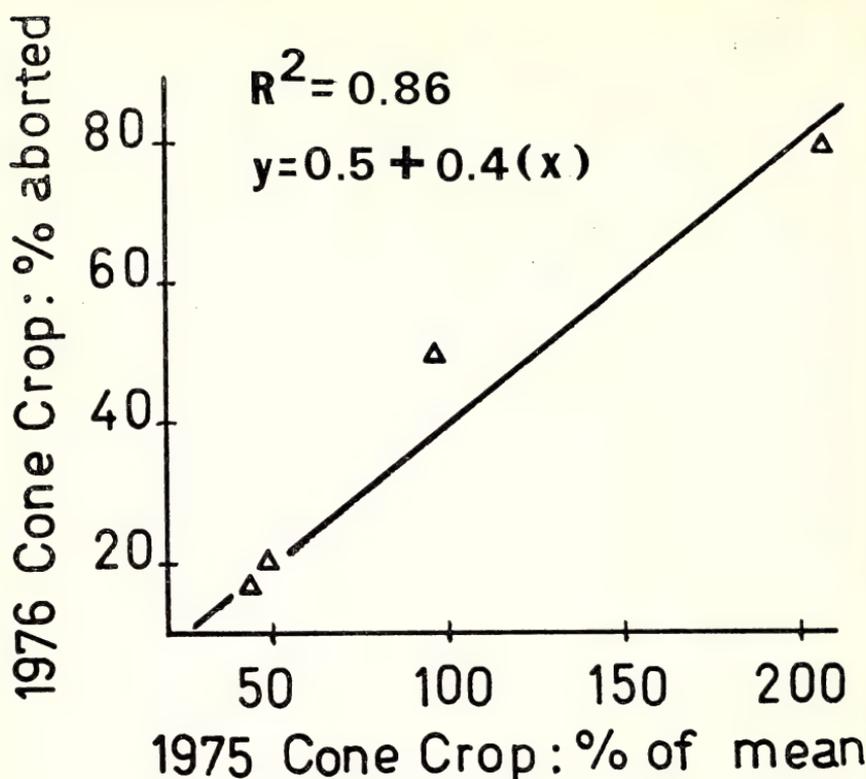


Fig. 1. The relative utilization of pinyon cone crops by *Eucosma bobana* (pine-cone moth) larvae as a function of the magnitude of the previous year's cone crop. The y-axis represents the percent of the 1976 cone crop that was aborted due to larval infestation. The x-axis represents the 1975 cone crop as a percent of the average of a 10-year cone production sequence for each *Pinus monophylla* community. If all cone predators were included in the analysis the slope of the regression line would be about 0.5.

K. T. Douglass, A. F. Johnson, P. G. Risser, and T. Weaver were all kind enough to edit and comment on the original version of this report. — FRANK FORCELLA, Department of Biology, Montana State University, Bozeman 59715 (Current address: Department of Botany-Microbiology, University of Oklahoma, Norman 73019).

NOTES ON THE FLORA OF EAST-CENTRAL IDAHO. — Although excellent treatments of much of Idaho's flora have been published (Davis, *Fl. Idaho*, 1952; Hitchcock et al., *Vasc. Plants Pacific Northw.*, 1955–1969, and Hitchcock and Cronquist, *Fl. Pacific Northw.*, 1973), some areas within the state remain relatively unknown floristically. With funding made possible by a C. R. Stillinger Grant, intensive botanical exploration of parts of east-central Idaho (Lost River, Lemhi, and Beaverhead Ranges of Custer, Lemhi, Butte, and Clark Counties) was initiated in the summer of 1973. As a result of three collecting seasons in the region, several plants worthy of mention have been encountered. Collection numbers are those of the author; specimens are deposited in ID.

*Aquilegia coerulea* James var. *coerulea*. Lemhi Co., E slope Lemhi Range, Targhee Nat. Forest. Moist, N-facing slope beneath Douglas fir, Mammoth Canyon, 2136 m, 15 July 1973, 1108. Although the var. *coerulea* is common in the central Rocky Mountain states, it is rarely encountered in Idaho, and this population, which is composed of about half var. *ochroleuca* Hook., may represent the NW limit of this blue-sepaled columbine. A second population in Butte Co., 7.5 km SE of Mammoth Canyon in a southern tributary of Meadow Canyon is composed of both varieties of *A. coerulea*, *A. formosa* Fisch., and *A. flavescens* Wats., as well as a wide array of putative hybrids apparently combining features of all three taxa, 1601, 1602, 1603, 1604.

*Saltha leptosepala* DC. var. *sulfurea* Hitchc. Lemhi Co., E slope Lemhi Range, Salmon Nat. Forest. Moist ground at head of small lake, headwaters of Middle Fork Little Timber Creek, 2834 m, 3 July 1973, 932; subalpine meadow above Mill Lake, 2800 m, 30 July 1974, 2096. This variety was previously known only from the Lost River Range, Custer Co., Idaho, but appears to be a common inhabitant of subalpine stream banks and lake shores of the central and northern Lemhi Range where substrates are primarily quartzitic.

*Draba oreibata* Macbr. & Pays. Lemhi Co., E slope Lemhi Range, Targhee Nat. Forest. Alpine tundra on NE side of peak 10,652, 2.5 km NW of junction of Meadow Canyon and South Fork, 3121 m, Sec 29, T11N, R28E, 24 July 1975, 2819; crest of Lemhi Range, summit rocks of Big Windy Peak, 3170 m, at head of Spring Mountain Canyon, 16 July 1973, 1116. This species was previously known in Idaho only from Pass Creek Gorge, Lost River Range, Custer Co. Its occurrence in the Lemhi Range is apparently restricted to limestone substrate.

*Lesquerella carinata* Rollins. Lemhi Co., Crest of Lemhi Range, summit rocks of Big Windy Peak, 3170 m, head of Spring Mountain Canyon, 16 July 1973, 1118; E slope Lemhi Range, NE ridge of peak 10,858 just S of junction of Meadow Canyon and South Fork, 2438 m, 24 July 1975, 2864; Crest of Lemhi Range, 0.7 km N of Bell Mountain, 3160 m, 29 July 1975, 2882. Butte Co., Crest of Lemhi Range, limestone rocks on summit of peak 10,400 at head of Middle Fork Eightmile Canyon, 3170 m, 3 July 1974, 1442. Clark Co., Crest of Lemhi Range at the head of Surret Canyon, 2926 m, 8 July 1975, 2593; E base of Lemhi Range, outwash of Eightmile Canyon, 1920 m, 4 June 1975, 2226; N side of Eightmile Canyon on limestone outcrop, 2011 m, 6 June 1975, 2289; W slope of Beaverhead Range, limestone outcrop in Peterson Canyon, 1804 m, 10 June 1975, 2357. Although apparently restricted to limestone in east-central Idaho and previously considered rare, this species is common in Custer, Lemhi, Butte, and Clark Counties from lower elevations to the highest summits, and has been reported recently from Montana by Lackschewitz (Madroño 23:361. 1976).

*Saxifraga debilis* Engelm. Lemhi Co., W slope Beaverhead Range, Salmon Nat. Forest, moist rocks near summit of Mountain Peak, 3050 m, near the head of Bull Creek, 22 July 1975, 2794. Although this species is listed by Davis (op. cit.), there is no discussion concerning its occurrence within the state. Hitchcock and Cronquist (op. cit.) state that it is probably in Idaho. It has been encountered but once in three field seasons of intensive exploration in the region and can most probably be considered rare for the state.

*Trifolium haydenii* Porter. Lemhi Co., E slope Lemhi Range, Targhee Nat. Forest, limestone rocks at junction of Meadow Canyon with South Fork, 2316 m, Sec 33, T11N, R28E, 7 July 1974, 1559; limestone rocks on summit of peak 10,652, N side of Meadow Canyon, 3246 m, 24 July 1975, 2844; W slope Beaverhead Range, Salmon Nat. Forest, quartzite talus on east side of Mountain Peak, 2926 m, 22 July 1975, 2761. Butte Co., E slope Lemhi Range, Targhee Nat. Forest, limestone rocks near summit of peak 10,858, 1 km S of junction of Meadow Canyon and South Fork, 3185 m, 10 July 1975, 2623. This plant is common in the Meadow Canyon drainage of the southern Lemhi Range and occurs from canyon bottoms with limber

pine and Douglas fir to the highest summits. It is particularly abundant on rocky alpine slopes and, in some cases, is the most abundant understory plant with Engelmann spruce at timberline. This is believed to be the first report of this species for Idaho.

*Gentiana tenella* Rottb. Custer Co., E slope Lost River Range, Challis Nat. Forest, moist, grassy bank of Pass Lake near outlet, head of W Fork Pahsimeroi River, 3079 m, 15 August 1973, 1169. This species is apparently rare in Idaho for searches of Pacific Northwestern herbaria (ID, IDS, WS, and WTU) and NY have failed to produce a single Idaho specimen. Hitchcock and Cronquist (op. cit.) indicate that it is reported from Idaho.

*Langloisia punctata* (Cov.) Goodd. Clark Co., Dry, rocky soil at Reno Point, S end of Beaverhead Range, 1646 m, 9 July 1975, 2604. This is a rather substantial population of several hundred plants and represents a significant N extension of its range. It has not previously been reported from Idaho although its occurrence has been noted in SW Idaho by Dr. Patricia Packard (pers. comm.).

*Phacelia incana* Brand. Clark Co., W slope of S Beaverhead Range Targhee Nat. Forest, moist limestone talus, Bare Canyon, 2103 m, 22 June 1975, 2482; limestone rocks at Reno Point, 1648 m, 9 July 1975, 2606. This species was previously known in Idaho only from a few collections and is rare in the state. The collections cited are populations composed of very few, widely scattered plants.

*Phacelia lyallii* (Gray) Rydb. Lemhi Co., E slope Lemhi Range, Salmon Nat. Forest, talus slope on saddle connecting Mill Lake with E Fork Hayden Creek, 2877 m, 1 August 1974, 2135. Gillett (Rhodora 62:205-222. 1960) reported two locations for this species in N Lemhi Co. Neither Davis (op. cit.) nor Hitchcock and Cronquist (op. cit.) indicate its presence in Idaho.

*Pedicularis contorta* Benth. var. *ctenophora* (Rydb.) Nels. & Macbr. Lemhi Co., E slope Lemhi Range, Targhee Nat. Forest, grassy slope of peak 10,652. 3 km NW of junction of Meadow Canyon and South Fork, 2746 m, Sec 21, T11N, R28E, 24 July 1975, 2859. The collection cited represents a W extension of the range of this variety of only about 75 km, but it has not previously been reported for Idaho. This plant is abundant in the Meadow Canyon area but has not been encountered elsewhere in the region. — DOUGLASS M. HENDERSON, Department of Biological Sciences, University of Idaho, Moscow 83843.

## REVIEWS

*Terrestrial vegetation of California*. Ed. by MICHAEL G. BARBOUR and JACK MAJOR. + map of the natural vegetation of California (1:1,000,000) by A. W. Küchler. John Wiley and Sons, New York. 1977. \$47.50.

California is one of the most diverse of states geologically, climatically, and biologically. In what other state than California grow plants of more than 5,000 native species? And in how many intricate ways do these plants become arranged into vegetational communities from tall forests to the almost barren bajadas of extreme deserts? From chaparral to alpine fell fields? Who would dare to make order out of such ecological chaos? Two people did, and to them we are indebted for this book. Without the leadership of Barbour and Major, *Terrestrial Vegetation of California* could not have been produced, even given the wealth of material and the cooperation of knowledgeable colleagues.

The wealth of plant species in the California Floristic Province, the endemics, the intricate genetic relationships, and the combination of rock and climate led to the dominance of taxonomy in California at mid-century and to the rise of biosystematics. Because of this natural pre-occupation with flora and its evolution, it is not too surprising that research on vegetational structure and classification in California was somewhat neglected, especially by academic scientists. This book could not have been written even as recently as twenty years ago. It comes none too early

in a region where even its ecologically enlightened people have overwhelmed many of the native biological communities.

The book is packed with information: 26 chapters, more than 1000 pages, and the large useful map. The introductory overview alone consists of six chapters and 220 pages, a book in itself. Do you want to know something about the California climate? Read Jack Major's Chapter 2. How about the flora? Peter Raven's Chapter 4. And what about California's paleoecology? Dan Axelrod's Chapter 5 comes as close in short space to summarizing the great changes that have taken place in western North America during the Tertiary and Pleistocene as could be done without writing a separate book. I notice only one omission in the overview section that would be helpful in such a relatively dry region — a chapter on the hard rock geology and perhaps another on the building and shaping of the mountains. Vegetation is almost as closely allied to substratum in much of California as it is to climate. Fortunately, there are very good books on California geology such as Jahn's "The Geology of Southern California" and Bailey's "Geology of Northern California".

There are 20 chapters on the main vegetational "types" of California. These are arranged into six large floristic provinces based upon their geographic affinities. Each chapter is an authoritative compilation. There is a uniform approach in all chapters, and there is cross-reference and integration among the chapters. Fortunately, no attempt was made to impose a hierarchical classification. Each chapter has one or more tables of actual vegetational data. Even though these are sometimes small samples, they provide some feeling for the vegetational and floristic structure.

There are several other things about each chapter that I like. For example, the title page of every chapter that deals with a vegetational type displays a physiographic map of California. On this map, the areas of the particular vegetation type are clearly marked. Details can be checked in Kùchler's excellent map. Each chapter includes a sampling of data (of varying richness) from physiological ecology. This is unusual in books on vegetation. Yet, if we are to understand vegetational composition, pattern, and function, we must have such information. This leads logically to another uniformity among chapters: suggestions for future research. What a gold mine of ideas for graduate students and active ecologists. All this, and the literature reviewed, too!

Further weak points are relatively minor. In such a book, one expects an abundance of clear photographs of the vegetation. There are relatively few, and the reproduction of some lacks clarity. Another money-saving device is the use of typewriter script for camera-ready tables and reference lists, which I don't begrudge.

Here, then, is a true classic that everyone interested in the Californian countryside, mountains, and deserts should have. The price? Entirely reasonable when it is realized that it is an encyclopedia of western vegetational ecology, and the book has scientific permanence. Its like will not appear again within the lifetime of its present readers. — W. D. BILLINGS, Department of Botany, Duke University, Durham, North Carolina 27706.

Ed. Note: No more than one review of a single volume is normally published in *Madroño*. However, *Terrestrial vegetation of California* is sufficiently significant as a landmark that more than one perspective is useful.

As members of (we suspect) the first upper division class to utilize *Terrestrial vegetation of California* as a text, we wish to communicate our reactions to the book. After a ten-day field trip through northern California, the class read and discussed 14 of the 20 chapters dealing with vegetation. As informed students we are meters of evaluation somewhere between the initiate and the professional botanist.

Th editors have handled burdensome layout problems well. However, there are a few prominent difficulties that must be mentioned. Most of the tables have been presented lengthwise so that they are not easily examined, and the spacing is so ex-

panded that unnecessary pages are added to an already large volume.

A. W. Küchler's "Native Vegetation of California" map is enclosed with an expanded legend in an appendix. In addition, each chapter is preceded by a diagrammatic map depicting the locations of vegetation types discussed. The latter could have been larger and more clearly contrasted for easy reference. Photographs tend to be dark, lacking in contrast, and of little assistance. Vegetation types are not consistently named throughout the book. Names should have been standardized or alternatives listed at the beginning of each chapter.

The "Research Natural Areas" and "Status of Vegetation Mapping" chapters are peripheral to the purpose of the book. The chapter on climate is essential, but lengthy and not easily read. It could have been a shorter review, as stated in the book's objectives.

Raven's discussion of California's flora in the introductory chapters is excellent, offering a good introduction to the highly endemic nature of California taxa and providing a firm basis for understanding the processes involved. Zinke's chapter, "Redwoods and Associated North Coastal Forests", lacks organization. He incompletely synthesizes a large amount of data, thus failing to guide the reader in speculation about redwood ecology.

Griffin's chapter, "Oak Woodland", is the best organized and most readable of all the contributions. He takes a ubiquitous vegetation type with little or no floristic unity and molds it into a presentation that at once gives a clear explanation of what is known (very little) and what is not known (a great deal).

"The Closed Cone Pines and Cypresses" displays the numerous problems in dealing with a difficult assemblage of arbitrary communities. Although the bibliography is superb, the chapter lacks cohesiveness and reflects a southern California viewpoint. The same bias is seen in the chaparral chapter.

Chapters on "Southern Coastal Scrub" by Mooney and "Vernal Pools" by Holland and Jain outshine others in the presentation of autecological studies. It is regrettable that knowledge of other vegetation types such as "North Coastal Scrub and Prairie" is not up to this level. The inconsistency of this last chapter may well be a reflection of its multiple authorship.

The "Montane and Subalpine Vegetation of the Sierra Nevada and Cascades" chapter presents a fine, although occasionally flawed, summary. In spite of controversy in the literature, only one interpretation of tree stand dynamics is offered.

The most important function of the volume will be as a reference rather than as a text — a kind of manual of vegetation types. Although cumbersome in the field or car, as most floras are, this book will be a valuable part of an herbarium, library, or botanist's reference shelf. A valuable feature is the extensive and current bibliography that follows each chapter.

This book is easily the best available review of California's vegetation, assembling diverse opinions and backgrounds from California's premier plant ecologists into a sizeable yet usable compendium that stimulates the reader not only to read and digest but to challenge with personal observation and research. — PETER STEKEL and EDWARD A. COPE, Department of Biology, Humboldt State University, Arcata, CA 95521.

#### MAP OFFER

The new map of the natural vegetation of California in full color at the scale of 1:1,000,000 will become available on 15 March 1978 with a brochure containing a commentary on the map and a detailed description of every vegetation type. Price: \$8 incl. brochure and postage; orders of 20 or more at a discount of 15%. Rolled maps, shipped in a tube cost \$12, postage extra. Make checks payable to A. W. Küchler and send orders with checks to A. W. Küchler, Dept. of Geography, University of Kansas, Lawrence, KS 66045.

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Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288, 1974. Institutional abbreviations in specimen citations should follow Holmgren and Keuken's list (*Index herbariorum, Part 1. The herbaria of the world*. Sixth edition, 1974. Regnum Veg. vol. 92). Abbreviations of names of journals should be those in *Botanico-Periodicum-Huntianum* (Lawrence, G. H. M et al. 1968. Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full title of the journal should be used. Titles of books should be given in full, together with the place and date of publication, name of publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted twelve pages in the journal over a two-year period. Beyond that number of pages, a required editorial fee of \$40.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Subject to approval of the Editor, articles may be published ahead of schedule, as additional pages of an issue. Editorial fees for such papers will be larger and will be determined on an individual basis.

## ANNOUNCEMENT

### CALIFORNIA BOTANICAL SOCIETY GRADUATE STUDENT MEETINGS

The California Botanical Society Graduate Student Meetings will be held at California Polytechnic State University, San Luis Obispo, on November 11 and 12, 1978. The meetings will take the form of a series of short research papers, or reports on work in progress, contributed by graduate students in all botanical fields. Members and non-members of the society are invited to participate. If you wish to receive further announcements concerning these meetings, please send your name and address to Malcolm McLeod, Biological Science Department, California Polytechnic State University, San Luis Obispo, CA 93407.

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# THE VEGETATION OF TWO CALIFORNIA MOUNTAIN SLOPES

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## ABSTRACT

Community characteristics and the distribution of woody species along complex elevational gradients are described for south-facing slopes in two California mountain ranges. In the inner North Coast Range, the low elevation (780–1250 m) community on Snow Mountain is a chaparral-woodland on serpentine substrate. At 1250 m, a sharp ecotone marks the change to nonserpentine soils and a mixed-coniferous forest that extends to the peak (2112 m). Along a northern Sierran transect (600–2040 m) is a series of three, well-defined forest communities. Species are distributed along this elevational gradient in a broad, overlapping manner with less correlation between community type and edaphic factors than found on Snow Mountain. The number of tree species in the Sierra is greater than on Snow Mountain, where serpentine soils and a drier climate are present. The number of shrub species and their relative importance is greatest in the serpentine chaparral where tree density and cover are low. On both slopes, overall woody species diversity decreases at higher elevations.

Montane forests are distributed in predictable patterns that vary with elevation. In California, the forests of the Sierra Nevada form a series of elevational zones dominated by one or several tree species. The distribution and composition of these forests have been characterized by Rundel, Parsons, and Gordon (1977), Ornduff (1974), Munz (1959), and Kylvér (1931). Within an elevational zone, each montane community is composed of a mosaic of site types, based in part on microclimatic and topographic positions. Diversity of soil and parent material also influences the composition and distribution of montane communities as shown by Kruckeberg (1969) and Whittaker (1960).

The objective of this study is to document quantitatively the composition and structure of montane forest communities along two California mountain slopes. The study is both a synecological description of several common forest communities and an example of how ordination techniques can be used to examine community characteristics and variation in response to environmental factors.

*Description of Study Areas.* A steep slope was located on Snow Mountain (Lake Co.) in the inner North Coast Range (N39°22', W122°45'). The transect extended from Bear Creek Ranger Station to the West Peak. The elevational gradient was from 780 m to 2040 m, over a linear distance of 9.6 km. A more gradual slope was located 135 km to the east in

the Sierra Nevada (N39°25', W121°05' to N39°38', W120°30'). The transect began 4 km south of Camptonville (Yuba Co.) and followed Highway 49 to Yuba Pass (Sierra Co.). The elevational gradient was from 600 m to 2040 m over a distance of 73 km.

Mean annual precipitation on the Sierran transect is 127 cm, 180 cm, and 102 cm at low, medium, and high elevations, respectively (U. S. Weather Bureau, 1964). Climatic records for the Snow Mountain area from low elevation stations (400 m) east of the mountain show mean annual precipitation of 50–76 cm, and mean annual temperature of 15.7°C (U. S. Weather Bureau, 1964). Mean annual temperature decreases with elevation along the Sierran transect from 11.5° to 6.0°C (U. S. Weather Bureau, 1964). Winter snow is found above 1400 m on the Sierran transect, and frequently above 1700 m on Snow Mountain.

Soils at low to medium elevations on Snow Mountain are predominantly red-brown, slightly acidic stony-loams (U. S. Forest Service, 1955). Above 1800 m, there are large colluvial areas of broken rock with little soil. Intermixed are areas of shallow, moderately acidic loams (U. S. Forest Service, 1955). The geology of Snow Mountain and most of the North Coast Range is dominated by rocks of the Franciscan formation (Page, 1966; Irwin, 1960). At low elevation sites there is a disorderly assemblage of sandstone, shale, and chert, with intrusions of serpentine. Above 1250 m is a more homogeneous formation of volcanic and metavolcanic greenstones with no reported or observed areas of serpentine (Dept. Nat. Res., 1966).

Below 1500 m on the Sierran transect the predominant soils are reddish-brown, slightly acidic loams (Soil. Con. Ser., pers. comm.). No data are presently available for soil types at higher elevations. The parent material below 1150 m is marine sedimentary mixtures of clay and shale. Mid-elevation sites are underlain by glacial deposits consisting of fluvio-glacial sand and gravel. Granitic rock predominates at higher elevations (Dept. Nat. Res., 1962).

#### METHODS

In the spring of 1977, vegetation was sampled at 90 m elevation intervals along both slopes. Only south to southwest slopes were sampled with inclinations of 5–30°. At each elevation interval a preliminary reconnaissance was conducted to record the presence of all woody species. A site was then chosen that had the desired aspect and that contained the representative species commonly encountered at that elevation. Sites were homogeneous in the sense that they were undisturbed and not topographically diverse.

A 20 by 25 m quadrat (0.05 ha) was marked and numbers of all woody species, including tree seedlings, were recorded. Basal area of stems with 1.0 cm dbh or greater was also recorded for trees, shrubs, and seedlings. Percent cover of all species was estimated along three 25 m line intercepts.

Two indices of relative dominance were used in the data analysis. The relative basal area of stems was calculated for most species at each site. For all species at each site an importance value (IV) was calculated by the formula:  $IV = 0.5 (RD + RC)$ ; where RD = relative density and RC = relative cover. This synthetic index was chosen because it expresses the different types of dominance that are found in the tree and shrub strata, as well as lessening the over-weighting effect of highly dominant species. Trees tend to dominate in terms of relative cover, even at low densities; shrubs may show higher densities, but lower cover.

A matrix of pair-wise, unstandardized sample similarities was calculated by the Bray and Curtis (1957) formula for percent similarity (PS):  $PS = \sum \min(x, y)$ ; where  $\min(x, y)$  is the smaller of the two IV values for a given species in sample sites X and Y. The matrices of site similarities for both transects were displayed by the polar ordination method of Bray and Curtis (1957) on two orthogonal axes. The two most dissimilar sites were chosen as two X axis endpoints. The site with the lowest mean similarity with all other sites was selected first, followed by the site least similar to it. The two Y axis endpoints were chosen according to the criteria suggested by Cottam, Goff, and Whittaker (1973).

#### RESULTS

Fig. 1 shows the relative basal area of dominant tree species at each site along the elevational gradients. In general, the important trees on Snow Mountain exhibit greater mean dominance as measured by relative basal area than on the Sierran transect.

The distribution of individual species and their relative importance is indicated in Tables 1 and 2. On the Sierran transect *Pinus ponderosa*, *Quercus chrysolepis*, *Pseudotsuga menziesii*, and *Calocedrus decurrens* have wide-ranging distributions. In contrast, there are few species on Snow Mountain with equally broad ranges, resulting in a greater change of species.

Fig. 2 shows the polar ordination of sample sites. Sites that are located close together in the ordination field are similar to one another in species composition. These clusters are considered one community type and named after the dominant species or vegetation type.

The demarcation of communities is especially apparent on the Sierran transect where three distinct forest belts are found. A yellow-pine belt extends from 600–1500 m with *Pinus ponderosa* dominating, and *Pseudotsuga menziesii*, *Calocedrus decurrens*, and *Quercus kelloggii* exhibiting lesser importance. A white-fir forest with *Abies concolor* and *Pinus jeffreyi* follows. Above 1860 m is the red-fir community consisting of mainly *Abies magnifica* with *Pinus contorta* ssp. *murrayana* in small patches. These elevational belts correspond with the montane communities described by Rundel et al. (1977) and Munz (1959). The Sierran transect, though of a greater elevational range, does not include a low-

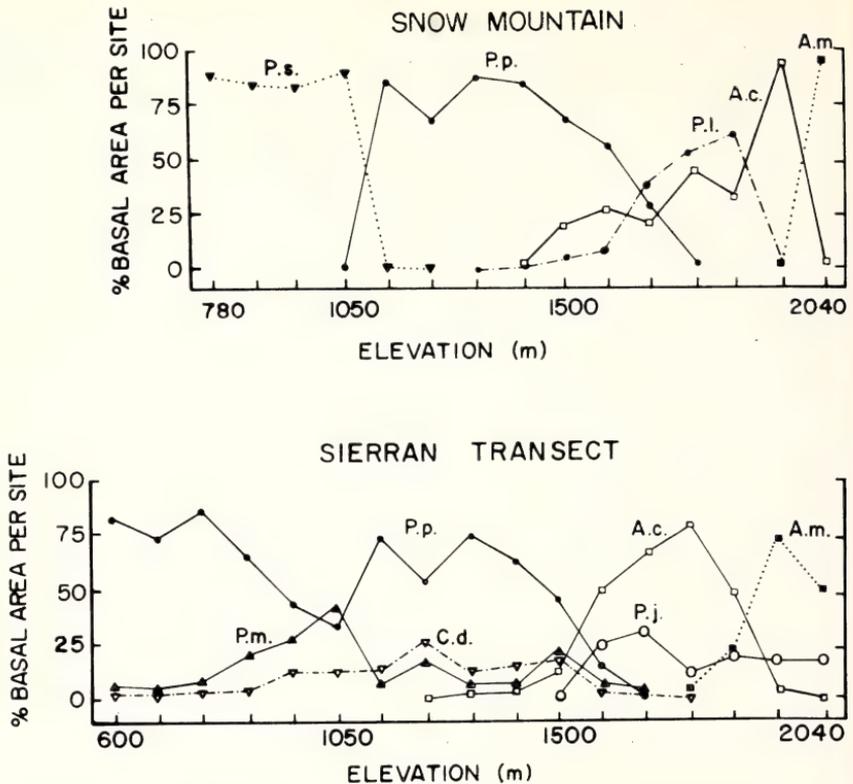


FIG. 1. Relative basal areas of dominant tree species along both elevational gradients. Only species with 25% or greater relative basal area per site are included. P.s. = *Pinus sabiniana*; P.m. = *Pseudotsuga menziesii*; C.d. = *Calocedrus decurrens*; P.l. = *Pinus lambertiana*; A.c. = *Abies concolor*; P.j. = *Pinus jeffreyi*; A.m. = *Abies magnifica*.

elevation foothill community. This vegetation is present below 400–500 m and is characterized by *Pinus sabiniana*, *Quercus douglasii*, and *Arctostaphylos* ssp.

Two main community types on Snow Mountain are indicated by the ordination of sites in Figure 2. Below 1250 m is a chaparral-woodland with *Adenostoma fasciculatum*, *Pinus sabiniana*, and *Quercus durata* sharing importance. Above is a montane coniferous forest showing successive dominance of *Pinus ponderosa*, *Pinus lambertiana*, and *Abies concolor* with increasing elevation. The chaparral community is common at low elevations in the North Coast Range where serpentine is abundant (Walker, 1954). The montane coniferous forest may be further separated into a yellow-pine belt (sites 7–10) and a white-fir belt (sites 11–14). However, sites 7–14 are considered one community type in this study because of their tendency to cluster together as closely related sites in the polar ordinations. This similarity is primarily due to the presence of

TABLE 1. IMPORTANCE VALUES (IV) FOR SPECIES AT EACH SITE ON SNOW MOUNTAIN.

Species	Sites														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. <i>Quercus dumosa</i>		2													
2. <i>Arctostaphylos stanfordiana</i>		4	3												
3. <i>Ceanothus cuneatus</i>	1	19	8	2	1										
4. <i>Umbellularia californica</i>	5	1			2										
5. <i>Adenostoma fasciculatum</i>	46	27	52	62											
6. <i>Pinus sabiniana</i>	22	18	17	18	3										
7. <i>Arctostaphylos viscida</i>				3	3										
8. <i>Quercus durata</i>	25	24	7		8	23									
9. <i>Quercus wislizenii</i>	1	3	7	6	26	17	17								
10. <i>Pseudotsuga menziesii</i>					1										
11. <i>Ceanothus integerrimus</i>					20	6									
12. <i>Cercocarpus betuloides</i>		2	6	9	4	7	2	5							
13. <i>Arctostaphylos glandulosa</i>						13		5			17				
14. <i>Pinus ponderosa</i>						17	19	43	55	53	31	17	4		
15. <i>Quercus chrysolepis</i>					13	9	28	31	27	32	25	22	49	45	
16. <i>Arctostaphylos canescens</i>					2	6	8		7		17		13		
17. <i>Pinus lambertiana</i>							2	4	4	19	12	35	20		
18. <i>Abies concolor</i>										9	18	12	39	18	50
19. <i>Ceanothus cordulatus</i>															5
20. <i>Abies magnifica</i>															
21. <i>Ribes lobbii</i>															

TABLE 2. IMPORTANCE VALUES (IV) FOR SPECIES AT EACH SITE ON THE SIERRAN TRANSECT.

Species	Sites																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. <i>Lithocarpus densiflora</i>			7	15													
2. <i>Arbutus menziesii</i>	7	4	5	4													
3. <i>Arctostaphylos viscida</i>	31	11	2	1	3												
4. <i>Quercus kelloggii</i>	11	20	31	25	9	7	13	6			3						
5. <i>Ceanothus integerrimus</i>					8												
6. <i>Pinus ponderosa</i>	33	31	35	24	28	17	34	23	50	40	14	12					
7. <i>Quercus chrysolepis</i>	4	31	2	1	8	4	11	20	4	6	20	3					
8. <i>Pseudotsuga menziesii</i>	11	3	13	25	35	48	17	14	11	13	20	8					
9. <i>Ribes nevadensis</i>									1								
10. <i>Calocedrus decurrens</i>	3		5	5	7	18	25	37	23	24	22	4	3				
11. <i>Pinus lambertiana</i>					2	6			4	4		2					
12. <i>Amelanchier alnifolia</i>									4		4						
13. <i>Arctostaphylos patula</i>										4			5				
14. <i>Ribes roezlii</i>											4	8	3	2			
15. <i>Garrya fremontii</i>												8		2			
16. <i>Castanopsis sempervirens</i>																12	
17. <i>Abies concolor</i>									3	8	14	41	56	50	58	14	12
18. <i>Ceanothus cordulatus</i>													13	14	22		
19. <i>Pinus jeffreyi</i>												12	21	7	6	8	13
20. <i>Pinus contorta</i> ssp. <i>murrayana</i>												2	4	3	6	6	19
21. <i>Abies magnifica</i>														5	8	72	56

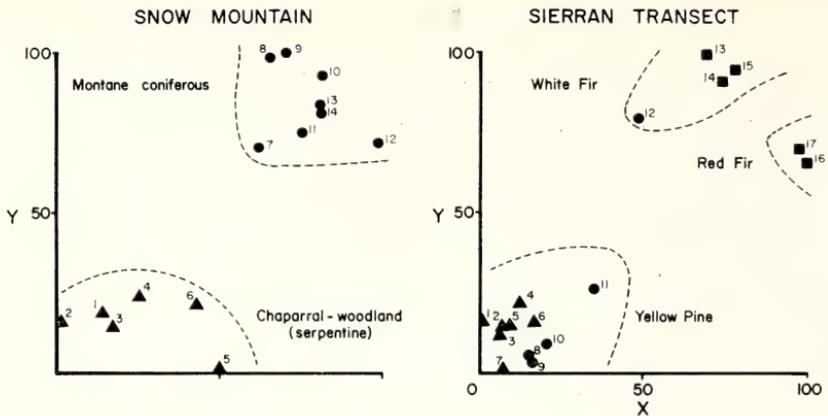


FIG. 2. Polar ordinations of sites along both elevational gradients. Sample sites are numbered and the underlying parent material indicated. Site 15 on Snow Mountain is not included. SNOW MOUNTAIN: triangles = Franciscan formation of sandstone and shale, serpentine present; dots = volcanic greenstones of the Franciscan formation, no serpentine. SIERRAN TRANSECT: triangles = marine sedimentary rock; dots = glacial deposits; squares = granitic rock.

TABLE 3. SPECIES DIVERSITY AND SHRUB IMPORTANCE VALUES FOR COMMUNITIES ON BOTH ELEVATIONAL GRADIENTS. Values calculated for each community type as indicated in Fig. 2.  $N_t$  = mean number of tree species/site;  $N_s$  = mean number of shrub species/site;  $IV_s$  = mean percent IV for all shrub species/site;  $H'$  = Shannon-Weaver index of diversity.

Community	$N_t$	$N_s$	$IV_s$	$H'$
SNOW MOUNTAIN				
Chaparral-Woodland	2.16	5.83	75.55	1.60
Montane-Coniferous	2.39	2.25	47.03	1.40
SIERRAN TRANSECT				
Yellow Pine	4.81	2.09	16.17	1.59
White Fir	4.75	2.75	23.21	1.49
Red Fir	4.00	0.0	0.0	1.01

*Quercus chrysolepis* and *Pinus lambertiana* in sites 7-14. *Quercus chrysolepis* is found at high densities in the understory of these sites as a small tree and shrub. The red-fir forest on the peak of Snow Mountain represents the southwest edge of a more extensive forest community that is found on the upper north and east slopes.

Table 3 lists the mean numbers of tree and shrub species, and total woody species diversity for each community. The mean percent of total importance values contributed by shrubs for each community is given as an index of relative shrub importance. Woody species diversity decreases with increasing elevation on both slopes, as does the importance of shrubs in the vegetation. Tree species richness is greatest in the Sierran transect; however, the number of shrub species in the serpentine chaparral is more than twice the number in any Sierran community.

## DISCUSSION AND CONCLUSION

The elevational transects in this study are complex climatic gradients along which temperature, precipitation, and length of growing season change. Species populations and community types are distributed along this environmental gradient in response to climatic factors (Whittaker, 1967). Edaphic conditions also change on both slopes and represent additional environmental factors that may account for variation in species and community types.

The ecotone between the chaparral-woodland and the montane coniferous forest on Snow Mountain is sharp as indicated by both the ordination and the individual distribution of the dominants. *Quercus durata* is a serpentine indicator (Kruckeberg, 1954, 1969) and is present on all but one of the chaparral-woodland sites. The discontinuity between this form of "serpentine chaparral" (Hanes, 1977) and the forest community at higher elevations corresponds to the edaphic disjunction.

No such disjunction based on edaphic factors is apparent in the Sierran transect. The dominants are distributed in an overlapping manner and there is less correlation between the ordination of communities and the underlying parent material. It appears that the distribution of communities along the Sierran transect is primarily a result of species distributions along a complex climatic gradient.

Although ordination methods are being used with increasing frequency in the analysis of vegetation, their effectiveness can be limited with certain types of data. Ordinations are subject to distortions of sample position when beta-diversity, the range of community variation, is great. Polar ordination has been shown to be the most resistant to this problem in comparison with other techniques (Gauch et al., 1977). There is no evidence of distortion from curvilinearity in the Snow Mountain ordination where beta-diversity is high; only a small amount exists in the Sierran ordination. Indeed, for both ordinations, the X axis or a diagonal axis parallels the main direction of change in community composition in response to elevation.

A major limitation of polar ordination is its vulnerability to the effects of different endpoint choices. When an extreme endpoint is selected with zero similarity with most other samples, the ordination can often become ineffective. If less extreme endpoints are chosen, the more extreme samples will always be found in the center of the ordination field, obscuring ecological interpretations of sample positions (Cottam et al., 1973). Because of this problem, site 15 on Snow Mountain was not included in the final ordinations presented in this paper. Thus, the interpretation of the Snow Mountain ordination is limited by the incomplete range of community variation presented, and a possible over-estimation of the dissimilarity between the two community types.

The following conclusions can be made about the composition and structure of the vegetation along the two mountain slopes:

(1) The observed pattern of species and community distribution can be related to an environmental gradient of climatic and edaphic factors. When environmental factors change abruptly, a sharp ecotone in vegetation may occur.

(2) Diversity of shrub and tree species decreases with increasing elevation on both slopes, which may result from the harshness of the high elevation environment.

(3) The numbers of tree species are less in the Snow Mountain communities than in the Sierra, primarily due to the presence of serpentine soils and a drier climate.

(4) The number of shrub species is greatest in the chaparral-woodland. Shrubs exhibit relatively high density forming a low, open vegetation with scattered pine trees. The increase in shrub species richness may be due in part to the low tree density and cover. This reduction in community structure can be attributed to the impoverished serpentine soils that limit biomass, productivity, and vertical differentiation of the vegetation (Whittaker, 1954).

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## REVIEW

*Northwest Botanical Manuscripts. An indexed register of the papers, 1867-1957, of Wilhelm Nicholas Suksdorf, William Conklin Cusick, Charles Vancouver Piper, Rolla Kent Beattie, and Harold St. John.* By TERRY ABRAHAM. 64pp., 7 illus. Washington State University Library, Pullman. 1976. \$5.00.

Botanical exploration of a country moves from travellers to residents, from the surgeon naturalist with the expedition to the storekeeper, ranchman or local physician whose keen interest in the local flora leads him afield. We now have a shelf of biographies of the explorers of Pacific Northwest: Douglas, Tolmie, Nuttall, Wilkes, Cook, Vancouver, LaPerouse, Lewis, and others. Terry Abraham, archivist at Pullman, has provided a checklist of the letters and papers of five important resident botanists: W. C. Cusick, whose papers date from 1906 to 1924; C. V. Piper, from 1888 to 1926; R. K. Beattie, from 1899 to 1956; W. N. Suksdorf, from 1867 to 1935; and H. St. John, from 1912 to 1957.

Two botanists had planned to write a history of botany in the Pacific Northwest, Albert Raddin Sweetser and R. K. Beattie. The Sweetser papers dating from 1897 to 1935, at the University of Oregon Library, are summarized in the *National Union Catalog of Manuscript Collections, 1959-1961* (1962) p. 73. They contain copies of letters and documents related to such a history, but his death in 1940 curtailed his plan. The Beattie papers at Pullman, numbering over 350 titles, listed in this publication, were likewise collected with a history in view. But Beattie died in 1960. The historian interested in tracing early figures or topics for this region will profit particularly from these two collections. For later twentieth century subjects, the letters at Pullman will likely prove most useful. The "Correspondence Index," pages 38-62, will ease the search since all five collections are integrated in this single index. Some

of the representative multiple entries include: L. R. Abrams, the Brandegees, F. V. Coville, A. Eastwood, M. L. Fernald, J. B. Flett, Martin Gorman, J. M. Greenman, H. M. Hall, A. A. Heller, A. S. Hitchcock, T. Holm, T. J. Howell, W. L. Jepson, I. M. Johnston, M. E. Jones, W. R. Maxon, A. Nelson, F. W. Pennell, B. L. Robinson, J. N. Rose, C. S. Sargent, W. A. Setchell, J. K. Small, W. Trelease, and C. A. Weatherby.

Abraham has prefaced his checklist of manuscripts with "a historic overview" of Northwest botany and illustrated it with photographs of the five botanists, unfortunately undated, and a group photograph of Harold St. John, then age 32, and associates, taken at the Pullman commencement of June 9, 1928. The "overview" includes some erroneous statements, for example, (1) that "Eaton's manual . . . has only an incomplete list . . . of eastern plants." Beginning with the fifth edition of the *Manual* (1829) western species were included, for example, *Pinus flexilis* (p. 331), *Quercus agrifolia* (p. 354), *Acer macrophyllum* (p. 90), *Vaccinium ovatum* (p. 434), etc. The eighth edition (1840) included California and Rocky Mountain species (see p. 16). (2) Abraham's statement that Pursh's plants were lost for nearly a century ignores the fact that Lambert's herbarium was consulted freely by botanists until its dispersal by auction in 1842. It was the American Philosophical Society series of Lewis and Clark collections that were "lost". (3) "Gray's Manual . . . through all its many nineteenth century editions never included the flora of the state of Washington" is indeed a strange statement! The scope of Gray's *Manual* was patently stated to be the *northeastern* United States. (4) To say T. J. Howell's *Flora* was "deficient in the identifying keys needed by the practicing botanists" and that it "did not prove very successful" can only reflect a want of understanding of Howell the botanist. "Considering the circumstances of its production," wrote W. L. Jepson in the *Dictionary of American Biography*, "his [Flora] is balanced, judicious, and highly useful." That Howell's *Flora* was not a mere compilation but rested on his own field studies—more than 50 species were new—was the mark of a vigorous mind.

To overlook Louis F. Henderson in an overview of Northwest botany would be unfortunate. He was in the first scientific party to enter the rain forest of the Olympic Peninsula (E. P. Thatcher in *Call Number* [Library University of Oregon] 22(1):20. 1960). A carefully prepared thesis entitled "A Contribution toward a bibliography of Oregon botany with notes on the botanical explorers of the state" by Katherine W. Hughes (*Oregon State College Thesis Series* 14, 1940), 93 pages, mimeographed, supplements Abrahams' very useful checklist.—JOSEPH EWAN, Department of Biology, Tulane University, New Orleans, LA 70118.

#### BOOKS RECEIVED AND LITERATURE OF INTEREST

*Nevada postal history 1861-1972.* By Robert P. Harris. Nevada Publications, Box 15444, Las Vegas, NV 89113. 1973. \$9.50 buckram. Of interest to botanists because of the large number of local and now "extinct" place names.

*Native plants for use in the California landscape.* By Emile L. Labadie. Sierra City Press, Box 2, Sierra City, CA 96125. 1978. \$8.95 paper. A quote from p. 93 perhaps characterizes the botanical sophistication of this potentially useful book: "*Chamaecyparis lawsoniana* . . . Flowers: Male flowers are bright red catkins."

BIOSYSTEMATICS OF PSILOSTROPHE  
(COMPOSITAE: HELENIEAE). II.  
ARTIFICIAL HYBRIDIZATION AND  
SYSTEMATIC TREATMENT

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*Psilostrophe* comprises seven species that grow in the semiarid regions of the southwestern United States and adjacent Mexico. Members of the genus are often conspicuous roadside weeds and are commonly known as paperflowers. In spite of their conspicuousness in the field, their suspected importance in livestock poisoning (Kingsbury, 1964; Schmutz, Freeman, and Reed, 1968), and their weedy nature, these species have remained poorly understood taxonomically.

*Psilostrophe* was first proposed by de Candolle (1838) from material collected by Berlandier from the vicinity of San Luis Potosi, Mexico. Three years later, the genus *Riddellia*, which would later prove to be synonymous with *Psilostrophe*, was erected by Nuttall (1841). *Riddellia* was typified by *R. tagetina* described from specimens collected by James in the Rocky Mountains. In 1849, A. Gray described a second species of *Riddellia*, *R. arachnoidea*, which he later realized (Gray, 1852, 1874) was the same as *Psilostrophe gnaphalodes*. Greene (1891) transferred the species of *Riddellia* to *Psilostrophe*. The first revisionary treatment of *Psilostrophe* came in 1903 when A. Nelson recognized six species. Rydberg (1914) reviewed the genus and named three additional species, bringing the total number of described species to ten. In the last comprehensive treatment of the genus, Heiser (1944) reduced the number of species to six. Heiser's work was revisionary and left room for a modern biosystematic study aimed at improving our understanding of the evolutionary relationships within *Psilostrophe*, which in turn provides the necessary background for further studies into adaptive strategies of species and roles of translocation heterozygosity, B-chromosomes, and polyploidy in the evolution of *Psilostrophe*.

DISTRIBUTIONS AND HABITATS

Populations of *Psilostrophe* are common elements of the summer flora in North American deserts. All species are weedy under the right circumstances and certain of the species exhibit disjunct populations that probably represent recent introductions. The variable *P. tagetina* is the most widespread of the species and is found throughout much of New Mexico, southeastern Utah, extreme eastern Arizona, Texas, mostly west of the Pecos River, and south to the Mexican states of Chihuahua and Coahuila (Fig. 1). It occurs in desert shrub, prairie grasslands, and pinyon-juniper woodlands, often in sandy soils from 600 to 2400 m in

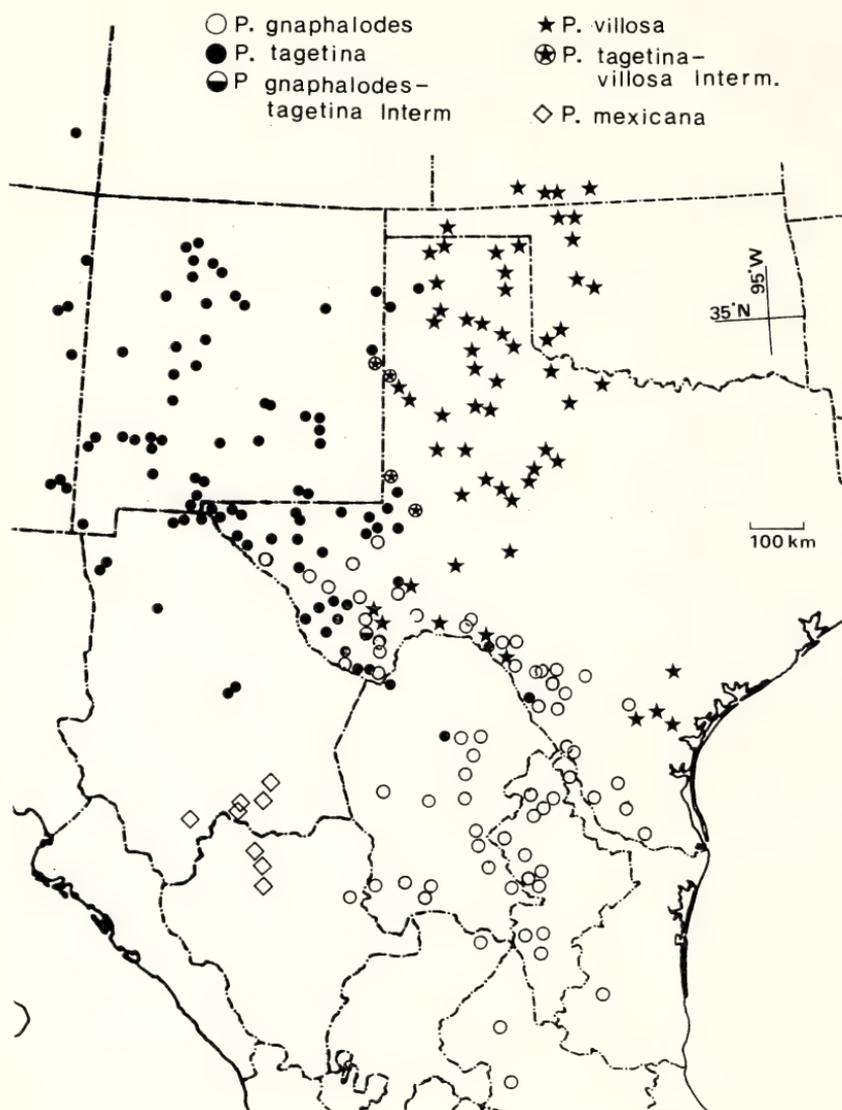


FIG. 1. Distributions of *Psilostrophe gnaphalodes*, *P. tagetina*, *P. gnaphalodes-P. tagetina* intermediates, *P. villosa*, *P. tagetina-P. villosa* intermediates, and *P. mexicana*.

elevation. The distribution of *P. tagetina* is overlapped by *P. gnaphalodes* and *P. villosa* in western Texas. Mixed populations containing *P. gnaphalodes* and *P. tagetina* occur in Brewster County, Texas. *Psilostrophe villosa* grows in prairie grassland from southwestern Kansas south to Texas at 300 to 900 m. *Psilostrophe gnaphalodes* grows in western Texas south to the Mexican state of San Luis Potosi from 300 to 2100 m. The remaining species with a Chihuahuan Desert distribution is the tetra-

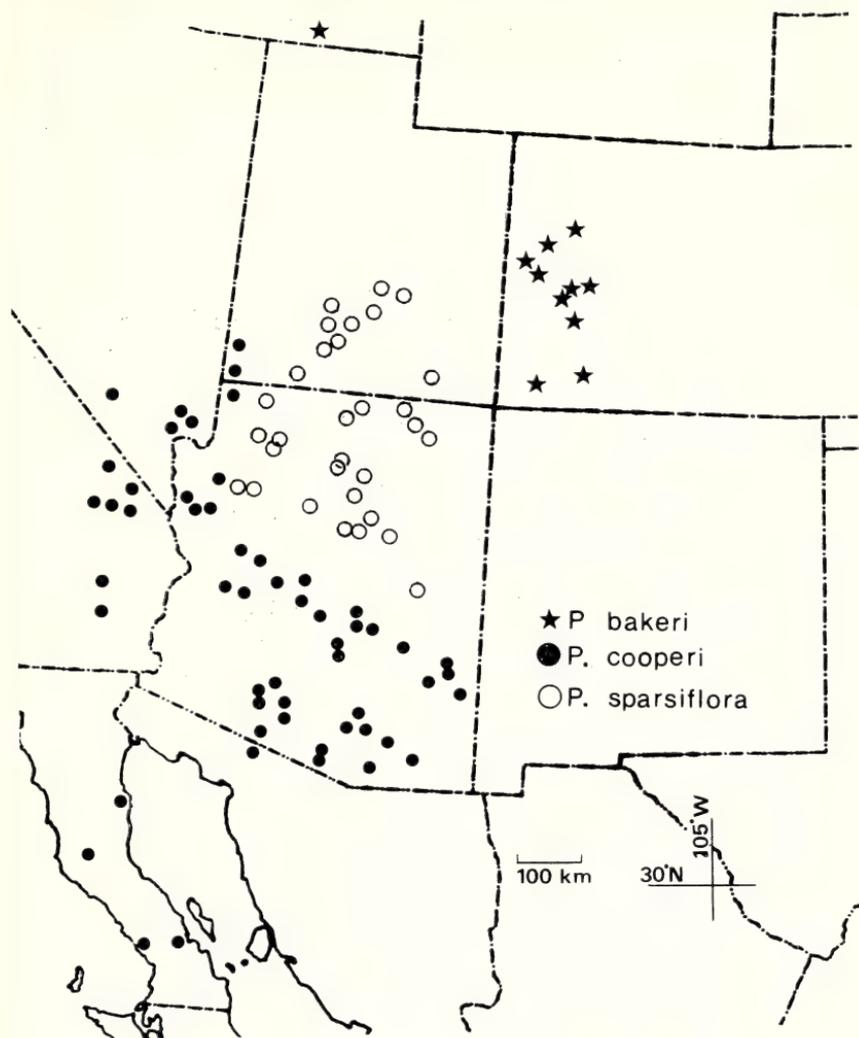


FIG. 2. Distributions of *Psilostrophe bakeri*, *P. cooperi*, and *P. sparsiflora*.

ploid, *P. mexicana*. It is encountered in hot desert shrubland to cool juniper woodlands in the states of Chihuahua and Durango, Mexico.

The three remaining species occur in or near the Mojave, Sonoran, and Great Basin Deserts (Fig. 2). *Psilostrophe cooperi* is encountered in the Mojave Desert and south and east to the northern Sonoran Desert in Arizona and Mexico along washes, rocky flats and hillsides, often in calcareous soils from 150 to 1500 m. *Psilostrophe sparsiflora* is generally found in sandy soils in sagebrush or pinyon-juniper communities in the cold Great Basin Desert from 900 to 2300 m. *Psilostrophe bakeri* is restricted to arid, rocky hills in western Colorado from 1350 to 2000 m

and is disjunct in Idaho. Housing development and increased cultivation through irrigation threaten the habitat of this species.

#### HYBRIDIZATION EXPERIMENTS

A program of experimental hybridization was initiated to study the crossing relationships of the species. A total of 2318 pistillate florets were crossed in two years. Parental strains used were plants transplanted from their native habitats or collected as seed and grown to maturity in the greenhouse.

Capitula to be used as ovulate parents were emasculated by removal of the hermaphroditic disc florets prior to anthesis. Pistillate ray florets were then dusted with the pollen of the desired pollen parent. Heads of both pollen and seed parents were covered with glassine bags throughout the entire crossing procedure beginning with the bud stage to insure against possible contamination. After pollination the cross was tagged and allowed to mature under cover of the glassine bag. Achenes matured in about six weeks. Crossability is expressed as percent filled achenes following artificial hybridization. Estimates of parent and hybrid fertility were based on percent pollen stainability in aniline blue-lactophenol. At least 500 grains were counted wherever possible. Pollen stainability of parent plants ranged from 91 to 99 percent.

Intraspecific crossability was measured in interpopulational crosses in *P. cooperi*, *P. gnaphalodes*, and *P. tagetina* and ranged from 48 to 57 percent achene set, with an overall crossability of 51 percent (Table 1). Interfertility among species was variable, ranging from 0 to 53 percent achene set (Table 1; Fig. 3). Table 2 summarizes morphological features of the species. In general the hybrids were intermediate to the parental strains with respect to critical morphological characters. In all cases reflexed ligules were dominant to horizontal ligules in fruit. Other characters examined apparently were quantitatively inherited. Complete data on pollen stainability, morphology, and meiosis in individual parental and hybrid plants are found in Brown (1974).

When coupled with morphological and geographical evidence, the degree to which plants cross and produce vigorous hybrids and the degree of fertility of the  $F_1$  offspring have long been used as indicators of genetic relationships of plants (Clausen, Keck, and Hiesey, 1941; Long, 1975). Crossability and fertility as determined in the greenhouse experiments are only of relative value and several limitations exist. Ability of species to cross in the greenhouse is a poor measure of their ability to hybridize in the field. Hybrids that apparently are vigorous in the greenhouse may not be competitive in the habitats of their parents. Furthermore, plants utilized in the experimental hybridizations represent only a minute sample of the total gene pool. That different plants in the same population may have different interspecific crossabilities is suggested by the crossing abilities of two individuals of *P. tagetina* collected from the same population in southeastern Arizona. All attempts

TABLE 1. CROSSABILITY IN *Psilostrophe*. <sup>a</sup>individuals/populations utilized.

Ovulate Parent	Pollen Parent	Total Ovules Crossed	% Achene Set Range
INTRASPECIFIC CROSSES			
<i>P. cooperi</i> (3/3) <sup>a</sup>	<i>P. cooperi</i>	29	48 (38-52)
<i>P. gnaphalodes</i> (3/3)	<i>P. gnaphalodes</i>	37	57 (50-78)
<i>P. tagetina</i> (5/4)	<i>P. tagetina</i>	163	50 (46-78)
INTERSPECIFIC CROSSES			
<i>P. cooperi</i> (5/3)	<i>P. sparsiflora</i> (1/1)	28	25 (19-50)
Reciprocal		26	0 (0)
<i>P. cooperi</i> (6/3)	<i>P. tagetina</i> (3/2)	45	7 ( 0-50)
Reciprocal		79	5 ( 0-13)
<i>P. cooperi</i> (4/3)	<i>P. villosa</i> (2/1)	24	0 (0)
Reciprocal		24	0 (0)
<i>P. cooperi</i> (3/3)	<i>P. bakeri</i> (1/1)	18	0 (0)
<i>P. cooperi</i> (2/1)	<i>P. gnaphalodes</i> (1/1)	55	29 ( 5-45)
Reciprocal		46	0 (0)
<i>P. sparsiflora</i> (4/2)	<i>P. tagetina</i> (4/3)	94	6 ( 0-23)
Reciprocal		50	6 ( 0-22)
<i>P. sparsiflora</i> (2/1)	<i>P. villosa</i> (2/1)	36	0 (0)
Reciprocal		21	0 (0)
<i>P. sparsiflora</i> (2/1)	<i>P. bakeri</i> (1/2)	23	4 ( 0-17)
<i>P. sparsiflora</i> (2/1)	<i>P. gnaphalodes</i> (3/3)	27	7 ( 0-22)
Reciprocal		98	4 ( 0-12)
<i>P. tagetina</i> (3/3)	<i>P. villosa</i> (2/1)	44	64 (44-72)
Reciprocal		24	42 (11-60)
<i>P. tagetina</i> (3/3)	<i>P. bakeri</i> (1/1)	43	21 ( 0-42)
<i>P. tagetina</i> (3/3)	<i>P. gnaphalodes</i> (3/3)	137	50 (36-77)
Reciprocal		195	44 ( 0-49)
<i>P. villosa</i> (1/1)	<i>P. bakeri</i> (1/1)	25	4 (4)
Reciprocal		20	0 (0)
<i>P. villosa</i> (1/1)	<i>P. gnaphalodes</i> (4/4)	35	26 (26)
Reciprocal		59	56 (33-69)
<i>P. gnaphalodes</i> (2/2)	<i>P. bakeri</i> (1/1)	30	0 (0)
F <sub>2</sub> CROSSES			
<i>P. cooperi</i> × <i>sparsiflora</i>	<i>P. cooperi</i> × <i>sparsiflora</i>	only 1 plant flowered	
<i>P. sparsiflora</i> × <i>tagetina</i>	<i>P. sparsiflora</i> × <i>tagetina</i>	75	0
<i>P. villosa</i> × <i>tagetina</i>	<i>P. villosa</i> × <i>tagetina</i>	89	0
<i>P. tagetina</i> × <i>gnaphalodes</i>	<i>P. tagetina</i> × <i>gnaphalodes</i>	73	1
<i>P. cooperi</i> × <i>gnaphalodes</i>	<i>P. cooperi</i> × <i>gnaphalodes</i>	only 1 plant flowered	

TABLE 1, continued.

## BACKCROSSES

<i>P. cooperi</i> × <i>sparsiflora</i>	<i>P. sparsiflora</i>	16	6
Reciprocal		28	4
<i>P. cooperi</i> × <i>sparsiflora</i>	<i>P. cooperi</i>	9	0
Reciprocal		8	0
<i>P. sparsiflora</i> × <i>tagetina</i>	<i>P. sparsiflora</i>	61	0
Reciprocal		38	11
<i>P. villosa</i> × <i>tagetina</i>	<i>P. tagetina</i>	12	0
Reciprocal		29	0
<i>P. villosa</i> × <i>tagetina</i>	<i>P. tagetina</i>	82	37
Reciprocal		40	20
<i>P. villosa</i> × <i>tagetina</i>	<i>P. villosa</i>	—	—
Reciprocal		24	38
<i>P. tagetina</i> × <i>gnaphalodes</i>	<i>P. gnaphalodes</i>	53	6
Reciprocal		39	21
<i>P. tagetina</i> × <i>gnaphalodes</i>	<i>P. tagetina</i>	38	0
Reciprocal		38	0
<i>P. cooperi</i> × <i>gnaphalodes</i>	<i>P. gnaphalodes</i>	—	—
Reciprocal		20	0
<i>P. cooperi</i> × <i>gnaphalodes</i>	<i>P. cooperi</i>	11	0

TABLE 2. SUMMARY OF MORPHOLOGICAL SIMILARITIES AMONG SPECIES OF *Psilostrophe*.

Species	Vestiture			Lower Lvs		Peduncles			Ligules			Achenes		Pappus					
	Phose	Villous	Pannose	Linear	Oblanceolate-Spatulate	Short < 1 cm	Int. 1-5 cm	Long > 5 cm	Reflexed	Horizontal	Short < 6 mm	Int. 6-10 mm	Long > 10 mm	Villous	Glabrate	Erose	Lacerate	> 1/2 achene length	< 1/2 achene length
<i>P. cooperi</i>			+	+				+	+				+	+	+	+			
<i>P. sparsiflora</i>	+				+	+			+		+			+	+				+
<i>P. bakeri</i>		+			+	+				+			+	+	+			+	
<i>P. tagetina</i>		+			+	+				+	+			+	+				+
<i>P. villosa</i>		+			+	+				+	+			+	+				+
<i>P. gnaphalodes</i>		+			+	+				+	+			+			+		+
<i>P. mexicana</i>		+			+	+				+	+			+			+		+

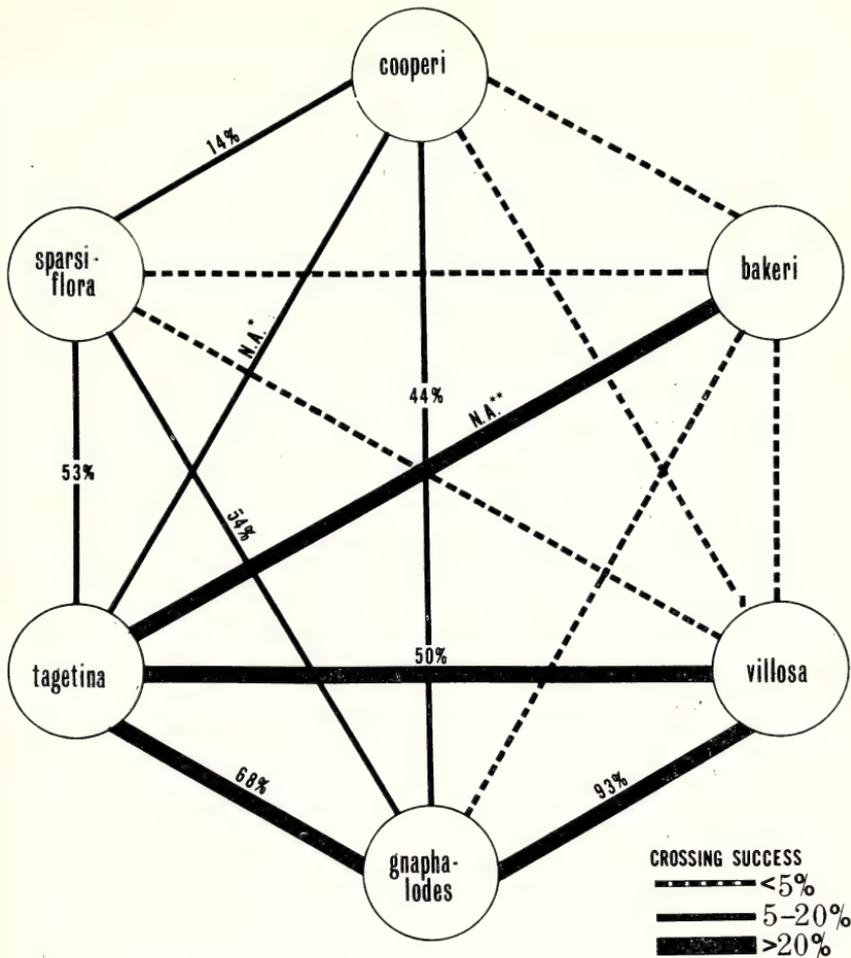


FIG. 3. Crossing diagram of the diploid species of *Psilostrophe* showing relationships based on percent interfertility. Mature  $F_1$  hybrids were not obtained from crosses with less than 5 percent interfertility. Percentages above cross-bars indicate mean pollen stainability in  $F_1$  hybrids (N.A.\* = no data, achenes failed to germinate; N.A.\*\* = no data, hybrids failed to flower).

to cross one individual with *P. sparsiflora* failed while attempts with the other were 23 percent successful (Brown, 1974). This suggests that all interspecific crossabilities would be higher if the ovulate parents were covered with pollen from a large number of plants (genotypes) as might occur under natural conditions. In addition, the backcrossing of  $F_1$  hybrids to their immediate parents increases the likelihood of poor seed set due to the operation of possible sporophytic incompatibility systems. Recently, Jones (1976) presented evidence that environmental factors may exert a considerable influence on the production of stainable and presumed normal pollen. Nevertheless, data on crossability and pollen

stainability in *Psilostrophe* seem in accord with morphological and geographical data.

Partial or complete internal barriers to gene exchange among species of *Psilostrophe* occur in the initial crossability and fertility of first-generation hybrids. Internal isolating mechanisms in *Psilostrophe* apparently are genic rather than chromosomal. Even though translocation heterozygosity is common in the genus, structural rearrangement has not been a major factor in speciation for interspecific hybrids possessed no more evidence of translocation heterozygosity than did their parents (Brown, 1977). In no case was evidence for inversions detected in the hybrids.

On the bases of morphology, geographical distribution, and crossing relationships, the diploid species of *Psilostrophe* fall into two categories: three distinct species in the Mojave, Sonoran, and Great Basin Deserts and a species alliance of *P. gnaphalodes*-*P. tagetina*-*P. villosa* in the southeastern portion of the range.

The southeastern species are very similar morphologically and are not always readily distinguishable. The ranges overlap considerably in western Texas, where intermediates occur. Artificial hybridizations showed initial crossabilities in any combination of these three species to be quite high (41 to 53 percent). Meiosis in the  $F_1$  hybrids was regular with pollen stainability ranging from 44 to 93 percent. The interspecific hybrids showed an ability to backcross to either parent, but a marked inability to produce second generation plants. Limited gene flow between species seems possible in areas of sympatry and may provide an important source of genetic variability. Field studies of *Psilostrophe* in trans-Pecos Texas should contribute to an understanding of the extent and consequences of natural hybridization among these species.

The morphology and ecology of the tetraploid *P. mexicana* suggests that it is closely related to the *P. gnaphalodes*-*P. tagetina*-*P. villosa* diploid complex. *Psilostrophe mexicana* was recognized late in the study and its crossing relationships have not been studied. Without this information additional speculation on the phyletic relationships of this interesting taxon is unwarranted. Further work emphasizing artificial hybridization is needed to trace the origin of *P. mexicana*.

*Psilostrophe bakeri*, *P. cooperi*, and *P. sparsiflora* occur in specialized habitats in the northern and western portions of the genus range. Each species is ecologically and geographically distinct. Major morphological gaps involving several characters are suggestive of major genetic discontinuities among these three species. The three species are well isolated reproductively by low initial crossability in addition to external factors. Taxonomic decisions within this group are relatively simple and misidentification rare.

The species are allied genetically to *P. gnaphalodes* and *P. tagetina*

of the southeastern alliance. Of 101 crosses attempted between *P. cooperi* and *P. gnaphalodes* 16 percent produced filled achenes. Six full achenes resulted from 125 hybridizations between *P. sparsiflora* and *P. gnaphalodes*, an overall crossability of 5 percent. Meiosis was regular in  $F_1$  hybrids of either combination with 16 bivalents undergoing an orderly segregation (Brown, 1977). Pollen stainability ranged from 44 to 60 percent. Complete chromosomal pairing occurred in hybrids of species widely divergent in geography, ecology, and morphology. The overall weakness and low pollen fertility in the hybrids suggest some genetic disharmony.

*Psilostrophe cooperi* and *P. sparsiflora* showed much less crossing affinity to *P. tagetina*: 5 and 6 percent overall crossability respectively. These figures may be misleading for individuals of *P. tagetina* from the same population exhibited differing abilities to hybridize as mentioned earlier. None of the achenes resulting from crosses between *P. cooperi* and *P. tagetina* germinated. Pollen stainability in four hybrids between *P. sparsiflora* and *P. tagetina* ranged from 51 to 55 percent. Low hybrid fertility in attempts to produce an  $F_2$  generation and backcrosses is evidence for internal isolation in addition to the eco-geographical isolation of these species.

*Psilostrophe bakeri* showed a 21 percent crossability with *P. tagetina* but little or no crossability with any other species. The simplest interpretation of this is to regard *P. bakeri* as derived from *P. tagetina* or its immediate ancestor. This distinct taxon is apparently reproductively as well as geographically isolated.

#### TAXONOMIC TREATMENT

The treatment of *Psilostrophe* is based on extensive field and herbarium studies in addition to studies of cytotaxonomy (Brown, 1977) and artificial hybridization. Most taxonomic difficulties in the genus arise because of substantial morphological similarities among the species. While in essential agreement with the capable revision of Heiser (1944), this study has brought to light additional characters useful in delimiting the species. A key to the species incorporating these characters is provided. In addition to reflecting increased knowledge about the geographical range and ecology of the species, this revision differs from that of Heiser in the recognition of *P. mexicana* and in the treatment of intraspecific variation in *P. tagetina*.

PSILOSTROPHE de Candolle, Prodr. 7:261. 1838. TYPE: *Psilostrophe gnaphalodes* de Candolle.

*Riddellia* Nuttall, Trans. Amer. Philos. Soc. n.s. 7:371. 1841. TYPE: *Riddellia tagetina* Nuttall.

Perennial or biennial, leafy-stemmed herbs. Stems simple below, clustered from a woody taproot often covered with old leaf bases, branching

above. Leaves both rosulate and cauline or all cauline, alternate. Lower leaves spatulate to oblanceolate or linear, margins entire or pinnately lobed. Upper leaves much reduced, sessile and usually entire. Vegetative organs sparingly pilose to densely woolly or sometimes floccose. Capitula subsessile to long pedunculate, solitary or in corymbose clusters. Involucres cylindrical; phyllaries 5–10, elliptic or lanceolate, herbaceous and uniseriate, or, if a second series is present, then the inner 1–7 bracts smaller than the outer and scarious. Corollas yellow to orange. Ray florets pistillate, fertile, 3–7 in a single series; the ligules becoming papery and persistent on the ripe achenes. Disc florets perfect, fertile; corolla tubes cylindrical, the 5 triangular lobes glandular-pubescent without. Achenes terete or slightly angled, sublinear, conspicuously striate, glabrate to villous. Pappus of 4–6 nerveless, lanceolate, subequal, hyaline squamellae; the margins frequently erose, sometimes lacerate-dissected. Base chromosome number,  $x = 16$ .

#### KEY TO PSILOSTROPHE

- Plants suffrutescent to subshrubby; pubescence of the stem densely white-pannose; lower leaves linear; heads scattered on peduncles 3–8 cm long . . . . . 1. *P. cooperi*
- Plants herbaceous; pubescence of the stem woolly to sparingly pilose; lower leaves spatulate to oblanceolate; heads in corymbose clusters, the peduncles less than 5 cm long.
- Stems green, sparingly pilose, upper foliage glandular-dotted; ligules tightly reflexed against the involucre at maturity . . . . . 2. *P. sparsiflora*
- Stems loosely villous to white-woolly; ligules remaining horizontal in fruit.
- Ray florets 5–6; disc florets 10–20; pappus scales less than one half the length of the disc corolla . . . . . 3. *P. bakeri*
- Ray florets 2–5; disc florets 5–12; pappus scales one half to equaling the disc corolla in length.
- Achenes and pappus glabrate; pappus scales entire or merely erose.
- Heads in open corymbs; peduncles 1–4 cm long; ligules 5–14 mm long, shallowly 3-lobed . . . . . 4. *P. tagetina*
- Heads in congested corymbs; peduncles nearly wanting to 10 mm long; ligules 3–6 mm long, deeply 3-lobed . . . . . 5. *P. villosa*
- Achenes and pappus long-villous; pappus scales lacerate-dissected.
- Heads in congested corymbs; peduncles nearly wanting to 10 mm long; disc corollas 3.5–4.0 mm long. 6. *P. gnaphalodes*
- Heads in open corymbs; peduncles 8–30 mm long; disc corollas 4.5–5.0 mm long . . . . . 7. *P. mexicana*

1891.—*Riddellia cooperi* A. Gray, Proc. Amer. Acad. Arts 7:358.  
 1868.—TYPE: Gray cited the following specimens as representative, "Gravelly banks at Fort Mohave, Dec. 1861, *Dr. J. G. Cooper*. On the Colorado, *Dr. Newberry*. Camp Grant, &c., Arizona, *Drs. Elliot Coues* and *Edward Palmer*." Gray (1874): clearly stated that the species was first collected by Cooper, and Heiser (1944) designated the Cooper specimen (GH!) lectotype.

Perennial suffrutescent plants, 20–60 cm tall. Stems densely white-pannose, becoming less so with age, freely branched. Leaves cauline, lanate to glabrate, linear, entire, 1–8 cm long, less than 0.5 cm wide. Heads scattered, terminating the many branches; peduncles slender, 3–8 cm long. Involucres loosely to densely lanate, cylindric, 6–8 mm high and 3–5 mm in diameter. Corollas yellow. Ray florets 3–6, ligules 8–18 mm long and nearly as broad, 3-lobed, enlarging and becoming reflexed in fruit. Disc florets 10–25, corollas 4–5 mm long. Achenes glabrous to sparsely glandular with sessile glands; pappus scales oblong-lanceolate, entire to erose, obtuse to acute, less than  $\frac{1}{2}$  the length of the disc corolla. Chromosome number:  $2n = 32$ . Flowering throughout the year; mainly March to June.

2. *PSILOSTROPHE SPARSIFLORA* (A. Gray) A. Nelson, Proc. Biol. Soc. Wash. 16:23. 1903.—*Riddellia tagetina* var. *sparsiflora* A. Gray, Synopt. Fl. N. Amer. 1(2):318. 1884.—TYPE: Gray cited two specimens from southern Utah in his description of this variety. Heiser (1944) selected the specimen of Captain *Bishop s.n.* as lectotype (GH!).—*Psilostrophe tagetina* var. *sparsiflora* (A. Gray) E. L. Greene, Pittonia 2:176. 1891.

*Psilostrophe divaricata* Rydberg, North Amer. Flora 34:8. 1914.—TYPE: United States: Arizona: "Grand Canyon of the Colorado," 1897, *D. T. Allen s.n.* (Holotype, NY!; isotypes NY! UC!).

Perennial herbs, 10–50 cm high. Stems sparingly pilose to glabrate, single or clustered from a woody caudex, often twisted and zigzag at the nodes; freely branched, the branches more or less strongly divergent. Basal leaves rosulate, villous when young, becoming glabrate with age, spatulate to linear, up to 14 cm long, usually less than 1.5 cm wide, entire or rarely pinnately lobed, frequently lacking in mature specimens. Cauline leaves smaller, sparsely villous to glabrate, narrowly oblanceolate to linear, entire, acute to obtuse, dotted with sessile glands particularly near the inflorescence. Heads born in loose cymes of 3–6 on slender peduncles up to 3 cm long. Involucres lightly villous, cylindric, 5 mm high and 3 mm in diameter. Corollas yellow. Ray florets 1–4, often 2 or 3, ligules 6–10 mm long and decidedly broader, 3-lobed, enlarging and becoming sharply reflexed in fruit. Disc florets fewer than 10, corollas 3–5 mm long. Achenes glabrous to sparsely glandular with sessile glands; pappus scales lanceolate to linear, subequal, frequently erose,  $\frac{1}{2}$  to  $\frac{2}{3}$

the length of the disc corolla. Chromosome number:  $2n = 32$ . Flowering from April to October.

3. *PSILOSTROPHE BAKERI* E. L. Greene, Pl. Baker. 3:29. 1901.—TYPE: United States: Colorado: Montrose, *Baker 14* (NDG). Greene based his description of this species on two collections, *Baker 14* from near Montrose, Colorado and *Baker 106* from near Grand Junction, Colorado. Both collections are large gatherings with many duplicates and either could have provided the characters used in the diagnosis. In citing the type locality as Montrose, Colorado, Rydberg (1914), without stating his reason, implied that *Baker 14* is type, hence the specimen in the Greene Herbarium is designated as lectotype, (isolectotypes, GH! MO! POM! US!).

*Riddellia tagetina* var. *pumila* M. E. Jones, Proc. Calif. Acad. Sci. ser. 2, 5:700. 1895.—TYPE: United States: Colorado: Grand Junction, in gravel, in open places, 21 Jun 1894, *M. E. Jones 5474* (Lectotype here designated POM!; isolectotypes BM! MO! NY! POM! UC!).—*Psilostrophe pumila* (M. E. Jones) A. Nelson, Proc. Biol. Soc. Wash. 16:22. 1903.

Perennial herbs, 5–30 cm high. Stems long-villous, one to several from a branched woody caudex. Lower leaves rosulate, loosely villous, spatulate to oblanceolate, up to 8 cm long, entire or rarely pinnately 3- to 5-lobed. Cauline leaves smaller, oblanceolate, entire. Heads in loose corymbs at the end of the branches on peduncles 1.5–5.0 cm long. Involucres lightly villous, cylindric, 7–10 mm high and 4–6 mm in diameter; of 9 distinct bracts. Corollas yellow-orange. Ray florets 5–6, ligules 8–15 mm long and nearly as broad, 3-lobed. Disc florets 10–20, tubular corollas 4–5 mm long. Achenes glabrous, striate; pappus scales unequal, short erose, decidedly less than  $\frac{1}{2}$  the length of the disc corolla. Chromosome number:  $2n = 32$ . Flowering May to July.

4. *PSILOSTROPHE TAGETINA* (Nuttall) E. L. Greene, Pittonia 2:176. 1891.—*Riddellia tagetina* Nuttall, Trans. Amer. Philos. Soc. n.s. 7:371. 1841.—TYPE: "The southern range of the Rocky Mountains, towards the sources of the Platte." Probably collected by Dr. James on Long's expedition (Gray, 1849) (Holotype BM!; isotype GH!). As pointed out by Heiser (1944) Nuttall's spelling in the original publication, "*Tagetinae*," was probably a misprint and subsequent workers have used the grammatically correct spelling, "*tagetina*."

*Psilostrophe tagetina* var. *lanata* A. Nelson, Proc. Biol. Soc. Wash. 16:21. 1903.—TYPE: United States: Texas: El Paso, Apr 1881, *G. R. Vasey s.n.* (Holotype US!).—*P. lanata* (A. Nelson) Hay, Miller & White, Proc. Biol. Soc. Wash. 16:186. 1903.

*Psilostrophe hartmanii* Rydberg, North Amer. Flora 34:8. 1914.—TYPE: MEXICO: Chihuahua: near Laguna de Guzman, *C. V. Hartman 726* (Holotype NY!; isotype GH!).

*Psilostrophe grandiflora* Rydberg, North Amer. Flora 34:8. 1914.—TYPE: United States: Arizona: Cochise Co.: near Cedar Gulch, Paradise, 21 Sept 1907, *J. C. Blumer 1709* (Holotype NY!; isotypes FM! GH! MO! ARIZ! UC!).—*P. tagetina* var. *grandiflora* (Rydberg) C. B. Heiser, Ann. Missouri Bot. Gard. 31: 292. 1944.

Perennial herbs, 15–50 cm tall. Stems loosely to densely villous, becoming less so with age, clustered from the crown of a woody taproot or single-stemmed in the first year of growth, usually freely branched above, forming globose clumps. Lower leaves rosulate, loosely to densely white-villous, narrowly oblanceolate to more commonly spatulate, up to 15 cm long, less than half as wide, entire to pinnatisect with lanceolate to broadly linear segments. Upper leaves smaller, oblanceolate to linear, lightly villous, eglandular or nearly so. Heads terminating the many branches in open corymbs; peduncles 1–4 cm long. Involucres densely white-villous, 5–6 mm high and 2–4 mm in diameter. Corollas yellow to orange. Ray florets 3–6, commonly 3, ligules 5–14 mm long and usually noticeably broader, broadly 3-lobed at the apex. Disc florets 5–12, corollas 3–5 mm long. Achenes glabrous or with a few stout trichomes when young, striate, terete or slightly angled. Pappus scales broadly to narrowly lanceolate, acute to obtuse, one half to equalling the disc corolla in length. Chromosome number:  $2n = 32$ . Flowering May to October.

Nelson (1903) and Heiser (1944) have commented on the morphological diversity of this species. It is also variable cytologically (Brown, 1977). In addition to the typical form, two varieties, var. *lanata* and var. *grandiflora*, were recognized by Heiser (1944) and others. Both varieties are based on differences in size, particularly of the ligules and peduncles, and degree of pubescence, characters that are extremely variable. My observations lead me to believe that recognition of infraspecific taxa is unjustified. I have visited the type locality of var. *grandiflora* on several occasions and found the population to be morphologically and chromosomally variable. The type collection is definitely extreme in size. Comparable plants as to size of parts and degree of pubescence are uncommon. No cytological character such as translocation heterozygosity or number of supernumerary chromosomes could be correlated with any morphological character. Unless further investigations prove otherwise, I favor a conservative treatment of this variable and widespread species.

5. *PSILOSTROPHE VILLOSA* Rydberg in Britton, Manual Flora North. States Canada. 1006. 1901.—TYPE: Original description and illustration (no authentic type specimen located).

*Psilostrophe cerifera* A. Nelson, Proc. Biol. Soc. Wash. 16:21. 1903.—TYPE: "Cheyenne Country, Indian Territory." Jun 1891, *M. A. Carleton 201* (Holotype RM, paratype US!).

*Psilostrophe cerifera* var. *biennis* A. Nelson, Proc. Biol. Soc. Wash. 16:21, 1903.—TYPE: United States: Kansas: Meade Co.: prairie near Crooked Creek 16 Aug 1890, *B. B. Smyth 140* (Holotype US!,

isotype NY!).—*P. biennis* (A. Nelson) Hay, Miller & White, Proc. Biol. Soc. Wash. 16:186, 1903.

Biennial or perennial herbs, 20–60 cm high. Stems loosely to densely long-villous, becoming less so with age. Basal leaves rosulate, densely long-villous, spatulate to oblanceolate, up to 10 cm long and less than 5 cm wide, entire or occasionally 3- to 5-lobed. Heads several at the ends of the branches in congested corymbs; peduncles subsessile to 5 mm long. Involucres densely white-woolly, 5–7 mm high and 3–4 mm in diameter. Corollas yellow-orange. Ray florets usually 3, ligules 3–6 mm long usually broader than long, deeply 3-lobed. Disc florets 5–10, corollas 3–5 mm long. Achenes glabrate; pappus scales linear-lanceolate, acute, one half to equaling the disc corolla in length. Chromosome number:  $2n = 32$ . Flowering from April to October.

6. *PSILOSTROPHE GNAPHALODES* de Candolle, Prodr. 7:261. 1838.—  
TYPE: Mexico: San Luis Potosi, *Berlandier 1336* (Holotype G, photographs FM! US!; isotype GH! probable isotypes BM! MO!).—*Riddellia gnaphalioides* (de Candolle) O. Hoffman in Loesner, Bull. Herb. Boissier 3:628. 1895.

*Riddellia arachnoidea* A. Gray, Mem. Amer. Acad. Arts ser. 2, 4:94. 1849.—TYPE: Three specimens are cited by Gray, “dry soil around Buena Vista and Saltillo, *Dr. Gregg, Dr. Wislizenus*: also near Monterrey, *Dr. Edwards*.” All three specimens are mounted on a single sheet in the Gray Herbarium. The Gregg specimen is here selected as lectotype (GH!).

Perennial herbs, 20–50 cm high. Stems loosely to densely villous, one to many from a woody taproot. Lower leaves rosulate, loosely to densely villous, spatulate to oblanceolate, up to 6 cm long and 1.5 cm broad, entire or occasionally pinnately 3- to 7-lobed. Upper leaves smaller, linear to oblanceolate, entire. Heads several at the ends of the branches in congested corymbose clusters; peduncles subsessile to nearly 1 cm long. Involucres densely white-woolly, 5–6 mm high and about 3 mm in diameter. Corollas yellow-orange. Ray florets 2–4, generally 3, ligules 4–7 mm long, usually slightly broader than long. Disc florets 5–9, corollas 3.5–4.0 mm long. Achenes and pappus scales long-villous, pappus scales linear-lanceolate, margins lacerate-dissected, about one half the length of the disc corolla. Chromosome number:  $2n = 32$ . Flowering throughout the year; mainly March to September.

7. *PSILOSTROPHE MEXICANA* R. C. Brown, Brittonia 26:115. 1974.—  
TYPE: Mexico: Chihuahua: desert shrub community dominated by *Larrea*, *Prosopis* and *Parthenium*, 8.1 mi N of junction to Jimenez along Hwy. 45, *Pinkava, McGill & Brown 788* (Holotype ASU!; isotypes to be distributed).

Perennial herbs, 15–50 cm tall, with one to many ascending, long-villous stems. Lower leaves rosulate, loosely to densely villous, oblan-

ceolate to linear-oblongate in outline, entire or rarely lobed to sub-pinnatifid. Cauline leaves smaller, narrowly oblongate to linear. Heads several at the ends of the branches in open corymbs, peduncles 10–30 mm long. Involucre cylindrical, woolly, 3–4 mm in diameter and 5–8 mm high. Corollas yellow-orange. Ray florets 3–5; ligules obovate to orbicular in outline, 5–8 mm long, 3-lobed. Disc florets 7–10; corollas 4.3–5.0 mm long. Achenes sublinear-oblong, long-villous with trichomes similar to those of the herbage; pappus scales lanceolate to linear, margins lacerate-dissected into long hairs. Chromosome number:  $2n = 64$ . Flowering from July to November.

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## GERMINATION OF COMANDRA (SANTALACEAE)

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In all parasitic angiosperms germination corresponds to a brief period of independence from host plants. During this short span of time, when growth is facilitated by nutrients present in endosperm and/or cotyledons, the seedling has an opportunity to establish structural and physiological contact with a host plant. It is a rather precarious transitional period of considerable biological interest. Surprisingly little is known, however, about the seedling stage of many parasites including members of Santalaceae, all of which are parasitic. The following structural details relate to the early establishment of *Comandra umbellata* (L.) Nutt. subsp. *pallida* (DC.) Piehl, as based on seedlings found in loose sand in Lethbridge, Alberta, 18 May 1976.

Seedlings of *Comandra* show exceedingly slender, erect stems with narrow, erect leaves when first emerging from the soil (Fig. 1A). They are difficult to spot among older plants, which normally have numerous sterile, unbranched shoots. About 6 or 7 cm below soil level the entire fruit was still recognizable, the fruit wall turned nearly black, and both it and the hard mesocarp split open on the apical pole. From this pole there protruded the withered endosperm still enclosing the 10 mm long cotyledons, which were separate at the base but closely adnate in the upper one-third (Fig. 1B, 1F). The cotyledons, which were only a fraction of a mm at the time of fruit dispersal (Piehl, 1965), remain in that position until they decay.

The initial stages of germination are clearly described and illustrated by Piehl. The precise origin of roots and rhizomes, however, needs further comment. Piehl states that the first rhizomes originate "in the transition or cotyledon region" of the axis. In my material there was no sign of lateral buds associated with cotyledons, while buds were clearly recognizable in the axils of the first one or two reflexed scale leaves (Fig. 1C). It is thus at this level, several cm below the soil surface, that the rhizomes originate in axillary positions. In several plants axillary roots had also formed in association with both these scale leaves and the cotyledons (Fig. 1C, 1D). Where both a bud and a root are formed in an axillary position, they already show the same regular position with respect to each other that characterizes the mature rhizome system (Fig. 1C; cf. Kujit, 1969, Fig. 3-6).

Haustoria are formed even two weeks following germination. Many haustoria in the seedling are closely similar to the so-called "haustorial rudiments" that Simpson and Fineran (1970) described for *Mida*. They are rather elongate, spur-like outgrowths clearly continuous with that

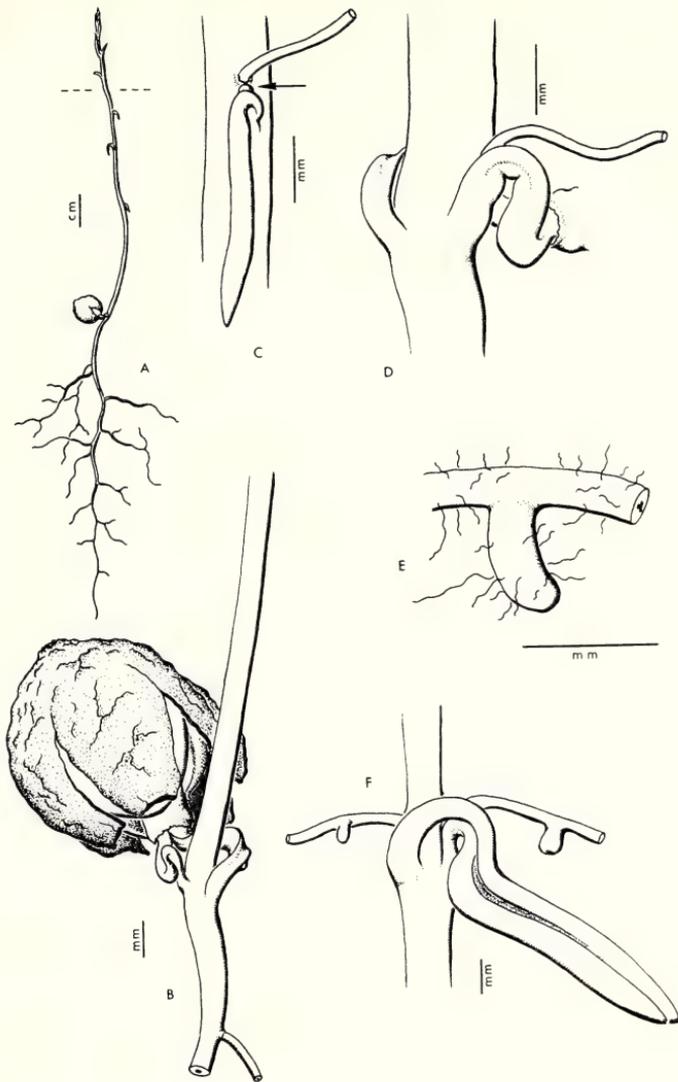


FIG. 1. *Comandra umbellata*. A. Seedling; soil level indicated by broken line. B. Cotyledonary zone. Within the cracked fruit wall the yellowish shell is visible, from which the tubular remnant of the endosperm, containing the twisted cotyledons, protrudes. Compare D and F. C. One of several subterranean nodes, about 4 cm above cotyledons, showing recurved scale-leaf and axillary root, between which is the axillary bud (arrow). The axillary root probably develops into a rhizome. D. Cotyledonary zone, showing twisted cotyledons still in exhausted endosperm, one cotyledon having an axillary root. E. Haustorial "rudiment", 4 mm along first lateral root, 5 mm below cotyledons. F. Cotyledonary zone with endosperm removed, the cotyledon tips cohering. Two axillary roots have formed, each bearing one young haustorium.

of the mother root (cf. Kuijt, 1969, Fig. 5). These rudiments thicken upon contact with host organs, and many eventually differentiate into haustoria. They develop on any root, whether below the cotyledonary node or above it, sometimes only a few mm away from the shoot in the latter cases (Fig. 1F), except for the upper portion of the primary root, which always seems to lack haustoria.

The only other Santalaceae where germination has been described are *Exocarpos* (Stauffer, 1959; Fineran, 1962) and *Santalum album* (Barber, 1906). Both these plants, and quite probably also *Buckleya* (cf. Kusano, 1902) are epigaeous and non-rhizomatous. Because *Comandra* is hypogaeous and rhizomatous it may be predicted that other rhizomatous genera such as *Arjona*, *Geocaulon*, *Nanodea*, and possibly *Nestronia* also have a hypogaeous type of germination.

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# CHROMOSOME NUMBERS IN XYLORHIZA NUTTALL (ASTERACEAE - ASTEREAE)

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*Xylorhiza* is a genus of eight species of the western United States and Mexico. The plants are suffruticose perennials or small shrubs that grow and flower in early spring. Most of the taxa have limited distributions in remote areas. Previously, the genus has been studied largely from the few specimens available in herbaria. Chromosomal data presented in this paper were obtained during the course of a biosystematic investigation of the genus (Watson, 1977).

Chromosome counts have been reported previously for only four species of the genus: *X. tortifolia* (Raven et al., 1960); as *Machaeranthera tortifolia*, *X. wrightii* (Turner, 1964; Powell and Sikes, 1970; as *M. wrightii*; Urbatsch, 1974), *X. glabriuscula* (Solbrig et al., 1969; as *M. glabriuscula*) and *X. frutescens* (Anderson et al., 1974; as *M. frutescens*). All plants counted previously were diploids with  $2n = 12$ .

## MATERIALS AND METHODS

Achenes and/or immature capitula for chromosome counts were collected from populations throughout the range of each species of *Xylorhiza*. Fruits and/or inflorescences were taken from one to five plants at each site. Immature heads were fixed in modified Carnoy's solution (4 chloroform: 3 ethanol: 1 glacial acetic acid; v/v/v). Aceto-carmine squashes of anthers were obtained by the method of Turner and Johnston (1961).

Seeds were germinated on moist filter paper in petri dishes. Emerging root tips were pretreated for four hours in a saturated solution of para-dichlorobenzene. The root tips were then fixed, hydrolyzed, stained, and squashed by the technique of Huziwara (1957).

## RESULTS AND DISCUSSION

Chromosome counts from 118 stands of *Xylorhiza* are recorded in Table 1. In addition, chromosome numbers for species previously thought to belong in *Xylorhiza* are included here or have been published elsewhere (Watson, 1973). Meiotic chromosome behavior was studied in the available taxa; chromosomes of most species were studied at mitotic metaphase.

Chromosome numbers of all taxa in *Xylorhiza* are now known; the base number for the genus is  $x = 6$ . Populations of most taxa are uniformly diploid with  $2n = 12$ . Tetraploids ( $2n = 24$ ) were found only in *X. tortifolia*, *X. venusta*, and *X. glabriuscula* var. *linearifolia*.

In most instances, meiosis in the diploids was regular with the forma-

TABLE 1. CHROMOSOME NUMBERS OF *Xylorhiza* spp. AND *Aster kingii*. Chromosome counts determined from mitotic cells are denoted by an asterisk (\*); other counts are from pollen mother cells. Populations with individuals having fragments are indicated by the superscript f. Collection numbers refer to *T. J. Watson*; vouchers are in TEX.

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*Xylorhiza cognata* (H. M. Hall) T. J. Watson  
 $2n = 12$  CALIF.: Riverside Co., 365, 366, 606.

*Xylorhiza confertifolia* (Cronquist) T. J. Watson  
 $2n = 12$  UTAH: Garfield Co., 312\*, 313, 696, 697.

*Xylorhiza glabriuscula* Nuttall var. *glabriuscula*  
 $2n = 12$  COLO.: Moffat Co., 891. MONT.: Carbon Co., 470<sup>f</sup>\*. UTAH: Daggett Co., 452. WYO.: Albany Co., 488, 489; Carbon Co., 479, 480, 481, 482, 484, 485, 487; Natrona Co., 473, 478; Sweetwater Co., 455, 458; Uinta Co., 462; Washakie Co., 463\*, 464, 465.

*Xylorhiza glabriuscula* var. *linearifolia* T. J. Watson  
 $2n = 12$  UTAH: Grand Co., 308\*, 435, 436, 908.  
 $2n = 24$  UTAH: Grand Co., 680, 905, 914, 916.

*Xylorhiza orcuttii* (Vasey & Rose) Greene  
 $2n = 24$  CALIF.: San Diego Co., 364\*, 603; Imperial Co., 604.

*Xylorhiza tortifolia* (Torrey & Gray) Greene var. *tortifolia*  
 $2n = 12$  ARIZ.: Mohave Co., 385, 386; Yavapai Co., 387, 388; Yuma Co., 610. CALIF.: Inyo Co., 376, 377, 727; Kern Co., 372, 373, 374, 375; Riverside Co., 607; San Bernardino Co., 384, 722, 723. NEV.: Clark Co., 380, 712, 715, 716, 717, 718, 720, 721; Nye Co., 378, 379, 728, 729, 730. UTAH: Grand Co., 316\*.  
 $2n = 24$  NEV.: Clark Co., 381, 382, 383, 713.

*Xylorhiza tortifolia* var. *imberbis* (Cronquist) T. J. Watson  
 $2n = 12$  UTAH: Grand Co., 309\*, 310, 911, 912, 913, 915.

*Xylorhiza venusta* (M. E. Jones) Heller  
 $2n = 12$  COLO.: Delta Co., 429\*, 430\*, 431\*, 665, 666, 667; Moffat Co., 655, 656, 894; Montrose Co., 427\*, 428\*, 668, 669; Rio Blanco Co., 449\*, 654, 898. UTAH: Carbon Co., 918; Emery Co., 304\*; Grand Co., 305\*, 306\*; Uinta Co., 451\*, 652<sup>f</sup>, 653, 895.  
 $2n = 24$  COLO.: Mesa Co., 432\*, 662\*. UTAH: Garfield Co., 900; Grand Co., 433\*, 682, 683, 687, 690, 901, 904.

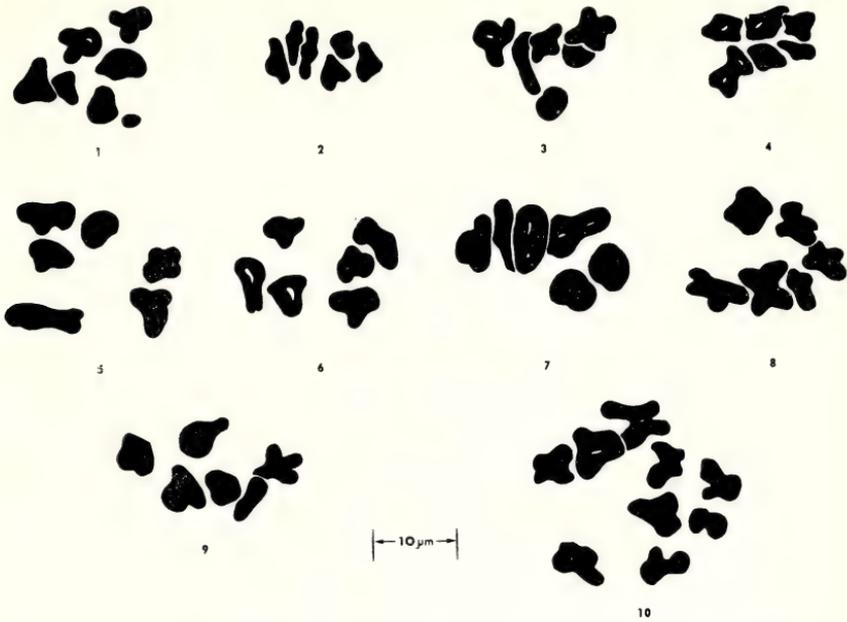
*Xylorhiza wrightii* (A. Gray) Greene  
 $2n = 12$  TEX.: Brewster Co., 401\*, 403\*, 626; Jeff Davis Co., 411\*; Presidio Co., 408\*, 409.

*Aster kingii* D. C. Eaton  
 $2n = 18$  UTAH: Salt Lake Co., 766.

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tion of six bivalents (Figs. 1–10) followed by normal disjunctions. In a few individuals of *X. glabriuscula* from Wyoming, a bridge at anaphase I was observed, suggesting that the plants were heterozygous for segmental rearrangements on one pair of chromosomes. Also, in a few individuals of *X. glabriuscula* and *X. venusta*, a pair of centric fragments was observed in pollen mother cells (Fig. 1) and/or in root tip cells. The fragments synapse and disjoin during meiosis I. At mitotic metaphase, the fragments are approximately one micrometer long and appear to be telocentric. The normal chromosome complement consists of submetacentrics that are 2.5–5.0  $\mu\text{m}$  long at mitotic metaphase.

The tetraploids characteristically form multivalents at meiosis and are morphologically indistinguishable from diploids of the respective



FIGS. 1-10. Camera lucida drawings of meiotic metaphase chromosomes of *Xylorhiza* spp. and *Aster kingii*. All collections are those of T. J. Watson. 1. *X. glabriuscula*,  $2n = 6_{II} +$  synapsed fragments, 470. 2. *X. glabriuscula* var. *linearifolia*,  $2n = 6_{II}$ , 908. 3. *X. confertifolia*,  $2n = 6_{II}$ , 697. 4. *X. venusta*,  $2n = 6_{II}$ , 669. 5. *X. tortifolia*,  $2n = 6_{II}$ , 372. 6. *X. tortifolia* var. *imberbis*,  $2n = 6_{II}$ , 911. 7. *X. wrightii*,  $2n = 6_{II}$ , 626. 8. *X. cognata*,  $2n = 6_{II}$ , 365. 9. *X. orcuttii*,  $2n = 6_{II}$ , 603. 10. *Aster kingii*,  $2n = 9_{II}$ , 766.

taxa, suggesting that the plants are autotetraploids. The tetraploids of *X. tortifolia* are located at the northern distribution limits in Nevada. Tetraploids of *X. venusta* are found at the southwestern margin of the range in Utah and Colorado. Diploids and tetraploids of *X. glabriuscula* var. *linearifolia* grow intermixed over the small range of the taxon in western Utah.

The taxonomic status and placement of *Xylorhiza* have varied (for a complete taxonomic history see Watson, 1977). Recent investigators (Cronquist and Keck, 1957; Turner and Horne, 1964) feel that *Xylorhiza* Nutt., *Machaeranthera* Nees (sensu stricto), and *Haplopappus* Cass. section *Blepharodon* DC. are closely allied. In their view, *Machaeranthera* series *Originales* Cronq. & Keck is a pivotal, infrasectional taxon through which the three groups are related. Cronquist and Keck (1957) consider *Xylorhiza* and the remainder of *Machaeranthera* to have been derived from an *Originales*-like ancestry and construe *M. blephariphylla* of this series to be the most primitive extant taxon in the *Xylorhiza*-*Machaeranthera* alliance. Chromosome numbers of the taxa involved seem instructive in these regards.

Most species of *Originales* and those species of *Blepharodon* related to *Originales* are reported to be on a base of  $x = 4$ . Although  $2n = 10$  has been reported from *M. blephariphylla* (Jackson, 1959; as *M. gymnocephala*), Hartman (1976) feels that the count was erroneous. He has recorded  $2n = 8$  from three populations of this species and has found plants from one of the populations to have 2 or 3 pairs of small, supernumerary chromosomes in addition to the normal complement of four pairs. Thus, Hartman regards *Originales* and related members of *Blepharodon* to be unibasic with  $x = 4$ . If *Xylorhiza* ( $x = 6$ ) has evolved from an *M. blephariphylla*-like ancestor or from another extinct or extant member of *Originales*, the chromosome number of the former is a result of an aneuploid gain. However, it is noteworthy that plants serving to link *Xylorhiza* to *Originales* by morphology and phenology and having a documented base number of  $x = 5$  are unknown. Species on a base of  $x = 5$  are found in *Machaeranthera* but these taxa belong to other subgeneric groups (i.e., series *Variables* and series *Verae* of Cronquist and Keck, and section *Psilactis* Turner and Horne) that cannot be related directly to *Xylorhiza*.

Some investigators (Raven et al., 1960; Solbrig et al., 1969) hold that the primitive base number for the Astereae as a whole is  $x = 9$  and that the lower chromosome numbers in the tribe were generally derived through aneuploid reduction (for a contrasting viewpoint see Turner et al., 1961). According to this hypothesis, the chromosome level at which *Xylorhiza* diverged would precede that of *Machaeranthera*. Also, Solbrig et al. (1969), Anderson et al. (1974), and Hartman (1976) have noted the frequent occurrence of  $x = 6$  in taxa that have been included in or bear relationship to *Haplopappus* and *Machaeranthera* (e.g., *Grindelia*, *Prionopsis*, *Xanthocephalum*, *Isopappus*, *Pyrrocoma*, *Isocoma*, *Hazardia*, *Xylorhiza* and the "phyllocephalus group" sensu Hartman, 1976). This observation led Hartman (1976) to suggest that  $x = 6$  is a more primitive number for this alliance and that the lower base numbers (i.e.,  $x = 4, 5$ ) are derived. It is interesting to note that one of the few documented cases of descending aneuploidy in natural populations is known from *Haplopappus* sect. *Blepharodon* (i.e., *Haplopappus gracilis*-*H. ravenii*; Jackson, 1962; 1965).

The foregoing observations suggest that *Xylorhiza* diverged early from the line that gave rise to *Machaeranthera* and *Haplopappus* in North America. However, before any credible phylogenetic interpretations can be made, it appears to me that the relationships of the North American Astereae to the poorly known *Haplopappus* sect. *Haplopappus* (sect. *Euhaplopappus* of Hall, 1928) of South America need to be explored. The latter taxon seemingly connects various elements in the *Xylorhiza*-*Machaeranthera*-*Haplopappus* alliance of North America (see Watson, 1977). Chromosome numbers for only ten of the South American species are known: most have  $2n = 10$  (Grau, 1976; L. C. Anderson, personal

communication), but *H. cuneifolius* has  $2n = 12$  (B. L. Turner and J. Bacon, personal communication).

The chromosome number of *Aster kingii* ( $2n = 18$ ) is reported here for the first time. This taxon was included in *Machaeranthera* sect. *Xylorhiza* by Cronquist and Keck (1957). However, it is phenologically, ecologically, morphologically, and chromosomally anomalous there. The plants of *A. kingii* flower in mid-summer and are found in coniferous forests in cracks of granitic outcrops at subalpine elevations in the Wasatch Mountains of Utah. Members of *Xylorhiza* flower in early spring and are distributed in relatively deep soils of deserts and semi-arid grasslands. Although plants of *A. kingii* have taproots surmounted by a caudex, the roots are small and resemble those of the alpine *Asters*, e.g., *A. alpigenus* (T. & G.) Gray. Individuals of *A. kingii* are caespitose and have relatively small capitula with phyllaries that have anthocyanic margins and squarrose tips; the disc florets are anthocyanic. None of these features is found in species of *Xylorhiza*.

The presence of taproots and squarrose phyllaries in *A. kingii* suggests *Machaeranthera*. However, with the exception of *M. brevilingulata* ( $2n = 18$ ; Turner and Horne, 1964; Powell and King, 1969), which is better placed in *Aster* or *Conyza* (Hartman, 1976), *Machaeranthera* consists of diploids with  $2n = 8$  or 10 and tetraploids with  $2n = 16$  (see Hartman, 1976).

*Aster kingii* is probably most closely allied with species of *Aster* in which  $2n = 18$  is a common number (Raven et al., 1960; Solbrig et al., 1964; Solbrig et al., 1969; Anderson et al., 1974; and others). Some members of *Aster* have taproots (e.g., *A. alpigenus*) and others have squarrose phyllaries (e.g., *A. conspicuus* Lindl.). The florets and capitula of *A. kingii* resemble those of the more widespread *A. integrifolius* Nutt., although the latter lacks squarrose phyllaries and differs in habit. This similarity was noticed by Gray (1884), who treated the two species together within *Aster* proper.

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INTERSPECIFIC HYBRIDIZATION BETWEEN NATIVE  
AND NATURALIZED CRATAEGUS (ROSACEAE)  
IN WESTERN OREGON

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ABSTRACT

Morphological evidence for hybridization between *Crataegus douglasii* var. *suksdorffii* and *C. monogyna* in the southern Willamette Valley, Oregon, has been derived from a population with intermediate leaf morphology. Experimental hybridization resulted in an average fruit set of 42 percent in ♀ *C. douglasii* × ♂ *C. monogyna*, and 7 percent in ♀ *C. monogyna* × ♂ *C. douglasii* crosses. Hybrid pollen was 66 percent stainable with aniline blue-lactophenol compared with 95 percent for *C. douglasii* and 96 percent for *C. monogyna*. This is the first documented hybridization between a European and a northwestern North American species.

Hawthorns (*Crataegus*, Rosaceae) are known to hybridize where species are sympatric (Standish, 1916; Bradshaw, 1954; Robertson, 1974; Byatt, 1975, 1976). None of the documented cases of hawthorn hybridization, however, has involved a species native to North America and a European species. In western Oregon, the native hawthorn, *Crataegus douglasii* Lindl. var. *suksdorffii* Sarg., and an introduced European species, *Crataegus monogyna* Jacq., have come together within the last 100 years. The native species has black fruit, five styles, and mostly unlobed leaves; the introduced species has red fruit, a single style, and deeply lobed or lacinate leaves. Hybridization has produced a population of intermediate plants with black fruits, variable style number, and a wide range of leaf shapes. The evidence presented here for the hybrid origin of these intermediate individuals is based on leaf morphology, the results of crossing experiments, and pollen stainability tests. All information gathered thus far supports the hybridization hypothesis.

The study was conducted on the Cogswell-Foster Reserve, a 36-ha tract 40 km north of Eugene in Linn County, Oregon. The Reserve was acquired by the Nature Conservancy in 1969. *Crataegus douglasii*, the black hawthorn, is native to the Reserve and is found throughout the Pacific Northwest, especially along streams, ditches, and valley bottoms. English hawthorn, *C. monogyna*, was introduced onto the Reserve about 100 years ago (Lucile Foster, pers. comm., 1976). It has spread vigorously throughout the area, forming dense thickets under canopies of *Quercus garryana* Dougl. Intermediate individuals can be found throughout the Reserve but are especially common along fence lines in open areas, where many individuals are large and produce abundant flowers and fruit. Increment cores suggest that most of these trees are less than 20 years old.

In May, both species and their putative hybrid bloom simultaneously, *C. monogyna* having the most abundant flowers. Hymenopterans and

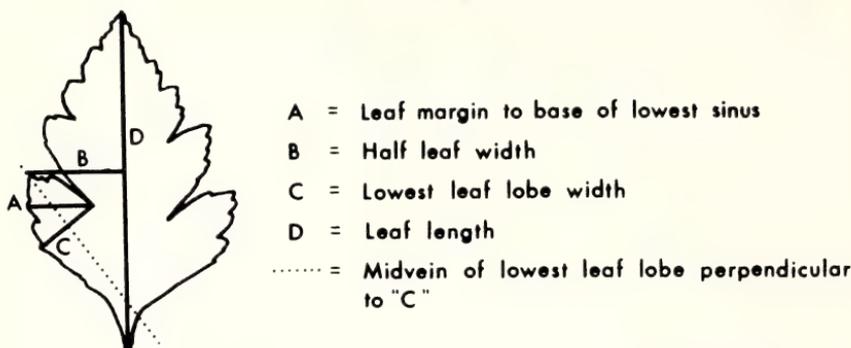


FIG. 1. Leaf measurements used in the scattergram (Fig. 2).

dipterans are attracted in large numbers. Honey bees (*Apis mellifera* L.) move among all three types on a single collecting flight. Frugivorous birds are known to be the principal agents of hawthorn seed dispersal (Hitchcock et al., 1969; Robertson, 1974) and are commonly seen devouring hawthorn fruits on the Reserve.

#### MATERIALS AND METHODS

*Leaf Variability.* Ten to 15 leaves from 114 randomly selected plants were collected in May and October, 1977. Four measurements were made on each leaf (Fig. 1).

*Artificial Crosses.* Hand crosses were made on May 1–13, 1976, and May 11–19, 1977. Crossing was done on calm, clear days, during mid-mornings and early afternoons. A corymb of 1–16 flowers was considered the "crossing unit" for each hybridization. Eighteen *C. douglasii* × *C. monogyna* crosses were made involving 203 flowers on 18 different plants. The pistillate parent was *C. douglasii* for ten corymbs and *C. monogyna* for eight corymbs. Hawthorn stigmas become receptive about two days before the petals open. Pollen is shed at anthesis. Therefore, flowers of the pistillate parent were chosen in the "popcorn" stage, just before bud opening. Stamens were removed with fine forceps, and pollen was transferred directly from the flowers of the male parent to the stigmas of the emasculated flowers. Corymbs were then bagged with cheesecloth and tied with string. Bags were opened in July to check fruit set and then reclosed to allow fruit ripening. All of the resulting fruits were saved for testing of seed viability.

Nine corymbs were bagged before bud opening to test for the necessity of pollen vectors. On eight plants, self-crosses were made to test for self-incompatibility, which has been reported in some Rosaceae (East, 1940).

*Pollen Viability Tests.* Pollen from 22 pressed hawthorn specimens was examined using aniline blue-lactophenol as an indicator (see Byatt, 1977). Percentages were based on microscopic examination of an aver-

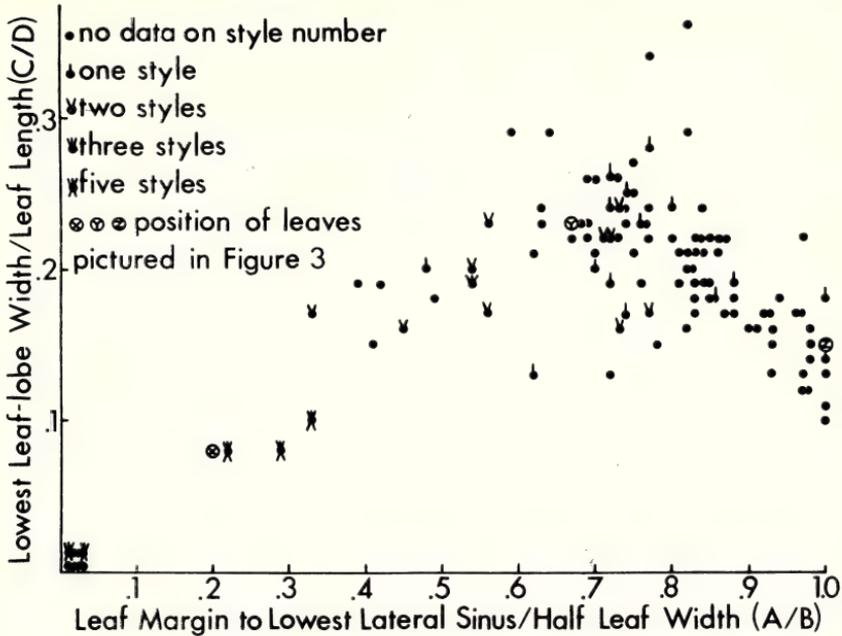


FIG. 2. Scattergram illustrating range of hawthorn leaf variability at the Cogswell-Foster Reserve. Each point represents the mean of leaves measured from an individual plant. One leaf each of *C. douglasii* (X), *C. monogyna* (Z), and an intermediate type (Y) from Fig. 3 are plotted to help indicate the relationship of leaf morphology to position on the scattergram.

age of 250 grains per plant. Grains that stained dark blue were assumed to be viable and unstained grains to be inviable.

#### RESULTS

*Leaf Variability.* Mean relative distance from the leaf margin to the base of the lowest sinus (A/B) was plotted against the mean ratio of the lowest leaf lobe width to leaf length (C/D) for each plant (Fig. 2). Distribution of points on the scattergram suggests the presence of a "swarm" of hybrid types that overlap the parental types in leaf morphology. *Crataegus douglasii* leaves are unlobed or shallowly lobed; *C. monogyna* leaves are usually deeply lobed or lacinate; while leaves of intermediate plants show wide morphological variation (Fig. 3).

*Artificial Crosses.* There is cross compatibility between *C. douglasii* and *C. monogyna* as judged by the high percentage of fruit set in ♀ *C. douglasii* × ♂ *C. monogyna* crosses. Fruit formation on ten corymbs ranged from 25 to 73 percent of treated flowers, with mean fruit set at 42 percent. The mean fruit set for *C. douglasii* corymbs left open for insect pollination was 29 percent.

Fruit set was much reduced in ♀ *C. monogyna* × ♂ *C. douglasii* crosses. Five out of eight corymbs set no fruit. The highest fruit set on

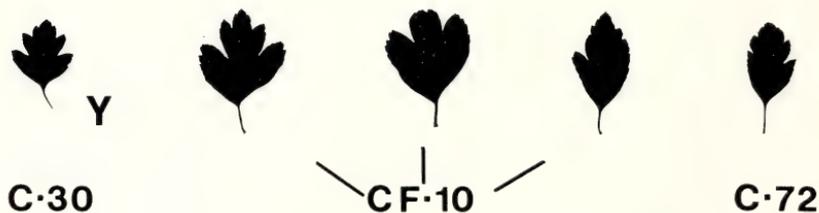
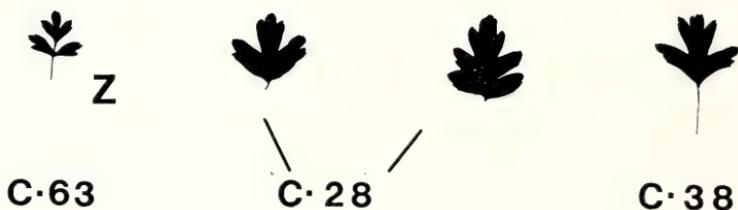
**C. douglasii****C. douglasii X C. monogyna****C. monogyna**

FIG. 3. Representative hawthorn leaf types from the Willamette Valley, Oregon. Letters and numbers refer to individual plants. Leaves X, Y, and Z have been plotted on the scattergram (Fig. 2).

one corymb was 25 percent and mean fruit set was 7 percent. Mean fruit set for *C. monogyna* corymbs left open to insects was 50 percent. The low fruit set is not thought to be an artifact of the experimental handling of *C. monogyna* flowers, because in other crosses, *C. monogyna* set significant amounts of fruit.

There was no fruit set on any corymb bagged before bud opening nor on any selfed corymb.

*Pollen Viability Tests.* Pollen from presumed hybrids showed significantly lower percentages of stainable grains than parental pollen. For pollen from nine individuals with hybrid morphology, the percentage of stainable grains ranged from 42 to 75 percent (mean = 66 percent). Stainable pollen from five specimens of *C. douglasii* ranged from 93 to 98 percent (mean = 95 percent); and from eight specimens of *C. monogyna*, stainability ranged from 93 to 98 percent (mean = 96 percent).

At least one hybrid individual at the Cogswell-Foster Reserve is completely male-sterile, all flowers having vestigial stamens that lack anthers. This plant is vegetatively vigorous, flowers heavily, and sets some fruit.

A comparison of the Willamette Valley hawthorns is given as Table 1.

#### DISCUSSION AND CONCLUSIONS

Evidence that the native *Crataegus douglasii* var. *suksdorfii* hybridizes with the introduced *Crataegus monogyna* in western Oregon can be summarized as follows:

1. There are many plants intermediate in leaf shape and style number and possessing a novel combination of parental characters: distinctly lobed leaves and black fruits.

2. Interspecific crosses resulted in substantial fruit set when *C. douglasii* was the pistillate parent. Partial unilateral sterility appears to be occurring because reciprocal crosses resulted in reduced fruit set. Insect vectors appear necessary for pollination, and all plants tested exhibited self-sterility.

3. Pollen stainability tests indicated significantly lower percentages of viable pollen grains in the putative hybrids than in the parents.

Most of the *C. douglasii* × *C. monogyna* hybrids on the Cogswell-Foster Reserve have 3–5 lobed leaves and 2–3 styles and, when in bloom, match the key description of *Crataegus oxyacantha* L., another hawthorn of European origin that is naturalized in the Pacific Northwest. [*C. oxyacantha* is now known in Europe as *C. laevigata* (Poiret) DC. See Byatt, 1974.] Hawthorn samples from the Reserve were sent to J. Byatt, Westfield College, London, whose determinations support the hybrid nature of the intermediate plants and confirm that they are not *C. oxyacantha*. Dr. Byatt reports (pers. comm., 1977) that *C. oxyacantha* is never black-fruited. She also writes, "It has already been sug-

TABLE 1. SOME DIAGNOSTIC CHARACTERS OF *Crataegus douglasii* var. *suksdorfii*, *C. monogyna*, AND THEIR HYBRIDS FROM THE WILLAMETTE VALLEY, OREGON.

Character	<i>C. douglasii</i>	Hybrids	<i>C. monogyna</i>
Petal color	White	White	White or pink
Style and pyrene number	5	(1) 2-3 (4)	1
Receptacle	Glabrous	Glabrous to hairy	Mostly hairy to woolly
Mature fruit color	Black	Black (Imm.: purple or red)	Red
Fruit shape	Globose	Globose	Ovoid
Mature leaf shape	Elliptic	Elliptic to obovate	Ovate or obovate
Leaf lobing	Unlobed or shallowly lobed	Variously lobed; sinuses of intermediate depth	Deeply lobed or lacinate
Leaf length	2-9 cm	1.5-6 cm	1.5-3.5 cm
Leaf pubescence	Both surfaces pubescent to glabrate	Glabrous to somewhat hairy, or with some hairs on veins below	Glabrous except for patches of hairs in axils of veins beneath
Leaf margins	Serrate or biserrate	Serrate or toothed	Entire or sparingly serrate
Lowest lateral leaf veins	Straight	Straight or slightly recurved	Strongly recurved
Termination of lateral veins	At tooth apices	Variable	At apices and sinuses
Fruit ripens	Jul-Aug	Aug-Sep	Sep-Oct
Chromosome number	2n = 34 (Calder et al., 1968)	—	2n = 34 (Clapham et al., 1962)
Geographic range	B. C. to S OR, W of Cascades	Willamette Valley, OR; possibly elsewhere	Eurasian native; naturalized sparingly but widely in N. A.

gested that black fruit colour is dominant in crosses between red and black-fruited taxa." This agrees with our observation that all presumed hybrids on the Cogswell-Foster Reserve are black-fruited.

Hitchcock et al. (1969) list both *C. monogyna* and *C. oxyacantha* as naturalized elements of our flora, distinguishing between them on the basis of leaf lobing and style number. Both are described as red-fruited. *Crataegus douglasii* × *C. monogyna* hybrids and *C. oxyacantha* may be distinguished in future treatments on the basis of fruit color.

*Crataegus monogyna* may be hybridizing with another North American species. J. B. Phipps (pers. comm., 1977) has noted probable hybridization between *C. monogyna* and the native *C. punctata* Jacq., in Ontario, Canada.

In this study we describe what we believe to be the first documented case of hybridization between a western North American species and a European native. At the present time, *C. douglasii* × *C. monogyna* hybrids are known only from Linn County in the Willamette Valley; however, they can be expected to occur in other locations in western British Columbia, Washington, and Oregon, where the parent species have co-existed for some time.

## ACKNOWLEDGMENTS

We thank Stan Cook, David Wagner, and Kenton Chambers for their support, reading of the manuscript, and helpful suggestions. We also thank Debra Ayres and Stan Love for their help in the field. Supported in part by NSF Grant DEB-7709472.

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A NEW SPECIES OF EUPATORIUM (ASTERACEAE)  
FROM CALIFORNIA

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*Eupatorium* (Asteraceae, Eupatorieae) is a highly diverse and widespread group of well over 1000 taxa. Numerous species are found in the American tropics, and the genus is well represented in the floras of more northerly areas of the globe, including North America. However, California is relatively depauperate in members of this large and complex genus, with only two native species recorded by Munz (1959). Consequently, the existence of a new, highly distinct, and narrowly endemic member of the genus in the state is of considerable interest.

***Eupatorium shastense*** Taylor & Stebbins, sp. nov.; a *E. occidentale* differt foliis basi opposita, folia caulina alterna. Capitulum plerumque solitarium, terminale. Flores albae. (Fig. 1)

Perennial herb from woody, enlarged or occasionally rhizomatous base. Stems clustered, 1.5–4.5 dm long, puberulent to pubescent, often with some glandular hairs above. Leaves opposite at base, alternate above; the juvenile orbicular, entire to slightly dentate; the adult ovate, obtuse to truncate at base, acute to acuminate at tip, coarsely serrodentate, often ciliate on margins with short hairs 0.3–0.9 mm long, glabrous to puberulent on laminar surfaces. Petioles 4–6 mm long, blades 15–31 mm long, 11–20 mm wide. Capitula mostly solitary (1–3) at ends of branches, often subtended by a small leaf-like bract, 12–16 mm diameter when pressed. Phyllaries 9–13, green, often ribbed at base, in two series, glabrous to pubescent. Phyllaries glabrous to pubescent, 9–14 mm long, 1.1–2.5 mm wide. Flowers all tubular, 30–60 per capitulum. Corollas 5–8 mm long, white. Style branches clavate, elongate, 3–5 mm long, with short stigmatic lines; appendage elongate, papillate. Achenes brown to black, puberulent to pubescent, 3.0–5.5 mm long, 5-nerved. Pappus of 20–40 whitish barbellate bristles. Chromosome number  $n = 17$ .

TYPE: CA, Shasta Co., 1.6 km E of Squaw Creek, T35N R2W (MDM), 762 m. *Stebbins & Ehrendorfer 5968*, 20 Jun 1959, Holotype (UC). Isotypes: MO, NY, GH, DAV.

Additional specimens examined: CA, Shasta Co., Shasta Lake, McCloud Arm opposite Bailey Cove, 487 m, on North Gray Rocks, *Stebbins and Gajewski 5949*, 18 Oct 1959 (UC, DAV); Devil's Rock, S28 T35N R2W, 670 m, along Low Pass Creek, *Stebbins 6177*, 9 Sep 1967 (DAV); N face Hirz Mt., S7 T35N R3W, 1066 m, *Taylor 2409, 2410*, 1 Jul 1972, chromosome voucher 2430, 1 Jul 1973 (DAV).

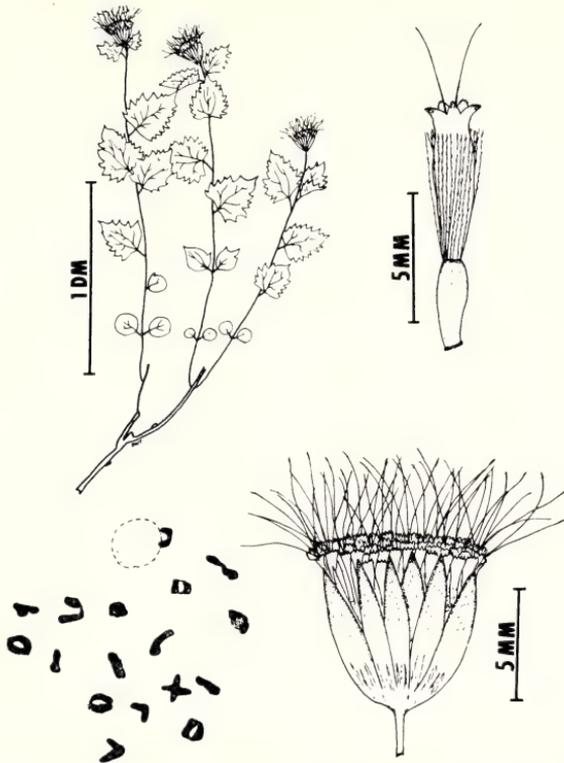


FIG. 1. *Eupatorium shastense*. Upper left: habit of plant. Upper right: detail of corolla. Lower left: camera lucida drawing of chromosome voucher  $\times 3100$ . Lower right: detail of single capitulum.

*Eupatorium shastense* is obviously related to the more widespread *E. occidentale* Hook., because these two taxa are similar in a number of vegetative characters. Both have numerous clustered stems that arise from an enlarged woody base and have very similar foliage and canopy architecture. Heteroblastic leaf development is typical of nearly all individuals of *E. shastense* observed, but this character is either absent or of rare occurrence for *E. occidentale*. The most striking differences separating these two species are characters of the capitulum. *Eupatorium shastense* has a solitary, terminal capitulum (occasional individuals possess a single subtending pair), whereas *E. occidentale* typically has  $>18$  capitula in a terminal corymbose cluster. The capitula of *E. shastense* are larger in most dimensional characters than those of *E. occidentale*, and the corollas of *E. shastense* are invariably white whereas the corollas of all *E. occidentale* we have observed are tinged with purple. *Eupatorium shastense* differs significantly at the 0.05 level of probability (based on *t* statistic comparisons) from *E. occidentale* for the following characters:

capitula per branch, capitulum width when pressed, and corolla width when pressed. The large, solitary heads of *E. shastense* are somewhat reminiscent of several species of *Brickellia*, but the 5-nerved achenes and chromosome number of  $n = 17$  of the former show that this resemblance is superficial.

*Eupatorium shastense* is a strict calcicole, being restricted to nearly vertical limestone cliffs of the Hosselkus formation from 450 to 1200 m between the Pit and McCloud river drainages in Shasta County. Plants of *E. shastense* establish on these cliffs wherever there is sufficient soil or organic matter lodged in cracks or on ledges to support their growth. *Eupatorium occidentale* and *E. shastense* are sympatric at all populations of the latter known to us. Ecologically, the two taxa occupy different habitats at a given site. *Eupatorium occidentale* occurs as an understory herb in rocky sites in a dense woodland dominated locally by *Pseudotsuga menziesii*, *Pinus ponderosa*, *Quercus chrysolepis*, and *Q. garryana* var. *breweri*. Plants of *E. occidentale* are absent from the vertical cliffs that are occupied by *E. shastense*. Elsewhere, *E. occidentale* is often a plant of cliff-faces, but it is not a strict calcicole. At all populations studied, no individuals of *E. shastense* have been found in the seemingly more favorable habitats in the surrounding woodland occupied by *E. occidentale*.

The Hirz Mountain population of *E. shastense* was surveyed during the summers of 1972–1975. The population during this period was stable and consisted of less than 100 individuals. Other known populations of the new species are similarly small. Individuals in small size-classes were observed in sufficient numbers on Hirz Mountain to suggest a stable population size.

#### ACKNOWLEDGMENTS

We thank Gerald D. Carr for the chromosome number determination.

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A NEW SPECIES OF VIGUIERA  
(ASTERACEAE-HELIANTHEAE) FROM NAYARIT, MEXICO

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*Viguiera* is a notably complex genus with relationships extending to such well-known genera or generic segregates as *Helianthus*, *Tithonia*, and *Hymenostephium*.

*Viguiera websteri*, described below, belongs to a group of species that Blake (1918) recognized as a distinct genus, *Hymenostephium*. D'Arcy (1975) sunk the latter into synonymy with *Viguiera*; this was also accepted by H. Robinson (1977). Neither author went so far as to include *Hymenostephium* within sect. *Diplostichis* of *Viguiera*, but I believe that its relationship is in, or near, this group and consequently concur with their generic disposition.

Detection of the relationship of *Hymenostephium* to *Diplostichis* (and consequently *Viguiera*) by D'Arcy and H. Robinson is not surprising, for Blake, himself, (1918, p. 7) notes, "They [*Hymenostephium*] are distinguished from the section *Diplostichis* of *Viguiera*, which they closely resemble in all other features, solely by their pappus . . .". The same may be said for the genus *Haplocalymma* Blake, which H. Robinson (1977) reduced to synonymy under *Viguiera*, a submersion to which I also subscribe, but again, this is not unexpected since Blake (p. 8) went on to state that *Haplocalymma* ". . . is clearly a lateral offshoot of the *Diplostichis-Hymenostephium* line, . . .".

And that is one of the problems in dealing with Blake's otherwise very scholarly treatment of the Compositae: he tended to let the absence of one, or perhaps two, characters *make* a genus. As noted by Cronquist (1968, p. 10) ". . . the absence of a character is a less reliable guide to taxonomic affinities than its presence". In the case of the pappus, very simple but loose, genetic control of its absence has been amply demonstrated by Clausen (1951) and many others.

***Viguiera websteri*** B. L. Turner, sp. nov. *V. hintonii* H. Robinson simulans sed capitulis pluribus majoribus, pedunculis longioribus, paleis receptaculi majoribus, plantis parvis erectis perennis caulibus comparata tenuibus, rhizomatibus ligeis cormoideis. (Fig. 1)

Perennial herb 30–65 cm tall, the stems slender, sparsely appressed pubescent to nearly glabrate, arising from woody, corm-like rootstocks, ca 20 mm long, 15–20 mm thick. Leaves opposite throughout, except for the several much-reduced leaves that subtend each of the flowering peduncles; petioles short, 3–8 mm long; blades ovate, 3–6 cm long, 1.5–2.5 cm wide, sparsely appressed-pubescent above and below, the margins crenate-serrate. Inflorescence loose, the heads remote, mostly (2)3–5 per

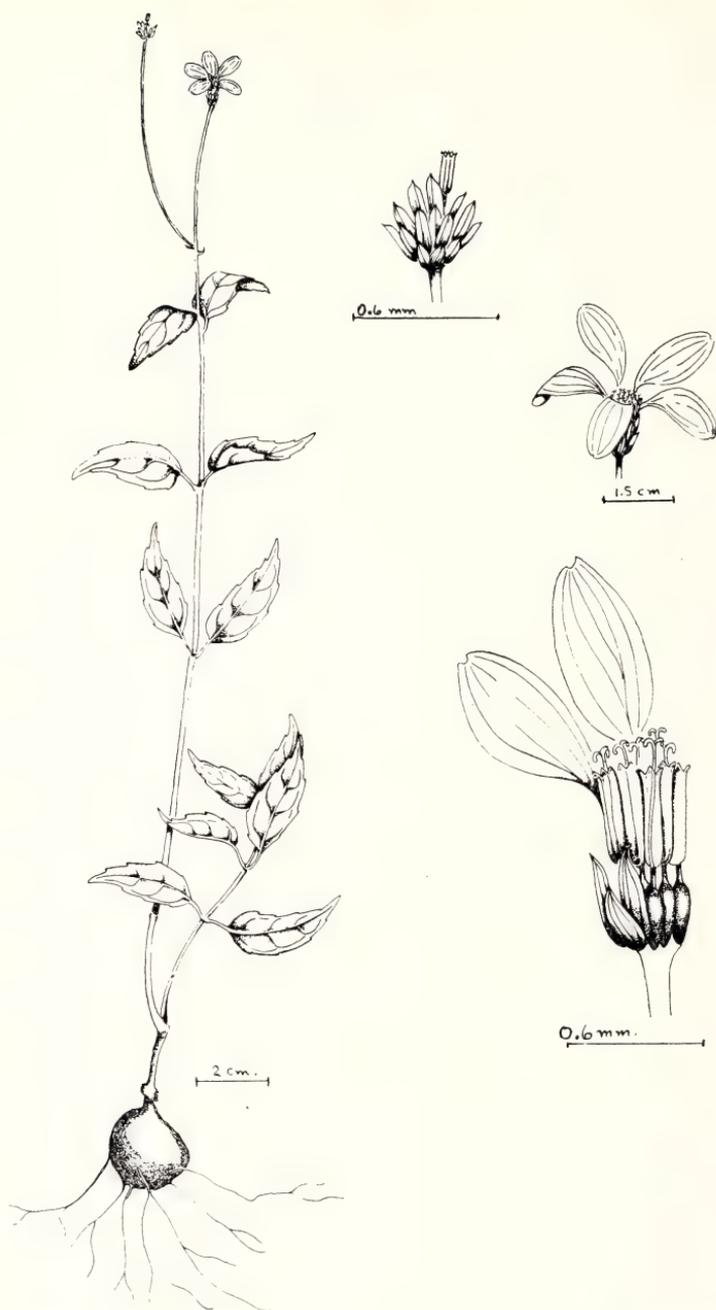


FIG. 1. Sketch of isotype (LL) of *Viguiera websteri* Turner: left, habit; upper right, involucre; middle right, individual head; lower right, partial head showing florets.

secondary branch, the ultimate peduncles (1)2–5 cm long. Involucre campanulate, 2-seriate; bracts, lanceolate-ovate, 2.0–3.5 mm long, ca 1 mm wide, moderately appressed-pubescent, 2–3 striate. Receptacle convex, knobby; bracts linear-ovate, acute or apiculate, ca twice as long as the involucre. Ray florets 8, yellow, neuter; ligule ca 5 mm long, 2–3 mm wide, the tube ca 0.8 mm long. Disk florets 20–30, yellow; corolla ca 4 mm long, the tube sparsely pubescent, ca 1 mm long; the lobes 5, ca 0.6 mm long; stylar appendages caudate, pubescent beneath, especially at the apex. Achenes black, sparsely appressed pubescent, somewhat tetragonally-flattened, ca 2 mm long, 1 mm wide; pappus absent.

TYPE: Mexico. Nayarit; "oak woods on volcanic rock 25 km by road S of Tepic" (between Tepic and Compestela), ca 1000 m, 18 Oct 1970, G. L. Webster and G. J. Breckon 15744. (Holotype DAV; isotype, LL).

The closest relationship of *Viguiera websteri* is probably with the recently described *V. hintonii* H. Robinson (1977) from Michoacan and Guerrero. It has the foliage and achene characters of this taxon but its habit is markedly different (low perennial from corm-like rootstocks vs. shrub 1–2 meters tall). Further, the heads of *V. websteri* are much larger (6–7 mm vs. 3–4 mm) with more numerous, larger florets.

The typification of *Viguiera hintonii* (McVaugh 22637, US) is unfortunate since H. Robinson has apparently described a plant whose inflorescence (to judge from the illustration accompanying his description) has been badly affected by insect egg deposition and larval development among heads, so that the peduncles of the capitula are described as 1–10 mm long. This range holds for isotypic material at TEX, but the heads are also badly infested by insects. Paratypic material (*Hinton et al.* 14182, LL), however, is relatively free of insects, possessing peduncles up to 30 mm long.

The section *Diplostichis* (including *Hymenostephium*) is in much need of detailed study. There is a perplexing array of variation in the group as noted by H. Robinson, especially along the Pacific Mountain slopes from Guatemala to Durango. Field work should do much to help unravel the complex and I suspect that several additional undescribed species will come to light in the process.

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A NEW SUBSPECIES OF *ABRONIA MARITIMA*  
FROM BAJA CALIFORNIA, MEXICO

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In the course of a survey of vegetation along the coasts of Baja California, Sonora, and Sinaloa, Mexico, I noted a pink-flowered *Abronia maritima* (Nyctaginaceae). It is presumed to be of hybrid origin.

*Abronia maritima* Nutt. ex Wats. ssp. *capensis* A. F. Johnson, ssp. nov. differt a *A. maritima* ssp. *maritima* foliis persucculentis, aggregatis, ovalibus v. subrotundis, crenatis, 1–3 cm longis, 0.8–1.5 cm latis, 3–5 mm crassis; perianthio bracteis 1.0–1.5plo longiore, tubo perianthii viridialbido, 7–9 mm longo, limbo perianthii roseo pallido centro albido et lobis non reflexis; anthocarpo glanduloso-puberulo omnino.

*Abronia maritima* Nutt. ex Wats. ssp. *capensis* A. F. Johnson differs from *A. maritima* ssp. *maritima* in that the leaves are very succulent, crowded, oval to suborbicular with crenate margins, 1–3 cm long, 0.8–1.5 cm wide, and 3–5 mm thick, the perianth is 1–1.5 times longer than the bracts, the tube greenish-white, 7–9 mm long, the limb pale pink with white center and unreflexed lobes, anthocarp glandular-puberulent throughout.

TYPE: Mexico, Baja California Sur, beach south of lighthouse at Cabo Falso NW of town of San Lucas, 18 Mar 1974, *A. F. Johnson* 711 (holotype, DAV). Paratypes: San Pedrito, B. Cfa. Sur, Dec 1972, *A. F. Johnson* 514 (UC); Migriño, B. Cfa. Sur, Dec 1972, *A. F. Johnson* 516 (CAS).

*A. maritima capensis* differs from *A. maritima maritima* primarily in perianth color and in having smaller, more crowded leaves (Fig. 1). Although obvious in the field, these characteristics tend to be lost in the preparation of herbarium specimens of this succulent species.

I have found subspecies *capensis* only along the Pacific shore of the Cape region of Baja California, Mexico, between Todos Santos and San Lucas (Fig. 2). A search of the collections of *A. maritima* in four herbaria (UC, CAS, DS, SD) failed to turn up any specimens collected along this 80-km segment of coastline. The purple-flowered ssp. *maritima* was not seen to co-occur with ssp. *capensis* along this stretch of coast, although it was observed on beaches 50 km north of Todos Santos and at San José del Cabo, 35 km northeast of San Lucas.

Several features, besides the morphological ones mentioned, serve to distinguish ssp. *capensis* from ssp. *maritima*. Estimated pollen viability of ssp. *capensis*, determined by staining with aniline blue-lactophenol, averaged 50 percent, much lower than that of ssp. *maritima*, which averaged 85 percent. The pollen of ssp. *capensis* when brushed on stigmas of

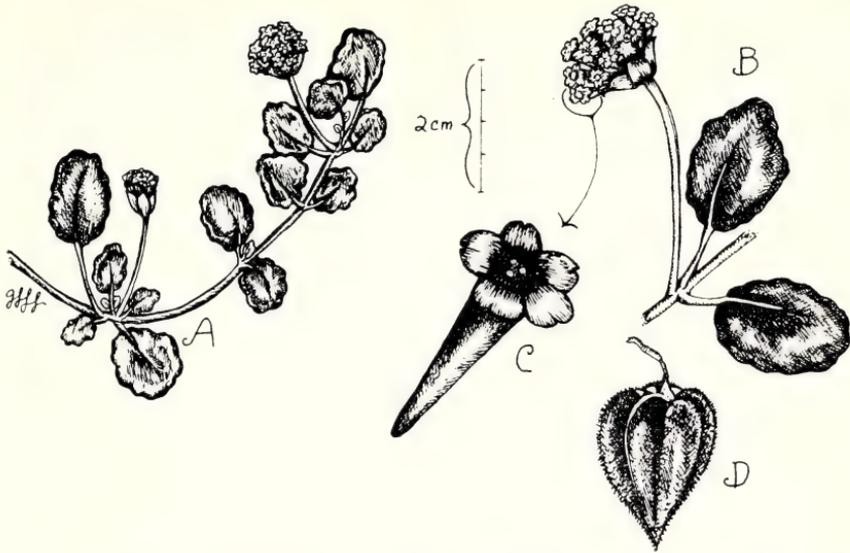


FIG. 1. *Abronia maritima* Nutt. ex Wats. ssp. *capensis* A. F. Johnson, drawn from live specimen growing in greenhouse. A) branch with flower head ( $\times 2/3$ ), B) detail of leaves and flower head ( $\times 1$ ), C) detail of flower ( $\times 3$ ), D) anthocarp ( $\times 2$ ).

ssp. *maritima* never produced seed, whereas the reverse procedure readily did so, a phenomenon often noted in autogamous species.

Secondly, ssp. *capensis*, grown in isolation in the greenhouse, is autogamous and produces copious seed, whereas ssp. *maritima* from California does not produce seed under these circumstances. However, ssp. *maritima* from the shores of the Gulf of California was found to be autogamous when grown in the greenhouse.

A third distinction is in the amino acid complement of the nectar, which includes tryptophan in ssp. *capensis* and lacks it in ssp. *maritima*. Baker and Baker (1976, 1977) have found the set of amino acids in the nectar to be constant within a species and useful for detecting hybrids, the nectar of which contain amino acids from both parents. This is the case with the nectar of hybrids between ssp. *capensis* and ssp. *maritima* which contains tryptophan.

Given the propensity of species of *Abronia* to hybridize (Tillett, 1960), it seems reasonable to suppose that ssp. *capensis* is the end result, after introgression and selection, of an initial cross between *A. maritima* and another species of *Abronia*. The closest candidate is *Abronia gracilis* Benth., a desert annual having a bright pink perianth with a white center, unreflexed limb, and small leaves with crenulate margins. Although this species does not presently occur in the Cape Region (ranging only as far south as the Magdalena plain), its nectar amino acid complement supports the hypothesis. Its nectar contains tryptophan

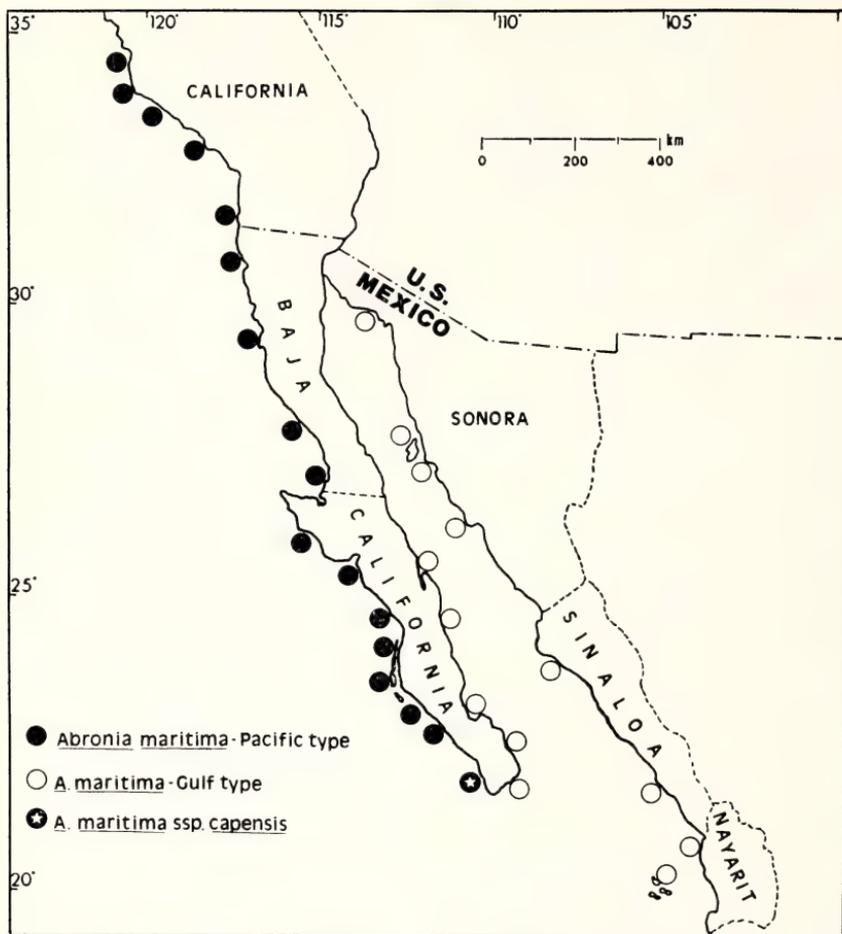


FIG. 2. Distribution of the variants of *Abronia maritima*.

and no other amino acids not found in *A. maritima maritima*. On this basis, another candidate, *A. umbellata* Lam., a northward-ranging annual morphologically similar to *A. gracilis*, can be considered less likely since its nectar contains lysine and leucine, not found in the nectar of *A. maritima capensis*. However, several attempts to cross *A. gracilis* with *A. maritima capensis* and *A. maritima maritima* from both the Pacific and Gulf coasts did not produce seed.

Populations of ssp. *maritima* from the Gulf of California resemble ssp. *capensis* and differ from Pacific coast populations of ssp. *maritima*, not only in being autogamous, but also in several morphological features (Johnson, 1978). The differences are maintained when plants from Pacific and Gulf coasts grown from seed in the greenhouse. Plants of ssp.

*maritima* from the Pacific coast north of Todos Santos have a reddish-purple perianth with reflexed limb and leaves with generally entire margins. Gulf coast plants have a shorter, bright purplish-pink perianth with unreflexed limb, and smaller, crenately-lobed leaves. The latter features are duplicated in some of the  $F_1$  progeny resulting from crosses between ssp. *capensis* and ssp. *maritima* from the Pacific coast (Silver Strand State Beach, California). It appears possible that the morphological differences between Pacific and Gulf coast populations of ssp. *maritima* are also the result of an earlier episode of hybridization, perhaps the same one that produced ssp. *capensis*.

#### ACKNOWLEDGMENTS

I thank Irene Baker for the nectar analyses and Annetta Carter for helpful suggestions.

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#### NOTES AND NEWS

*Lasthenia californica* (COMPOSITAE), ANOTHER NAME FOR A COMMON GOLDFIELD.— In conjunction with a systematic study of certain Californian Helenieae (Johnson. Systematics of Eriophyllinae (Compositae). 1978. Ph.D. dissertation. Univ. California, Berkeley.), we had opportunity to examine type specimens that were previously unavailable (see Ornduff. 1966. Univ. Calif. Publ. Bot. 40.). The holotype of *Lasthenia californica* DC. ex Lindley, 1 Aug 1835, Edwards's Bot. Reg. 21: facing pl. 1780 ("HHS [Hort. Horticultural Society of London]", *J. Lindley*. CGE!) was found to be referable to what until now has been called *L. chrysostoma* (Fischer & Meyer) Greene (basonym: *Baeria chrysostoma* Fischer & Meyer, Jan 1836, Index Seminum Hert. Petrop. 2:29) and not *L. glabrata* Lindley, Edwards's Bot. Reg. 21: facing pl. 1780 (lectotype designated here by Ornduff: California, "1833 [22 Dec 1830-18 Aug 1832]", *D. Douglas*. CGE!). Because publication of the epithet *californica* predates that of *chrysostoma*, the name in use for this conspicuous plant of southwestern Oregon, California, southern Arizona, and northern Baja California must be changed to *L. californica*. — DALE E. JOHNSON, Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, PA 15213, and ROBERT ORNDUFF, Department of Botany, University of California, Berkeley 94720.

PUBLICATION OFFER — Robert Ornduff (address above) has a number of copies of "A Biosystematic Study of the Goldfield Genus *Lasthenia*" Univ. Calif. Publ. Bot. 40, 1966. He would be glad to send gratis copies to individuals or libraries upon request.

RANUNCULUS GERANIOIDES H.B.K. EX DC.  
IN COSTA RICA AND PANAMA

THOMAS DUNCAN

Department of Botany and University Herbarium  
University of California, Berkeley 94720

Authors of recent floras and previous authorities on *Ranunculus* have reported *R. repens* L. and *R. pilosus* H.B.K. ex DC. from Costa Rica and Panama (Standley, 1937; Benson, 1948; Duke, 1962). Recent studies of the *Ranunculus hispidus* Michx. complex have revealed that *R. geranioides* H.B.K. ex DC. has been treated erroneously as *R. pilosus* H.B.K. ex DC. (Benson, 1948; Duke, 1962) and occurs in both Costa Rica and Panama. The purpose of this paper is to note these corrections to the floras of Costa Rica and of Panama and to document the distribution of *R. geranioides* and its differences from *R. repens* in these countries.

Sepals reflexed; petals lanceolate, commonly 7–10, rarely 5; achenes papillate . . . . . 1. *R. geranioides*  
Sepals patent; petals obovate, commonly 5, rarely as many as 10; achenes smooth . . . . . 2. *R. repens*

1. *Ranunculus geranioides* H.B.K. ex DC. Syst. 1: 286. 1818

Plants stoloniferous and rhizomatous; sepals reflexed, 4.0–7.0 mm long, 2.0–3.5 mm wide, one-half to fully as long as the petals; petals yellow, (5)7–10, 6.0–11.7 mm long, 2.8–6.0 mm wide, the widest point above the middle; nectary scale obovate; achene wall with minute to conspicuous papillae, achene beak one-third to one-half as long as the body, the tip often slightly curved and tapering from a broad base;  $n = 16$  (Panama, *Duncan 2331*).

FLOWERING AND FRUITING DATES: Throughout the year.

HABITATS: Paramos, meadows, fields, streambanks, and roadsides.

DISTRIBUTION: Primarily South American from Colombia to northern Peru; northern limit of range on Volcán Baru, Chiriquí Province, Panama, and near Orosi and on Volcán Turrialba in Costa Rica; 1300–3300 m in Costa Rica and Panama.

SPECIMENS EXAMINED: Costa Rica: *Cartago*: At foot of Orosi waterfall, 5 May 1957, *Rodriguez C. 428* (UC, MICH). Volcán Turrialba, 2000 m, Jan 1899, *Pittier 7550* (GH). Volcán Turrialba, ca. 3300 m, 13 Feb 1922, *Greenman and Greenman 5582* (MO). Volcán Turrialba, 2900 m, 17 Sep 1969, *Weston and Kincaid 6136* (UC). Volcán Turrialba, ca. 20 km by road above Turrialba and 8 km by road N of Pastora, 7000 ft, 16 Feb 1974, *Duncan 2314* (MICH, UC). *San José*: Potrero of Finca Santa Rosa north of El Alto de Cabeza de Vaca on Río Sucio, 14 Nov 1929, *Dodge and Thomas 4949* (MO). Sables du Río Parrita au Copey,

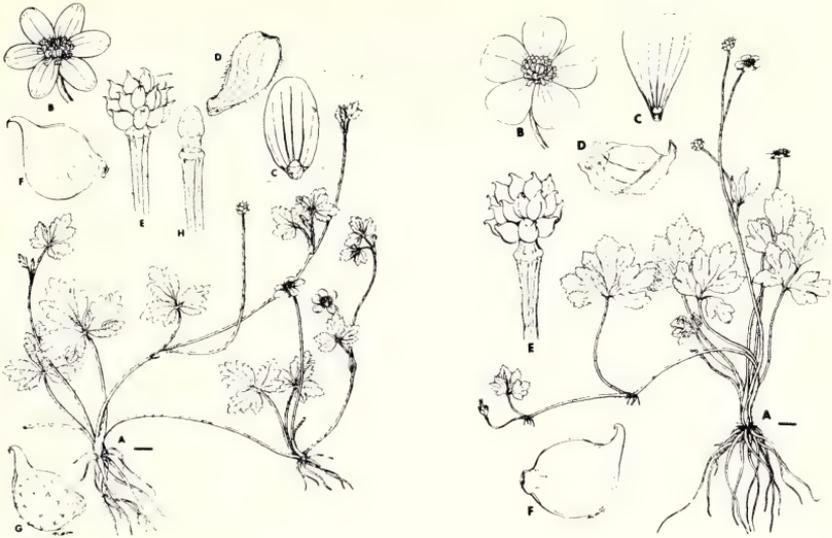


Fig. 1. (Left) *Ranunculus geranioides* from Colombia. A. Whole plant. B. Flower. C. Petal. D. Sepal. E. Infructescence. F. Achene. G. Achene (from Volcán Baru, Panama). H. Receptacle. Scale line represents ca. 3 cm in A, 1.5 mm in C and D, 5 mm in B, 2 mm in E and H, and 1 mm in F and G.

Fig. 2 (Right) *Ranunculus repens* from Volcán Turrialba, Costa Rica. A. Whole plant. B. Flower. C. Petal. D. Sepal. E. Infructescence. F. Achene. Scale line represents ca. 3 cm in A, 1.5 mm in C and D, 5 mm in B, 2 mm in E, and 1 mm in F.

1800 m, Feb 1898, *Tonduz 11873* (GH). PANAMA: *Chiriquí*: Valley of the upper Rio Chiriquí Viejo, vicinity of Monte Lirio, 1300–1900 m, 27 Jun–13 Jul 1935, *Siebert 159* (MO). Along the trail between Cerro Punta and the Quebrado Bajo Grande, 2000–2100 m, 28 May 1970, *Wilbur 11924 with Luteyn and Armond* (GH, DS, MO). Along Quebrado Bajo Grande below road to Cerro Punta and ca. 1 km from Cerro Punta, 6000 ft, 24 Feb 1974, *Duncan 2331* (MICH, UC). Vic. of Bajo Chorro, 1900 m, 20–22 Jul 1940, *Woodson and Scherry 646* (GH). Boquete District, Bajo Chorro, 7000 ft, 26 Mar 1938, *Davidson 444* (GH).

The name most frequently applied to these populations, *R. pilosus* H.B.K. ex DC. is based on material collected by Humboldt and Bonpland in Colombia. This name is currently treated as a synonym of *R. praemorsus* var. *praemorsus* (Duncan, 1979), which is widely distributed in the Andean paramos from Venezuela to Argentina. Earlier authors treated *R. pilosus* as conspecific with *R. petiolaris* H.B.K. ex DC. var. *petiolaris*. The latter is a widespread Mexican, Central American, and northern South American taxon and is what earlier workers thought *R. geranioides* to be. Benson (1948) emphasized the lack of stolons for *R. petiolaris* var. *petiolaris*. However, the plants from Costa Rican and

Panamanian populations are distinctly stoloniferous. Additionally, the short, stout-based, slightly curved achene beaks, clavate receptacles, and fibrous roots readily distinguish *R. geranioides* from *R. petiolaris* var. *petiolaris*, which possesses long, easily broken, straight achene beaks, conical receptacles, and tuberous roots. The illustration in Duke (1962) is not from material of *R. geranioides* from Panama. Apparently a specimen of *R. petiolaris* var. *petiolaris* was used. This taxon does not occur in Panama or Costa Rica.

An additional specimen of *Davidson 444* is reported to be at MO. A search of their collections has not resulted in the discovery of this duplicate. Duke (1962, based on the identification of Benson) reports that this specimen is *R. repens*. I doubt this report because *R. repens* is currently not known to occur in Panama and the duplicate at GH is *R. geranioides*.

2. *Ranunculus repens* L. Sp. Pl. 554. 1753.

Plants stoloniferous and rhizomatous; sepals appressed 4.0–6.0 mm long, 2.0–4.0 mm wide up to two-thirds as long as the petals; petals yellow 5–7 (10), 6.0–10.0 mm long, 5.0–12 mm wide, the widest point above the middle; nectary scale flabellate; achene wall smooth, the margin narrow, inconspicuous, or absent; achene beak less than one-third as long as the body, the tip slightly curved and tapering from a broad base;  $n = 16$  (Costa Rica, *Duncan 2302*).

FLOWERING AND FRUITING DATES: Throughout the year.

HABITATS: Disturbed roadsides, fields, and wet meadows.

DISTRIBUTION: Native of Europe with a cosmopolitan distribution; in Costa Rica in the provinces of Cartago, Heredia, and San José: 1500–2500 m.

SPECIMENS EXAMINED: Costa Rica: *Cartago*: Near stream, beyond Pa-cayas, 9 Jun 1957, *Rodriguez C. 471* (UC). Lower potrero of Finca Coli-blanco, 1620–1910 m, 17 Oct 1929, *Dodge and Thomas 4530* (MO). Volcán Turrialba, ca. 2900 m, 17 Sep 1969, *Weston and Kincaid 6135* (UC). Volcán Turrialba, ca. 20 km by road above Turrialba at town of Pastora, 7000 ft, 16 Feb 1974, *Duncan 2314* (MICH, UC). *Heredia*: Along roadside between Los Cartagos and Vara Blanca on road to Vol-cán Poás, 6000 ft, 20 Feb 1974, *Duncan 2322* (MICH, UC). *Vara Blanca de Sarapiquí*, north slope of Central Cordillera, 1500–1750 m, Jul–Sep 1937, *Skutch 3249* (MO, GH). *San José*: Potrereros of Rancho Redondo, 2200–2600 m, 18 Nov 1929, *Dodge and Thomas 4946* (MO). La Palma, 1460 m, Aug 1898, *Tonduz 7402* (GH). *State Unknown*: Vic. of Los Nubes, 1800 m, 1 Dec 1937–1 Jan 1938, *Allen 714* (GH).

The three specimens cited by Duke (1962) as *R. repens* from Pana-ma are treated here as *R. geranioides*. *Ranunculus repens* is currently not known to occur in Panama. Standley (1937) included all material of *R. geranioides* in *R. repens*. He was correct in doubting the previous treatment of these populations as *R. petiolaris* var. *petiolaris* (*R. pilosus*

sensu other authors) but apparently considered no possibilities other than *R. repens*. Standley (1937) suggested that *R. repens* was introduced from Europe with grass seed.

## ACKNOWLEDGMENTS

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## NOTEWORTHY COLLECTIONS

Ed. Note: With this issue a new format is inaugurated for "range extensions" and similar notes. Its purpose is to provide a greater array of useful data in more telegraphic style than has been customary. Prospective authors of these notes should study carefully the conventions of the new format.

TEESDALIA CORONOPIFOLIA (Bergeret) Thellung (CRUCIFERAE).—USA, CA, Sonoma Co., W edge Santa Rosa, SW of intersection of Fulton and Piner roads, locally common in wet areas with *Blennosperma*, 7 Mar 1977, C. F. Quibell 1392 (BM, CDA, GH, ROPA, RSA, UC). Basionym: *Thlaspi coronopifolium* Bergeret; for discussion of synonymy, see Thellung, A. 1912. Repert. Spec. Nov. Regni Veg. 10:289-290.

*Previous knowledge*—Native to S Europe and N Africa; adventive in N Europe. (Herbaria consulted: CAS, DS, JEPS, UC; published sources: Clapham, A. R. et al. 1962. Fl. Brit. Isles, 2nd ed.; Tutin, T. G. et al., eds. 1964. Fl. Europaea, vol. 1.) The only other member of the genus, *T. nudicaulis* (L.) R. Br. [≡ *Iberis nudicaulis* L.], is native to W and central Europe and has been recorded as locally adventive in B.C. (Taylor, R. L. and B. MacBride. 1977. Vasc. Pls. Brit. Columbia), WA and OR (Hitchcock, C. L. and A. Cronquist. 1973. Fl. Pacific Northw.), and in E USA from MA to NC (Fernald, M. L. 1950. Gray's Man. Bot., 8th. ed.). *Diagnostic characteristics*—Our plants differ from *T. nudicaulis* principally in having acutely (vs. bluntly) lobed leaves, subequal (vs. unequal) petals, and 4 (vs. 6) stamens.

*Significance*—Apparently, first record of species for N.A. (In Gleason, H.A. 1952. New Britton and Brown Ill. Fl., vol. 2, plant figured as *T. nudicaulis* may be *T. coronopifolia*); first record of genus for CA (sources in addition to those cited above: Abrams, L. 1944. Ill. Fl. Pacific Sts., vol. 2; Munz, P. A. 1959. A Calif. Fl.; ———. 1968. Suppl. Calif. Fl.; ———. 1974. A Fl. S. Calif.). The value of documenting introductions and migrations has been discussed by Shinners (1965. Sida 2:119-128) and by Strother and Smith (1970. Taxon 19:871-874).—CHARLES F. QUIBELL, Department of Biological Sciences, Sonoma State College, Rohnert Park, CA 94928 and JOHN L. STROTHER, Botany - Herbarium, University of California, Berkeley 94720.

*AGROSTIS HUMILIS* Vasey (POACEAE).—USA, CA, Tuolumne Co., moist alpine meadow at outflow of Blue Canyon Lake, 3048 m, (NE¼ S9 T5N R20E), 22 Jul 1976., *Neisess 67* (OBI, US). Mixed community, including *Carex nigricans* C. A. Mey., *Pedicularis groenlandica* Retz., *Potentilla breweri* Wats., *Dodecalheon alpinum* Greene, *Caltha howellii* Greene, *Aster alpigenus* Gray var. *andersonii* Peck, *Salix anglorum* Cham. var. *antiplasta* C. K. Schneid., *Castilleja culbertsonii* Greene, *Trisetum spicatum* Richt. var. *molle* Beal, *Juncus longistylis* Torr., and *Claytonia nevadensis* Wats. Collection verified by T. R. Soderstrom, US, Apr 1977.

*Previous knowledge*—Range: Cascade and Olympic Mts. of B.C., WA, OR; across NV and UT (Uinta Mts.); Rocky Mts. from MT south to NM (Herbaria consulted: US; UC and JEPS kindly checked by Alan R. Smith; published sources: Hitchcock, A. S., *Man. Grasses U.S.*, 1950; Hitchcock, C. L. et al., *Vasc. Pls. Pac. Northw.*, Cronquist et al., *Intermountain Flora*, 1977.). *Diagnostic characters*—Small tufted perennials; culms 3–18 cm tall; ligules 0.5–1.5 mm long, obtuse to truncate; blades 0.5–1.2 mm broad, mostly basal; panicles loosely contracted, 1.5–4 cm long; glumes subequal, 1.5–2.2 mm long, lanceolate, acute, purple; lemma 1.5–1.8 mm long, awnless; palea shorter, about  $\frac{2}{3}$  its length; rachilla vestige lacking or very short. Blue Canyon population exhibits maximum dwarfing.

*Significance*—Previously unlisted in State and local floras. Full distribution in California unknown. Habitat and range suggest that it is relictual in sierran alpine tundra.—KURT R. NEISESS, Department of Botany and Plant Sciences, University of California, Riverside 92521.

*ASPLENIUM SEPTENTRIONALE* (L.) Hoffm. (ASPLENIACEAE).—USA, CA, Lassen Volcanic Natl. Park: Raker Peak, SW slope, 21 Jun 1976, *D. Showers 3533* (SFSU); 1 km W of Lost Creek Camp, 2 Sep 1976, *D. Showers 3748* (SFSU, CAS). Rare. Other localities include: Eagle Peak, Loomis Peak, and the North Domes. Scattered populations, in crevices of dacite volcanic rock, fully exposed, 1800–2700 m. Frequent associates are *Penstemon newberryi*, *Cryptogramma acrostichoides*, and *Polystichum scopulinum*. Verified by J. T. Howell, Apr. 1977 (*D. Showers 3748*).

*Previous Knowledge*—Known from SD and OK, W to OR and Baja Calif.; also WV; Eurasia. Known in CA from, Tulare Co., Columbine Lake, collected by J. T. Howell in 1942. Single locality in OR, Douglas Co., Copeland Creek on the N Umpqua River collected by F. Lang. (Herbaria consulted: CAS, DS, UC, SFSU; published sources: Munz, *Supplement to a California Flora*, 1968; Amer. Fern J. 59: 45–47. 1969). *Diagnostic characters*—small tufts consisting of grasslike fronds, the stipe longer than the blade, the latter divided into 2–3 linear segments.

*Significance*—A second locality in CA. The Lassen populations are between the two known localities for the southern Cascades-Sierra Nevada axis. They are 310 km SE of the Douglas Co, OR locality and 520 km N of the Tulare Co, CA locality.—DAVID W. SHOWERS, Department of Ecology and Systematic Biology, San Francisco State University, San Francisco 94132.

## NOTES AND NEWS

**ENDANGERED SPECIES IN CALIFORNIA: FEDERAL PROCEDURES AND STATUS REPORT.**—There is considerable confusion about the various federal actions that have taken place relating to rare plants. This is exemplified by the statement in the April 1978 Madroño (25:107) that *Cordylanthus mollis* ssp. *mollis* has *Endangered* status under the Endangered Species Act. This is not yet so. It may be well to review the steps necessary to attain this status.

To be legally recognized as *Endangered* or *Threatened* under this act, a taxon must have been the subject of a proposed and a final rulemaking published in the Federal Register. *Critical habitats* are given legal standing in the same manner. These rulemakings are the responsibility of the U. S. Fish and Wildlife Service. So far it has

taken the following steps concerning plants: A Notice of Review appeared 1 Jul 1975 and included essentially the national list compiled by the Smithsonian Institution (H.R. Doc. No. 51; 94th Congress, 1st Session, Report on endangered and threatened plant species of the United States, compiled for the Committee on Merchant Marine and Fisheries by the Smithsonian Institution, 15 Dec 1974). This is a permissible, but not mandatory, step. On 16 Jun 1976 a rulemaking proposing 1783 taxa for *Endangered* status appeared. There has been no proposed rulemaking for *Threatened* status. Final rulemakings based on the 1976 action have appeared sporadically since then. The first such action for the nation listed four San Clemente Island taxa on 11 Aug 1977. It covered *Lotus scoparius* ssp. *traskiae*, *Malacothamnus clementinus*, *Delphinium kinkiense*, and *Castilleja grisea*. On 26 Apr 1978 a second group was listed; included, along with the notorious Furbish's lousewort, were five more California plants: *Oenothera deltoidea* var. *howellii* and *Erysimum capitatum* var. *angustatum*, both of the Antioch Dunes in Contra Costa County; *Oenothera avita* ssp. *eurekaensis* and *Swallenia alexandrae*, both of the Eureka Dunes in Inyo County; and *Dudleya traskiae* of Santa Barbara Island. On 28 Sep 1978 four more California plants joined the select list: *Arabis macdonaldiana* of Red Mountain, Mendocino County; *Orcuttia mucronata* of a single vernal pool in Solano County; *Pogogyne abramsii*, an inhabitant of rapidly disappearing vernal pools in San Diego County; and *Cordylanthus maritimus* ssp. *maritimus*, a coastal salt marsh taxon from Southern California. Only two *Critical Habitats* have been proposed for California taxa so far, for the two Antioch Dunes plants mentioned above. Both were the subject of a final rulemaking on 31 Aug 1978.

Of the 22 plant taxa now listed for the nation as *Endangered* or *Threatened*, thirteen are from California. This impressive proportion testifies not only to the large number of very rare taxa in the California flora but also to the hard work of the many amateurs and professionals that have assisted in the California Native Plant Society's Rare Plant Project, begun in 1968 at the instigation of G. Ledyard Stebbins, president from 1966 to 1971.—ALICE Q. HOWARD, Chairman, Rare Plant Committee, CNPS, University Herbarium, University of California, Berkeley 94720.

Note added in proof: Amendments to the Endangered Species Act passed on the final day of the 95th Congress in mid-October will change somewhat in the listing process outlined above.

A CORRECTION ON THE INDIGENEOUS DISTRIBUTION OF KNOBCONE PINE.—In a recent note (Madroño 25:106. 1978.) I reported a population of *Pinus attenuata* Lemm. along Beasore Road N of Bass Lake as a southward range extension. This population was thought to be indigenous based on the confirmation by the Timber Management Officer for the Sierra National Forest that neither knobcone pine nor any knobcone mixture had been planted in this area. However, a recent communication from Frank G. Hawksworth (Forest Pathologist, Rocky Mtn. For. Range Expt. Sta.) and an article in the *Fresno Bee* from 1971 describe planting by the Forest Service in the early 1960's of a knobcone-monterey pine hybrid (*P. × attenuradiata* Stockw. and Right.) along Beasore Road. Much of the present population is apparently offspring from these hybrids, many having lost most monterey pine characteristics.—JON E. KEELEY, Department of Biology, Occidental College, Los Angeles, CA 90041.

Ed. Note: Jim A. Bartel, Botanist with the Sierra National Forest, Fresno, has provided the following further information: *Pinus × attenuradiata* was planted as a timber tree in several harshly dry sites in the Sierra National Forest in the early 1960's. The hybrid pine was promoted for its rapid growth but has not been a good timber tree because it is readily bent or broken by snow.

GYNODIOECY IN *MAMMILLARIA DIOICA* (CACTACEAE).—Virtually every flora and monograph treating *Mammillaria dioica* K. Brandegee describes the species as incompletely or partially dioecious. In her description of the species Brandegee stated that many plants were either male or female, and others hermaphroditic or “imperfectly dioecious in all degrees” (*Erythea* 5:115–116. 1897). Our observations of plants in Anza Borrego Desert State Park in SE San Diego Co., CA in 1968 and 1978 indicate that populations of *M. dioica* in this area are in fact gynodioecious, the plants being either hermaphroditic or pistillate. Both hermaphrodites and pistillate plants set fruit with apparently normal seed. Compared with hermaphrodites, the flowers of pistillate plants are smaller, with narrower petals, but larger stigmas (Fig. 1.). The pistillate flowers bear stamens with indehiscent anthers that contain no pollen. Self-incompatibility, self-compatibility, autogamy, cleistogamy, and agamospermy are known in the Cactaceae (Ganders, *Cact. Succ. J. Gt. Brit.* 38:39–40. 1976), but *M. dioica* is apparently the only species in the family with imperfect flowers. Brandegee’s description was based only on plants from near the coast, so



FIG. 1. Pistillate (left) and hermaphroditic flowers of *Mammillaria dioica* (scale in mm).

it is uncertain whether the breeding system of the species differs in coastal and inland populations, or whether she misinterpreted the situation. The distribution of floral forms in this species merits more extensive observation by botanists in the San Diego region.—FRED R. GANDERS and HELEN KENNEDY, Department of Botany, University of British Columbia, Vancouver, B.C., Canada V6T 1W5.

ADDITIONS TO THE FLORA OF THE FARALLON ISLANDS, CALIFORNIA. — The flora of the Farallon Islands, San Francisco County, California, was recently described by Coulter (Coulter, *Madroño* 21:131–137. 1971) based on observations made in 1968. Since 1968, I have noted 14 additions, eight previously unreported and six previously reported species, possibly missed in 1968. A new variety of a previously noted species has also been observed. I have not noted any extinctions. I report here on the additional species noted from 1968 through the summer of 1975.

Before the 1968 flora only two papers had been published on the plants of the islands. Blankenship, who was on the islands 3–6 July 1892, collected 28 species, 11

native and 17 introduced plants (Blankenship and Keeler, *Zoë* 3:144-165. 1892). Ornduff, who was there for a short time in May 1960, found only 20 species, 10 native and 10 introduced, but noted the addition of 3 new ones to the islands (Ornduff, *Leafl. West. Bot.* 9:139-142. 1961). For the 1968 flora, I was present on the islands for three months during the spring and summer of 1968 and found 36 species, 14 previously unnoted. Of the 36 species, 13 were native and 23 were introduced. With the 14 additions noted here, the island list contains 50 species, 18 native and 32 introduced.

Following is a list of the additional species. Previous listings of species by Blankenship and Ornduff are noted. For a description and map of the islands, see the 1968 flora (Coulter, *Madroño* 21:131-137. 1971). Names are given according to Munz (Munz, *A California flora*. Univ. of Calif. Press, Berkeley, 1959) and where they have been changed Munz's names are in synonymy. Names with asterisks are those of introduced species. Specimens have been placed in the Dudley Herbarium (DS) except as noted.

\**Anagallis arvensis* L. f. *caerulea* (Schreb.) Baumg. Although this taxon was reported by Blankenship, Ornduff, and Coulter, the population consists almost exclusively of the pin-orange variety. A few plants of the blue variety were found near East Landing about 2 m south of the tram tracks in 1971. They have not been found in subsequent years.

*Bromus* cf. *maritima* Hitchc. Previously unreported, this grass was found in 1975 in a few patches 15 to 30 south of the lighthouse on Lighthouse Hill. It has not been collected; a photograph of the plant was identified by B. Crampton.

\**Cerastium viscosum* L. This is likely the *C. glomeratum* Thuill. of Blankenship. It has not been reported since 1892. In 1975 a few plants were found by B. Lewis along the sidewalk northeast of Heligoland Hill. It has not been collected.

\**Gnaphalium luteo-album* L. A new species on the islands, in 1975 a few plants were found along the tram tracks by B. Lewis.

*Juncus bufonius* L. Jim Lewis (PRBO) found viable seeds in the damp area between the living quarters and the paint locker in 1975. Plants grown from these seeds were collected and identified. The species was reported by Blankenship and Ornduff but missed by Coulter in 1968.

\**Leontodon leysseri* (Wallr.) G. Beck. Observed in 1972, this plant is new to the islands. It grows along the tram tracks between East Landing and the Power House.

\**Malva parviflora* L. In 1974 many plants were found by R. Boekelheide around the living quarters and from the living quarters to the water. This plant was reported by Blankenship but not listed by Ornduff or by Coulter in 1968.

\**Medicago hispida* Gaertn. In 1975 scattered plants were found in the southeast section of the island. Perhaps this is *M. denticulata* Willd. recorded by Blankenship. It has not been collected.

*Montia hallii* (Gray) Greene. Found in 1972 but not observed earlier, this plant grows along the path near the top of Lighthouse Hill.

\**Plantago coronopus* L. A new plant to the island, many plantains were found along the south slope of Lighthouse Hill near the living quarters and between the living quarters and the Power House.

\**Polycarpon tetraphyllum* (L.) L. Found on the island for the first time in 1972, this plant grows commonly along the tram tracks near the living quarters.

*Psilocarphus tenellus* Nutt. var. *tenellus*. Listed by both Blankenship and Ornduff but missed in 1968, this plant grows commonly where the soil is hard and gravelly in the southeast part of the island.

\**Rumex crispus* L. One plant was found among the gull colony in the southeast part of the islands in 1974. It bore fruit in that year and again in 1975. This plant has not been found on the islands before.

*Sagina occidentalis* Wats. This plant grows commonly in the southeast part of the

island where the soil is hard and gravelly. It was noted by Blankenship and Ornduff but missed in 1968.

\**Vulpia myuros* (L.) K. C. Gmelin var. *hirsuta* Hack. (*Festuca megalura* Nutt.) In 1975 many patches of this grass were found near the lighthouse on Lighthouse Hill. This is a new species to the islands.

Some species such as *Psilocarphus tenellus* and *Sagina occidentalis*, reported by both Blankenship and Ornduff, were probably present but overlooked in 1968. *Cerastium viscosum*, *Malva parviflora* and *Medicago hispida* were recorded by Blankenship but not by Ornduff or by Coulter in 1968. In 1892 these plants may have persisted in fenced gardens, protected from rabbit grazing, as suggested by Ornduff. The gardens have since been abandoned. Between 1972 and 1975 the Point Reyes Bird Observatory carried on a program to eliminate the rabbits, which were finally completely eliminated in 1975. With the reduction in the rabbit population these plants may have been able to recolonize the islands; or, perhaps, these species persisted as repressed populations, expanding with the reduction in rabbit numbers.

The location where some new species were first recorded suggests the ways in which these plants came to the islands. *Anagallis arvensis* forma *caerulea*, *Leontodon leysseri*, and *Polycarpon tetraphyllum*, found along the tram tracks where there is much human activity were likely brought by man. *Bromus maritima*, *Montia hallii*, and *Vulpia myuros* were found near the top of Lighthouse Hill where most migrant passerine birds first land on the islands. These plants may have been transported by passerines. Finally, *Rumex crispus*, found in the gull colony, may have been brought by gulls, which fly between the islands and the mainland.

I thank R. Boekelheide, J. and B. Lewis, D. Manual, and D. Gaines for pointing out new plants. Dr. H. Baker, Dr. B. Crampton, and G. True helped in identification. This paper has been improved through discussions with J. and B. Lewis and through comments by Dr. P. Raven and R. Boekelheide on an earlier draft. I very much appreciate the encouragement of Dr. P. Raven, Dr. H. Baker, and Dr. J. H. Thomas. The U. S. Coast Guard kindly provided logistic support and the Point Reyes Bird Observatory generously made possible my stay on the island. I thank the personnel of the Farallon Island Wildlife Refuge for permission to work on the island.

This is contribution number 151 of the Point Reyes Bird Observatory. — MALCOLM C. COULTER, Department of Biology, University of Pennsylvania, Philadelphia 19104.

## REVIEW

*Manual of the vascular plants of Wyoming.* By ROBERT D. DORN. Illustrations by Jane L. Dorn. 2 vols. 1498 pp. 1977. Garland Publ. Co., New York. ISBN 0-8240-9905-2. \$95.

Wyoming now has a flora! A conspicuous blank spot has been filled in for plant taxonomists, biogeographers, ecologists, resource managers, users of Wyoming's natural resources, and those who appreciate and have the opportunity to enjoy its rich natural beauty.

Many of Wyoming's political leaders and residents are salivatingly eager to exploit its coal, oil, forests, rangelands, wildlife, water soils, scenery, and other operationally non-renewable natural resources. Others wish to apply a conservation ethic, or legal restrictions, to unregulated use. Both groups have had a most useful tool handed to them free, more or less, by an independent, dedicated, skillful scientist.

The manual is excellent. Dorn is a practiced, perceptive, industrious plant collector. He mentions giving himself only three years to do the flora. Thus, some weeds and all infraspecific taxa are not included, distributions are given only within Wyoming and in broad categories, habitat information is minimal. 2144 species are well described. Leading families are *Compositae* (with 17.3% of the species), *Gramineae*

(10.2), *Leguminosae* and *Cruciferae* (5.8 each), *Cyperaceae* (5.5), *Scrophulariaceae* (4.6), *Ranunculaceae* (3.0), *Umbelliferae* (2.6), and *Boraginaceae*, *Caryophyllaceae*, and *Chenopoliaceae* (2.4). Dorn's keys are direct, imaginative, practical for field use, and have been tested (p. 2). Keys to fruiting plants are provided for some groups (*Cruciferae*, *Umbelliferae*, *Astragalus*, *Salix*); vegetative characteristics are often used. Taxa are arranged alphabetically. References are given to recent monographic treatments, and sources of original descriptions are given. Synonymy seems adequate.

Improvements in a new edition might include a less lavish use of paper simply to condense volume and weight. More detailed distributions are desirable, particularly since the Rocky Mountain Herbarium at Laramie has a file of dot maps for Wyoming plants, and many of the species are mapped in Hultén's Alaska flora and his other publications and still others in the monographs Dorn gives as references. Reference should have been made to Wyoming taxonomic work already done. These include Beetle and May's (1971) treatment of the grasses, Beetle's on the section *Tridentatae* of *Artemisia* (1960), Porter's series on families through the *Fumariaceae* (1962-1972), theses, local floras such as Shaw's for Teton County (1976), Despain's for Yellowstone National Park (1975), Nelson's unfortunately unpublished one for the Medicine Bow Mts. (1974). All of these contain valuable information on the flora of Wyoming that Dorn's flora does not.

Some comments can be made on individual taxa. Beetle's treatment of *Artemisia tridentata* and its allies is more perceptive, and an exception could have been made here for including subspecies. *Puccinellia-Glyceria-Torreyochloa* is less confusing if attention is paid to the species' habitats. A few species from Teton County are not included (*Antennaria plantaginifolia*, *Dodecatheon jeffreyi*, *Carex subfusca*).

A condensed appendix supplies some of the accessory information vital for understanding the flora. The map at  $1/5.8 \times 10^6$  could have been at  $1/3 \times 10^6$  and still fit the page but supply more information. A paleobotanical discussion adds to the material on geography, climate and floristic elements given by Porter (1963:6-8). Dorn's floristic discussion adds some interesting ideas but omits some of Porter's details. "Vegetation types" recognizes 47 plant associations that can be seen in the field. It avoids to a large extent both problematic casual explanations and physiognomic groupings. Soils limitations of several species are first mentioned here. Is grassland diversity slighted? Are data on these kinds of vegetation so lacking that no hierarchical arrangement at all is possible? desirable? References here are too selective. Rare and endangered species are listed by counties, and this list is a first for Wyoming. Early collectors are briefly mentioned. A systematic summary lists numbers of genera and species by division, subclass, and families. The glossary and drawings, by Jane L. Dorn, are excellent and very useful. The volumes are fully indexed. Eight pages of Additions conclude the manual.

Dorn's book is a valuable gift to the people of Wyoming and to botanists everywhere. Both groups have needed it. The high cost obviously makes the work less available. Unfortunately no one will benefit from the \$95 price. One must conclude that our present methods of getting floras written, or not written for North America, are wasteful of a valuable resource, namely skilled botanists — their industry, imagination and training. — Jack Major, Botany Department, University of California, Davis 95616.

## DUES INCREASE ANNOUNCEMENT

Because of increasing costs, the Council of the California Botanical Society has reluctantly voted to increase regular dues for 1979 from \$12 to \$15 and student dues from \$8 to \$10. Institutional subscriptions will rise from \$20 to \$22.

The size of MADROÑO has remained fairly constant since 1973, but cost per page has increased about 50 percent since then — from \$35 to \$53. These figures do not include expenses of the Treasurer, Secretaries, or Editor, which now total about \$1000 per year. Expenses have exceeded income since 1974, and our endowment fund has dwindled to the point that the current total assets of the Society would sustain only about six months of normal activity. Meanwhile, the number of life memberships, from which no further income may be anticipated, has increased to more than 30.

To insure a firm financial footing allowing the publication of 200–250 pages a year in MADROÑO, a dues increase now is absolutely necessary. Simultaneously, policies on editorial fees for longer papers are being clarified and made more stringent; and ways to lower publication costs are being sought. Nevertheless, it seems likely that small increases will be necessary as long as costs continue to inflate.

## REVIEWERS OF MANUSCRIPTS

The Editor thanks Barbara D. and Grady L. Webster, the members of the Board of Editors, and authors of papers for their cooperation and help in many ways. Special appreciation goes to John L. Strother, Alan R. Smith, and Alice Q. Howard, without whose generous assistance the mid-volume editorial transition would have been much more difficult.

Reviewers of manuscripts for Volume 25 are gratefully acknowledged below. Inadvertent omissions, if any, are sincerely regretted.

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