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The California Botanical Society dedicates volume 21 of Madroño to WALLACE ROY ERNST, former member of the Board of Editors and at heart a western botanist. His careful studies of the floral morphology of the Papaveraceae reflect original and fresh interpretations of the relationships among the genera of this difficult and complex family. In the Loasaceae and the genus *Lamourouxia* (Scrophulariaceae) his correlations of variation patterns in floral morphology with different pollination mechanisms represent a novel and pioneering effort in explaining the adaptive significance of these morphological patterns. The importance of his work in these and other groups lies not only in the solutions he offered to perplexing systematic and biological problems, but also in providing models of a broad and eclectic methodology and of a rigor of interpretation. His wide store of knowledge extended to a diversity of wild and cultivated plants and was available freely to colleagues and students. His pervasive love of plants was reflected in many ways, including a strong interest in gardening. Whenever the opportunity was available he exhibited a remarkable horticultural expertise and a highly refined aesthetic sense. Though a native Californian and one who loved the "wide open spaces" of California, Wally took a great pride in Washington, D.C. He delighted in showing the city and its numerous sights to visiting botanists from all parts of the world. His favorite tour was one of the city at night, including unusual perspectives of illuminated monuments and fountains—a memorable experience indeed. In many respects, he functioned as an unofficial host for the Department of Botany at the Smithsonian Institution and frequently entertained visiting botanists in his home. Wally's sense of perfection and his highly critical intellect were evident in every task he undertook, botanical or otherwise, and these qualities were particularly evident in the careful and meticulous critiques of manuscripts that he reviewed for others. Those who knew Wally Ernst miss him.

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ERRATA

p. 70. Second paragraph, third line, should read ". . . subject *of* the present paper . . ."

p. 71. Map: The small dot under the N of SAN BERNARDINO should be a square.

p. 423. Line one should read **Mimulus** for **Minulus.**

p. 455. Line one in Note should read **Licea deplanata** for *Licea deplanata.*

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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

SECOTIACEOUS FUNGI FROM WESTERN UNITED STATES

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It is always pleasing to obtain good material of any unfamiliar fleshy basidiomycete but particularly material of species which are at the center of discussion and conjecture, whose name is based on some obscure collection or whose name is based on collections inadequately de-described. These conditions apply for most any secotiaceous fungus, for it appears that collections are so irregularly made that affinities are always in dispute. So much of our knowledge of the bolbitiaceous and strophariaceous gastromycetes is based on single collections that Singer (1963) considers only one species of *Galeropsis, G. andina,* has been obtained in enough quantity to study it really extensively. When several collections of two species of so-called *Galeropsis* from widely separated areas came to hand, the opportunity was taken to critically review their taxonomy. The two fungi can be assigned to *Galeropsis cucullata* and *G. polytrichoides.*

A note on recent collections of another secotioid fungus, *Setchelliogaster,* appends the discussion.

Smith has recently (1965) described *Weraroa coprophila* (figs. 1–3) from Payette National Forest, Idaho, which is distinguished primarily by the lack of a spore-print, the color of the gleba, carpophore coloration, the spore dimensions and spore attachment to the basidium. He drew attention in his account of the similarity of his fungus to *Bolbitius cucullatus* Seaver & Shope, the type of which was examined by one of us (R.W.) during the tenure of a National Science Foundation Grant (G 13282–03779, made available to me while at the University of Michigan). The hymenial color of the type approaches "bone brown" of Ridgway and thus closely resembles that of many dark-spored agarics, i.e., *Psilocybe* spp. and *Stropharia spp.* Even under the microscope the spores have a slight purplish flush, and do not approach the gill colors found in either *Agrocye* or, as indicated by Singer (1963), in *Conocybe.*

Opportunities have been taken over several years by one of us (R.W.) to examine the types of many so-called bolbitiaceous fungi, both agaricoid and secotioid. *Bolbitius cucullatus,* it seems, is unique in this group in some of its anatomical details. The cheilocystidial shape (fig. 8), pore characters and gill color lead one to place this species along with Smith's fungus in the strophariaceous genus *Weraroa* as it is presently understood. *Galeropsis* (type species—*G. destertorum* Vel.), the genus to which *Bolbitius cucullatus* was transferred by Singer (1936), differs

markedly in gill and spore color; moreover it is considered by us (Watling, 1964), as it stands at present, to be an artificial assemblage of secotiaceous fungi, and a revision is being prepared.

The following new combination is proposed:

Weraroa cucullata (Seaver & Shope) Thiers & Watling, comb. nov. *Bolbitius cuculattus* Seaver & Shope, Mycologia 27:649. 1935. *Galeropsis cucullata* (Seaver & Shope) Singer, Beih. Bot. Centralb. 56:137. 1936. *Secotium longpipes* Zeller, Mycologia 33:209. 1941.

Pileus 9–35 mm high, 4.5–15 mm broad at the base, not or hardly expanding, typically conic often ending in a long, relatively sharp point which may curl on drying (fig. 7), wrinkled, fibrillose to fibrillose-scaly from remains of a floccose, "mustard yellow" (Color terms defined in Ridgway (1912) are placed in quotes.) to "ochraeous tawny" veil, dry, almost "apricot yellow" to "mustard yellow" when young becoming rich "chrome yellow" at the base, finally more "old gold" or "buffy citrine" at the base and "tawny" or near "buckthorn brown" toward the apex; margin incurved and tightly fitted around the stipe, joined in the young specimens to the stipe by a distinct, although fugacious, veil which leaves distinct flecks and which can be seen even in the most mature pilei upon careful examination; sometimes becoming free and expanded but retaining a frill of velar flecks. Stipe columella 50–110 × 1–4 mm, equal or slightly swollen at the base in larger specimens, dry with appressed fibrils at the apex or fibrillose toward the base from velar remnants, "pale ivory yellow" at apex and near "Saccardo's umber" to "sepia" downwards, then "ochraceous buff" to "clay color" at the apex with hint of cinnamon yellow but base unchanging. Gills fusing and anastomosing to form elongate compartments, "Verona brown" at first then becoming flushed with "warm sepia," finally "bone brown" except for white or pale yellow margin. Flesh soft, yellowish in pileus, more buff in stipe, particularly in the base, and drying bright yellow; odor and taste not unpleasant, mild.

Basidia 4-spored, hyaline to slightly colored in KOH, clavate or constricted about the middle, 25–35 × 10–12 μ, pedicellate. Basidiospores (fig. 9) 11.5–13 (14.5) × 6.5–7.5 (8) μ, elliptic to slightly amygdaliform, flattened in side view with a low shoulder over a prominent, although not large, apiculus, thick-walled, truncate by a slightly eccentric or apical pore, deep honey with a bister tint in water and KOH. Pleurocystidia rare, up to 25μ long, langeniform and slightly mucronate, mixed with more vesiculose cells up to 15μ broad, described by some as pseudoparaphyses. Cheilocystidia (fig. 8) numerous, forming a distinct fringe on the gill, filamentous-cylindric, hyaline or slightly yellowish, 35–70 × 5–7.5 μ; caulocystidia lageniform, up to 30 μ long and 5–8 μ broad at apex. Hymenophoral trama of irregularly arranged, ± enlarged cells some of which have yellow contents. Pileus trama of irregularly arranged, ± swollen cells and up to 16 μ in width with some colored con-
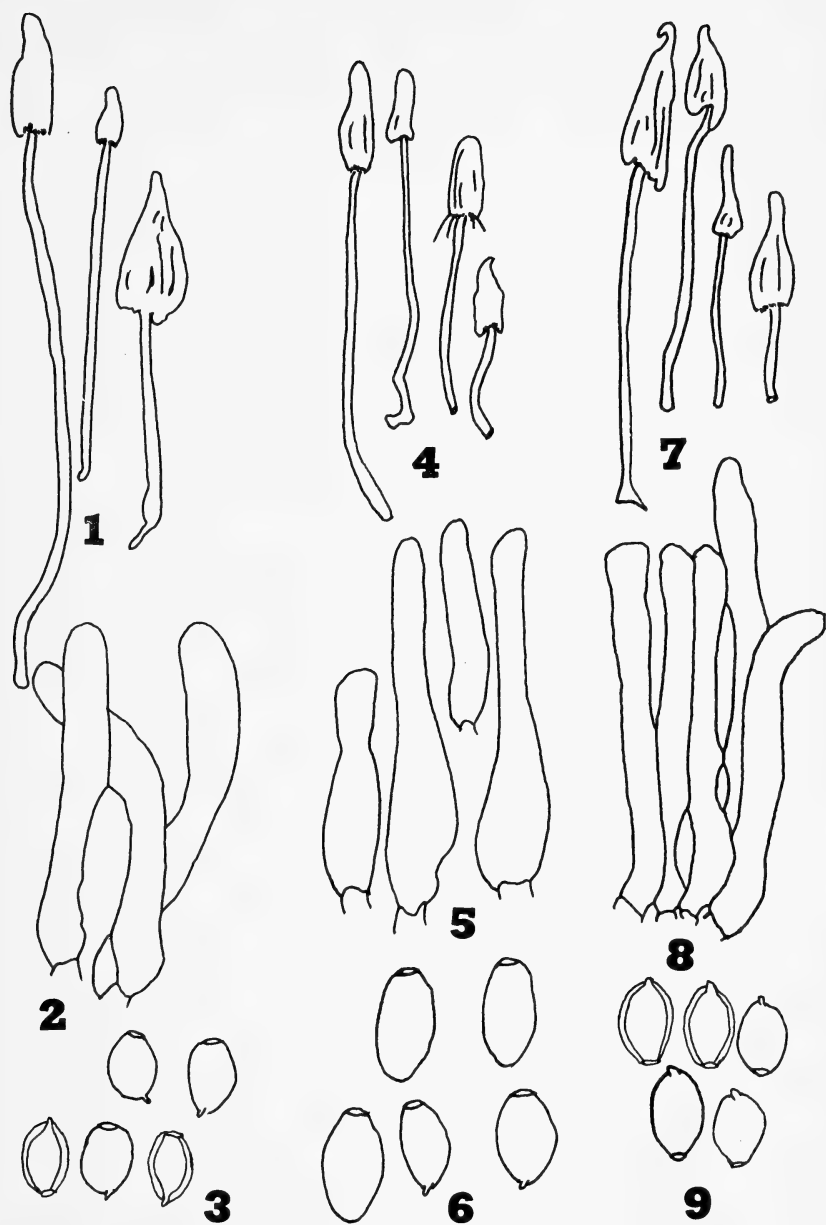
FIGS. 1–9: 1–3, *Weraroa coprophila;* 1, carpophores, × 1; 2, cheilocystidia, × 400; 3, basidiospores, × 900; 4–6, *Galeropsis polytrichoides;* 4, carpophores, × 1; 5, cheilocystidia, × 400; 6, basidiospores, × 1000; 7–9, *Weraroa cucullata;* 7, carpophores, × 1; 8 cheilocystidia, × 400; 9, basidiospores, × 800.

tents and covered in a distinct filamentous pellicle of ± colored, ± faintly colored granulose cells 2–3 μ in diam. and up to 35 μ long. Clamp connections infrequent but present.

On ground among grass and sedges, elev. 9,600 ft, University of Wyoming Summer Camp, near Laramie, Wyoming, 2 July 1929, *F. J. Seaver* a *F. Shope* (Type: MICH, ex herb. Univ. Colorado No. 249. A permanent slide is also in NY).

Gregarious, often in large troops, in boggy or marshy areas; elev. 7,500 ft., Haskner Creek, Sierra Madre, Carbon Co., Wyoming, June, 1950, *Smith 36246* (MICH); Hot Lake Area, elev. 6,300 ft., Lassen Volcanic Nat. Park, Shasta Co., California, 8 June, 1965, *Thiers 12923* (E, San Francisco State College); Silver Lake, elev. 7,200 ft., Amador Co., California, 6 June, 1966, *Thiers 16904* (E, San Francisco State College).

This fungus is very close to *Weraroa coprophila* as already indicated, and it may be necessary to reassess the position of the Idaho fungus when more material is collected. When the type collections of the two species are compared one gets the impression that *W. coprophila* (fig. 1) is a much more robust fungus. Smith (1965), however, has indicated three main differences between his taxon and *W. cucullata;* namely, the darkening stipe, the smoky grey to pale fuscous gills when fresh and the narrow spores (fig. 3). The first difference still applies, however the stipe is very dark at the base from the beginning in *W. cucullata;* the gills of *W. cucullata* are nearer "Verona brown" than has been indicated earlier and, after comparing the types of both species directly, one besides the other, the colors are indeed very close. The spores are slightly narrower but one must treat this with some caution for the statement is based on only a single collection. Similarities are also seen in cheilocystidial shape. Although Smith did not observe cheilocystidia, they are present in the type material of *W. coprophila* and resemble those of the type of *W. cucullata;* the contents are much more yellow in KOH in *W. coprophila.* Now that more and more collections are being made of gastromycetoid fungi, the full range of differences between individuals, which belong to the same taxon, are becoming evident.

Galeropsis polytrichoides was described by Zeller (1941) from collections made by W. B. Cooke on Mount Shasta, and, although not found for several years it has appeared in the last few collecting seasons in several localities elsewhere in California. A full description based on these fresh collections and subsequent microscopic examination is given.

GALEROPSIS POLYTRICHOIDES (Zeller) Zeller, Mycologia, 35:410. 1943. Figs. 4–6. *Secotium polytrichoides* Zeller, Mycologia 33:211. 1941.

Pileus 5–15 mm high, 3–10 mm broad at the base, narrowly to acutely conic, subacute or ellipsoid or pinched in at the top, attenuate or becoming truncate at the base at maturity, moist or slightly lubricous when fresh and immature but soon becoming dry; glabrous to silky

appressed fibrillose, becoming rimose, tan on the disc, darker towards the margin, becoming "sudan brown" to "bone brown" at maturity, drying with distinctly paler disc and in herbarium material the disc is "ochraceous tawny" to "yellow ochre" and the margin "date brown" to almost "umber"; margin joined to the stipe when young with white fibrils which darken slightly with age becoming very pale tan to ochraceous and separate at maturity, forming a fimbriate fringe with long dangling "ciliae" up to 10 mm long. Veil consisting of parallel hyphae 25–42 (68) μ long and 4.5–7 μ wide, fused or adhering tightly together. Stipe columella 30–90 mm $\times$ 1–2 mm, equal or slightly enlarged at the base, glabrous to silky fibrillose often showing a twisted pattern of fibrillosity, tan to "buckthorn brown", finally "Verona brown" and in dried material with a peculiar steel blue at the very base when seen in certain light. Gills joined by a few thin, anastomosing lamellar partitions, pale brown, on drying becoming "buckthorn brown" to "Prout's brown" to "raw umber" in dried material. Flesh pale tan in pileus and upper stipe, darker brown in lower stipe.

Basidia (1-, 2-) 4-spored 25–29 $\times$ 7–8 μ, short pedicellate, usually hyaline in KOH although some are distinctly yellow-brown. Basidiospores (fig. 6) 10–13 $\times$ 5–6 $\times$ 6–6 μ, ellipsoid, slightly flattened in side view and swollen upwards in face view (obovate of Zeller), slightly tapered, with an apical germ-pore, although fairly thick-walled not strongly pigmented. Pleurocystidia not found; cheilocystidia (fig. 5) lageniform to slightly subcapitate with apex 5–6 (8) μ broad and up to 25 μ long. Caulocystidia similar to cheilocystidia, although more variable in shape and often with a tapered apex, 20–42 $\times$ 18–12 μ (apex 8.5–10 μ or 1.5–2 μ). Hymenophoral trama consisting of interwoven, swollen hyphae up to 8.5 μ broad. Pileus trama filamentous, consisting of interwoven, swollen cells up to 17 μ broad with a distinctly filamentum cutrill of hyphae 2–4 μ in diameter. Clamp connections present.

Gregarious on moist ground, in boggy areas about streams, and in open seepage areas in conifer woodlands; Lassen Volcanic National Park, elev. 6,000 ft., Shasta Co., California, 3 July, 1965, *Thiers 12912* (E, San Francisco State College); Big Meadows Campground, elev. 7,000 ft., Calaveras Co., California, 30 May, 1966, *Thiers 16874, 16875,* and *16878* (E, San Francisco State College); Sagehen, California, 29 May, 1966, *D. McLaughlin* (E).

It must be pointed out that in all the collections examined the basidiospores are slightly larger than those indicated in the original description. However, authentic material collected on 24 July, 1941, by W. B. Cooke from a site only a few yards from the type locality and now in MICH under No. 136 Mycobiota of North America, Mycobiota of Mt. Shasta, California, is similar to our collections in every way. The type material has not been examined.

A very interesting observation which needs further ecological examina-
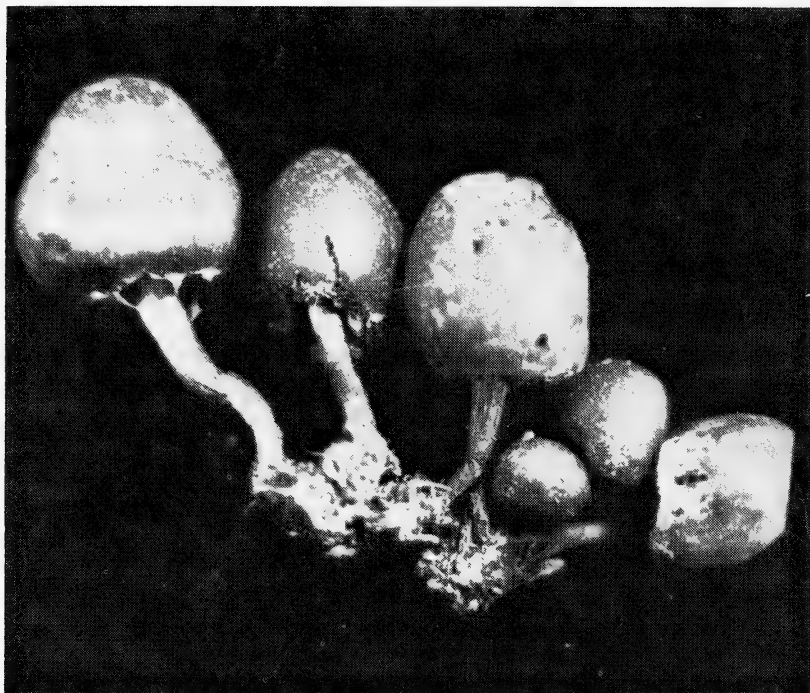
Fig. 10. *Setchelliogaster tenuipes,* × 1.

tion is that on these different occasions *Werarora cucullata* and *Galerop-sis polytrichoides* have been found at the same localities, in Lassen National Park, in Silver Lake area and in the type locality for *G. polytri-choides* (from which the type of *Secotium longipes,* =*W. cucullata* fide Singer, was also described).

We believe that all *Galeropsis*-like fungi are xerophytic derivatives, many of which are, perhaps, quite restricted in distribution, of a whole series of familiar agaric groups. It does not follow, however, that we think all secotiaceous fungi exhibit convergance in this way and are such end-products. We envisage these gastromycetes as paralleling the aquatic mammals; although the latter are all adapted to water and live successfully there, they can be quite unrelated, except that they are all mammals.

Several factors convince us that they are end-products: particularly the well-developed stipe, the well-developed cheilocystidia, the well-developed cuticular structure of the stipe and pileus, and the lamellar nature of the "gleba." It has been shown by one of us (R.W.) that in *Conocybe farinacea* dye entering a water column maintained in the stipe finally finds its way into the cheilocystidia and then into external, apical droplets. It is postulated that the cystidia which develop on the most exposed parts of the gill have developed in response to water uptake

phenomena. This will be expanded in greater detail elsewhere but the question must be posed here, if this is so what would be the part played by the cheilocystidia in such a fungus as *Galeropsis cucullata* and when would they begin to play a part in the economy of the gill-edge if evolved within the fruit body.

Should, therefore, the Secotiaceae or the majority of its members be placed alongside the units to which they are closest? Martin (1956) has already expressed similar ideas on the subject but from a more general point of view. Also should not *Weraroa* and *Galeropsis* be reorganized into genera which show some relationship to the geophiloid agarics and separate out the bolbitiaceous element, if one exists?

There is little doubt that these questions will cause much discussion and possibly disagreement and we sincerely hope it does, so that, when further material is available to us, it can be examined with new thoughts in mind; we are anxious to see more material to support our present approach.

Pouzar (1958) described the genus *Setchelliogaster* in 1958 basing the taxon on *Secotium tenuipes,* a fungus originally described by Setchell (1907) who collected it on the University of California campus at Berkeley, California. As early as 1950 Heim discussed the possible connection between this fungus and the bolbitiaceous agarics mainly on the basis of the cellular cuticle and spore color, but its affinities are still problematic. It is always difficult to make convincing comparative studies from limited herbarium material; we are, for example, ignorant of how the cuticle of this fungus actually develops. The development of such carpophore tissues is considered by Reijnders (1963) and Watling (1963) to be very important in the understanding of relationships between different groups of higher fungi. After examination of several herbarium collections it appears that the cuticular structure, although cellular, does not, in fact, develop in the same way as that of typical members of the Bolbitiaceae, e.g., *Conocybe farinacea, Bolbitius vitellinus,* or *Agrocybe praecox.* The cells of the outer layer are not pyriform with the pedicels developing from an active zone as described by Watling (1964), but more studies are required.

All the studies so far carried out were based on material from the small area embraced by Alameda and Santa Clara counties, California, although Singer and Smith (1959) mention a collection in the New York Botanical Garden from Oregon. The material described below is from San Francisco State College Campus and adjacent Marin Co. and are the only recent collections with full field notes made by one of us (H.T.). Grateful appreciation is extended to Mrs. Alix Wennekens for transmitting the collections from Marin Co.

SETCHELLIOGASTER TENUIPES (Setchell) Pouzar, Ceska Mykol. 12:34. 1958. Fig. 10. *Secotium tenuipes* Setchell, J. Mycol. 13:239. 1907. Gastro-

carp 5–25 mm high, 10–20 mm broad at maturity; convex to somewhat cylindric to globose when fully developed, never completely expanding, dry to moist, glabrous, colored near "Hessian brown" to "carob brown" when young, unchanging with age or becoming near "hazel" to "Kaiser brown" to "chestnut brown"; unchanging when bruised; margin typically incurved during all stages; when young typically attached to the stipe columella by white veil fragments, usually breaking free with age, but always remaining incurved to straight, entire to often eroded. Stipe-columella distinct, well-developed and apparent in all gastrocarps, 5–20 mm long, 3–4 mm broad, solid, extending through the entire gleba, more or less concolorous with the gleba or peridium, surface dry, more or less appressed fibrillose; white mycelium at the base. Gleba distinctly lamellose to broadly and highly irregular lacunose; lamellae plates very thin and fragile but not becoming pulverulent with age or when dried, typicallly folded, convolute and irregular, strongly intervenose with numerous, large air spaces interspersed, "ochraceous tawny" to "hazel" during all stages of development. Peridium less than 1 mm thick, fragile, concolorous with the surface, unchanging when exposed; taste and odor mild.

Basidia 27–38 $\times$ 8–12 μ, typically 2-spored with the sterigmata often large and strongly developed. Basidospores 15–17.6 $\times$ 9–11.2 μ, ovoid to subellipsoid, with well-developed sterigmal appendage, germ-pore typically present but often poorly differentiated and difficult to interpret, bright ochraceous to "tawny" in KOH and Melzer's, surface roughened, episporium with numerous small canals extending from inner-wall to surface and sometimes causing an obscure reticulation on the surface. Cystidia not seen, but often large, $\pm$ cylindric to fusoid cells with obtuse apices present in hymenium (possibly undeveloped basidia). Trama of lamellae plates irregular to subparallel, staining pale ochraceous to yellow in KOH and Melzer's. Peridial trama typically loosely interwoven; cutis differentiated as a layer of globose to vesiculose cells, "ochraceous tawny" in KOH and Melzer's, wall not incrusted, 12–18 μ in diam.

Gregarious in soil under *Eucalyptus globulus* and *Cupressus macrocarpa.* All collections except one made by Mrs. Alix Wennekens in vicinity of Mill Valley, Marin Co., California, *Thiers 21893, 21911, 29112, 21913, 21914,* and *21924.* An additional collection was made on the campus of San Francisco State College, San Francisco, California, *Thiers 12413.* All collections are deposited in the herbarium of San Francisco State College.

Setchell (1907) noted this fungus growing under *Eucalyptus globulus,* and *Quercus* spp. in the vicinity of *Eucalyptus* spp.. Our more recent collections are from under *Eucalyptus globulus* and *Cupressus macrocarpa;* the latter, although native to California, has presumably been planted in Marin Co. *Eucalyptus* spp. are mainly native of Australia, a few extending into the East Indies, and it is interesting to speculate

as to the habitat of Setchell's fungus. Various *Eucalyptus* spp. are widely planted now for ornament in Mexico, South Africa, the southern states of the United States, India, S.E. Asia, etc., and it is possible that native species of fungi have taken up association (mycorrhizal or not) with *Eucalyptus* when once introduced, e.g., *Scleroderma* in India (Thayer, et al., 1967), *Pisolithus tinctorius* in S. Africa (Thayer, et al., 1967). The qeustion arises as to whether *Setchelliogaster* is an endemic western North American fungus or has it been introduced along with the *Eucalyptus* trees? It has not been found in Australia yet, but there is every possibility that a fungus can exist for very long periods as a mycorrhizal associate simply reproducing vegetatively or being distributed along with seedlings of mature trees and rarely producing fruit bodies. The climate offered by California may be more favorable to the fungus than its native area, and so regular fruiting can be accomplished in its new environment.

LITERATURE CITED

HEIM, R. 1950. Le genre Galeropsis Vel. (= Cytarrophyllum Heim) trait d'union entre agarics and gastrales. Rev. Mycol. (Paris) 15:3–28.

MARTIN, G. W. 1956. On Lentodium squamulosum. Proc. Iowa Acad. Sci. 63:280–286.

POUZAR, S. 1958. Nove rody vyssich hub. Ceska Mykol. 12:31–36.

REIJNDERS, A. F. M. 1963. Les problems du development des carpophores des agaricales et de quelques groupes voisins. Hague.

RIDGWAY, R. 1912. Color Standards and color nomenclature. Washington, D.C.

SETCHELL, W. A. 1907. Two new hypogaeous Secotiaceae. J. Mycol. 13:236–241.

SINGER, R. 1936. Studien zur systematik der basidiomyceten. Beih. Bot. Centralb. 56:137–174.

————. 1960. Three new species of Secotiaceae from Patagonia. Persoonia 1:385–391.

————. 1963. Notes on secotiaceous fungi Galeropsis and Brauniellula. Kongl. Ned. Akad. Wetensk. 66:106–117.

————., and A. H. SMITH, 1958. Studies on secotiaceous fungi. III. The genus Weraroa. Bull. Torrey Bot. Club 85:324–334.

————. 1959. Studies on secotiaceous fungi. VI. Setchelliogaster Pouzar. Madroño 15:73–79.

SMITH, A. H. 1965. New and unusual basidomycetes with comments on hyphae and spore-wall reactions with Melzer's solution. Mycopathol. Mycol. Appl. 26:385–402.

THAYER, H. S., S. BALWART, and B. K. BAKSHI. 1967. Mycorrhizae in Eucalyptus. Indian Forester 93:756–763.

WATLING, R. 1963. *In* REIJNDERS, A. F. M. Les problems du development des carpophores des agaricales et de quelques groupes voisins. Hague.

————. 1964. Taxonomic characters of the Bolbitiaceae with particular reference to the genus Conocybe. Ph.D. thesis. Edinburgh Univ.

————. 1965. Observations on bolbitiaceae. 2. Conspectus of the family. Notes Roy. Bot. Gard. Edinburgh 10:287–323.

ZELLER, S. N. 1941. Further notes on fungi. Mycologia 33:196–204.

MYXOMYCETES NEW TO CRATER LAKE NATIONAL PARK, OREGON. I.

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During the winter months an over-abundance of precipitation generally in the form of snow is deposited in the High Cascades of Crater Lake National Park. Each year, the accumulated annual snow depth often exceeds 50 feet from November to May. Early in the spring slimemolds or Myxomycetes are frequently exposed as the snow melts away from forest litter and fallen logs. Decaying, moist organic matter such as bark, wood, and fallen twigs is characteristically noted as the habitat for Myxomycetes. In contrast, the summer is normally quite dry since very little rain falls during the months of July and August. However, during mid-August, 1968, succeeding storms (snow followed by several days of rain) brought 5.34 inches of precipitation which almost doubled any previous weather record set in the park for that month. Following the storms in late August and early September many specimens of slimemolds were collected. Interestingly, some of these are not commonly found in montane areas.

Most of the Myxomycetes reported thus far for Crater Lake National Park were recorded by Peck and Gilbert (1931) as occurring from the High Cascades to the Coast Range in northwestern Oregon. Exceptions include one species reported by Martin (1932), three new species described by Kowalski (1966, 1968), and I (Curtis, 1968) mentioned *Barbeyella minutissima* Meylan as well as eight additional species (Curtis, 1969) as being new to the State of Oregon.

All the specimens for this paper were collected on some form of decaying wood at elevations from 6,000 to 7,000 feet during the summer of 1968. Previously, this author (Curtis, 1969) indicated the presence of 43 different species in a preliminary report of the slimemolds from the park. The 11 species, included here, bring the total number of Myxomycetes found in Crater Lake National Park to 54. At least one collection of each species has been deposted in the University of Iowa Herbarium, Iowa City, Iowa and where possible, duplicate specimens have been given to the Crater Lake National Park Herbarium, Crater Lake, Oregon. The numbers for the collections are my own and they indicate only those specimens given to the University of Iowa Herbarium. The names of the organisms are those accepted by Martin (1949).

RETICULARIACEAE

Reticularia splendens Morgan. On a decorticated fallen log, Kerr Valley, 6,800 feet, *1522,* Sept. 4, 1968. Only two aethalia were found, one 5 mm and the other 13 mm in diameter. Both were brownish-copper colored with a white conspicuous margin about the base of the hypothallus. Spores were generally reticulate over two-thirds of their surfaces.

TRICHIACEAE

Arcyria globosa Schw. On a decorticated fallen coniferous log, west Goodbye Bridge area, 6,100 feet, *1479,* Aug. 30, 1968. Several small, short-stalked sporangia about 0.4 to 0.8 mm in diameter were scattered throughout the grooves of a decaying log. The peridium, in most cases, was fugacious while the capillitium and spores were the typical drab, ashen-grey color. Several specimens were collected at elevations from 6,000 to 7,000 feet.

A. incarnata (Pers.) Pers. On decayed wood, Kerr Valley, 6,800 feet, *1520,* Sept. 4, 1968. The sporangia were generally short stalked with a saucer-like base from which there was a greatly expanded, loose capillitum. Most were rosaceous to brown in color. This slimemold was found in many areas of the park.

STEMONITACEAE

Enerthenema papillatum (Pers.) Rost. On decayed wood, 2 miles west of Annie Springs, 6,000 feet, *1442,* Aug. 27, 1968. The sporangia, for the most part, had a total height ranging from 0.8 to 1.5 mm. The stipe expanded at the tip of the columella to form a disk from 0.05 to 1.5 mm in diameter. The peridium was fugacious and the spores appeared to be black in mass.

Stemonitis axifera (Bull.) Macbr. On decayed wood, west Goodbye Bridge area, 6,100 feet, *1476,* Aug. 30, 1968. This collection was obtained on the underside of a decayed stump. The sporangia were densely clustered, a bright rusty-brown, and 7–8 mm in height. The spores (about 5μ in diameter) were minutely warted.

S. palliada Wing. On decayed wood, northeast of Goodbye Bridge area, 6,100 feet, *1461,* Aug. 29, 1968. Small clusters of 5 to 10 sporangia (3–4 mm high) were found scattered over an area of approximately 4 square millimeters. The sporangia were slightly elongate-ovate in shape and lilaceous-brown in color.

S. hyperopta Meylan. On decayed wood, 2.4 miles southeast of Park Headquarters, 6,700 feet, *1423,* June 23, 1968. The sporangia were sometimes scattered but generally gregarious in small clusters, lilac-brown in color and 1–2 mm tall.

PHYSARACEAE

Leocarpus fragilis (Dicks.) Rost. On decayed wood, Kerr Valley, 6,800 feet, *1518,* Sept. 4, 1968. Sporangia were gregarious with a shiny, smooth, reddish-brown and very brittle peridium. The spores appeared black in mass.

Physarum leucopus Link. On needles and fallen twigs, west side of Munson Ridge, 6,900 feet, *1500,* Sept. 1, 1968. Sporangia were somewhat scattered. The peridium and stalk were frosty-white with lime deposits.

P. newtoni Macbr. On a decayed broken limb, northwest of Goodbye Bridge area, 6,200 feet, *1443,* Aug. 27, 1968. The two collections con-

tained hundreds of gregarious sporangia, stalked, bright rose-purple with red lime nodes. Most stalks were as long or longer than the diameter of the sporangium, thereby, differing from the descriptions of Lister (1925) and Martin (1949) who both indicated that the sporangia were short-stalked or sessile. The stalk was not translucent and therefore this Myxomycete could not be *Physarum roseum* Berk. & Br. Although this Myxomycete has been reported previously from Oregon (Peck and Gilbert, 1931), it is considered rare.

P. notabile Macbr. On bark and wood of a fallen coniferous tree, west side of Munson Ridge, 6,900 feet, *1498,* Sept. 1, 1968. This slime-mold was primarily sessile with a few sporangia merging into short plasmodiocarps while others had short, furrowed stalks. The peridium appeared to be uncrusted with an ashy, bluish-white lime deposit.

LITERATURE CITED

CURTIS, D. H. 1968. Barbeyella minutissima, a new record for the Western Hemisphere. Mycologia 60: 708–710.
————. 1969. New records of Myxomycetes from Oregon. I. Madroño: 20:75–77.
————. 1969. A preliminary report of the Myxomycetes of Crater Lake National Park, Oregon. Madroño: 20: 278–282.
KOWALSKI, D. T. 1966. A new species of Lamproderma from California. Mycologia 58: 808–810.
————. 1968. Three new species of Diderma. Mycologia 60: 595–603.
————. 1968. Observations on the genus Lamproderma. Mycologia 60: 756–768.
LISTER, A. 1925. A monograph of the Mycetozoa. 3rd ed. by G. Lister, Brit. Mus. Nat. Hist. London.
MARTIN, G. W. 1932. New species of slime molds. J. Wash. Acad. Sci. 22: 88–92.
————. 1949. North American Flora 1:1–190.
PECK, M., and H. GILBERT. 1931. Myxomycetes of northwestern Oregon. Amer. J. Bot. 19: 141–147.

NOTES AND NEWS

RATIBIDA COLUMNIFERA (COMPOSITAE) IN CALIFORNIA.—*Ratibida columnifera* has previously not been known from California, although it is widespread from British Columbia to Minnesota and south to Arizona, Mexico, and Tennessee. Recently we collected specimens of this species on dry rocky soil on the west side of Eagle Lake in Lassen Co. at the Eagle Lake Field Station (*Santamaria & Ediger 721,* CAS, UC). The local population consists of about 100 plants.—ROBERT EDIGER, Chico State College, Chico 95926, and NICK SANTAMARIA, Tahoe-Truckee High School, Truckee, California 95734.

TRANSFER OF PHRYGILANTHUS SONORAE
TO PSITTACANTHUS (LORANTHACEAE)

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When *Phrygilanthus sonorae* (Watson) Standley, a mistletoe from southern Baja California and adjacent Sonora, was first assigned to *Phrygilanthus* (Standley, 1919) the genus had representatives in both the Old and the New World. More recently, concepts have swung to the exclusion of Old World species (Barlow, 1962). Even the New World remnant is currently under considerable question as a coherent taxonomic unit. It is no wonder that the appropriateness of *P. sonorae* in this genus is also at issue. In particular, the possibility of the species belonging in *Psittacanthus* seemed to warrant exploration.

The major criterion of *Psittacanthus* at this time is the absence of endosperm in the mature fruit. All other Loranthaceae, *sensu stricto,* have endosperm. A recent study of Bhatnagar and Chandra (1968) has, however, demonstrated the presence of normal endosperm in *Psittacanthus cuneifolius* (Ruiz & Pavon) Blume from Argentina. While the systematic position of this species may be questioned, the reliability of the endosperm—less condition as the major generic criterion is equally insecure. Little doubt exists, nevertheless, that species lacking endosperm are to be included in *Psittacanthus*. The author, therefore, visited the area of Bahia de los Angeles, Baja California in early January, 1969, in order to study fruits in the fresh condition. Detailed results will be published elsewhere at some future date. The main result, however, is a confirmation of the complete absence of endosperm in mature fruits, the cotyledons having taken over the storage function. There is no alternative, therefore, to transfer this mistletoe to *Psittacanthus*. As the internal organization of the genus *Psittacanthus* has not been adequately worked out it is impossible to place *P. sonorae* accurately in relation to other species.

PSITTACANTHUS **sonorae** (Watson) Kuijt, comb. nov. *Loranthus sonorae* Watson, Proc. Amer. Acad. Arts 24:73. 1889. *Phrygilanthus* sonorae (Watson) Standley, Contr. U. S. Natl. Herb. 20:212. 1919. *Dipodophyllum diguetii* Van Tiegham, Bull. Soc. Bot. France 42:177. 1895?

Watson designated this species *"Loranthus (Psittacanthus) Sonorae."* While does this not constitute a nomenclaturally valid publication of *Psittacanthus sonorae,* it leaves no doubt as to Watson's ideas of affinity.

A noteworthy fact observed in several instances near Bahia de los Angeles was the hyperparasitism of the common desert mistletoe, *Phoradendron californicum* Nuttall, on *Psittacanthus sonorae* (fig. 1). In one case more than a dozen hyperparasitic plants of various sizes grew

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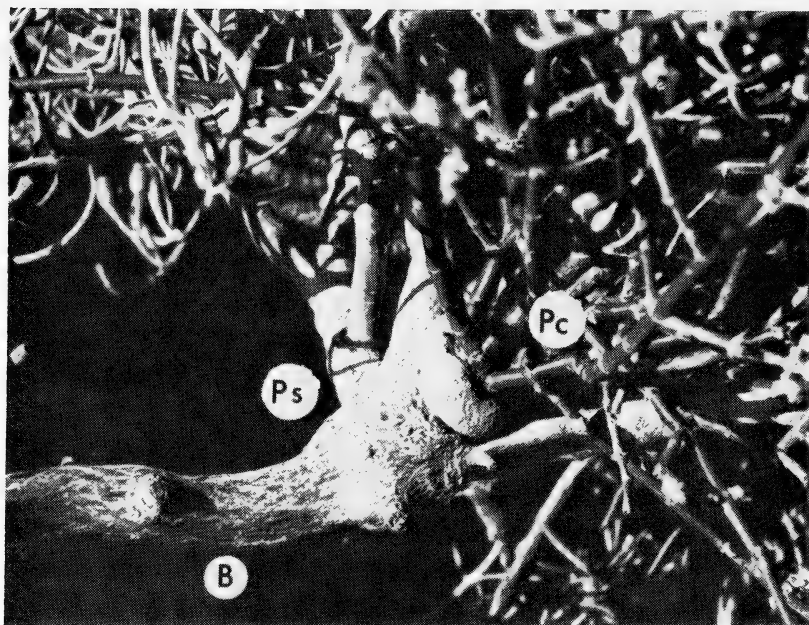
Fig. 1. Hyperparasitism of *Phoradendron californicum* (Pc) cn *Psittacanthus sonorae* (Ps), in turn parasitic on *Bursera microphylla* (B). The chalk-white bark belong to *Psittacanthus sonorae*.

on a single individual of *Psittacanthus sonorae.* The haustorial organs of the hyperparasite were surrounded by a crater-like formation of *Psitta-canthus* wood, and were greatly restricted when compared to their normal development on desert trees. A similar phenotypic variability in haustorial development has been reported in other cases of hyperparasitic mistletoes (Kuijt, 1964). This kind of hyperparasitism in mistletoes is undoubtedly an indication of the fact that local fruit-eating birds eat the berries of both species, the seeds thus being voided together. No evidence was seen of self-parasitism of *Psittacanthus sonorae* on members of the same species.

I would like to thank Reid Moran and P. D. Warrington for assistance in the matter of transportation, and F. A. Stafleu for nomenclatural advice.

LITERATURE CITED

BARLOW, B. A. 1962. Studies in Australian Loranthaceae. I. Nomenclature and new additions. Proc. Linn. Soc. New South Wales. 87:51–61.
BHATNAGAR, S. P., and S. CHANDRA 1968. Endosperm in Psittacanthus. Curr. Sci. 37:704–706.
KUIJT, J. 1964. Critical observations on the parasitism of New World mistletoes Canad. J. Bot. 42:1243–1278.
STANDLEY, P. C. 1919. Studies in tropical American phanerogams—No. 3. Contr. U. S. Natl. Herb. 20:173–220.

THE GENUS CHLOROPHYLLUM (LEPIOTACEAE) IN CALIFORNIA

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Chorophyllum molybdites (Meyer ex Fr.) Massee, the only species in the genus, was first reported from Southern California by Smith (1936), but without an accompanying description. While conducting a regional taxonomic study of *Lepiota* S. F. Gray and related genera (Sundberg, 1967), I verified the occurrence of *C. molybdites* in Southern California. Subsequent field work and herbarium studies indicated that its range extended much further north than Los Angeles, the northern limit reported by Smith (1936). Since *C. molybdites* is poisonous to some individuals (Singer, 1948; 1962; Smith, 1954), and often appears in cultivated areas such as lawns and gardens, it seems important to report on the characteristics and extended geographical distribution of California material.

A detailed morphological and anatomical description is included because few exist in the literature and published descriptions of California specimens are non-existent. Colors in quotation marks are those of Ridgway (1912). Where Ridgway's terminology may be unfamiliar to those lacking access to his color standard, approximations of his colors are included in general terms. Thirty-four collections were examined and deposited in either the herbaria of San Francisco State College or University of California, Berkeley. The distribution map (fig. 2) is based upon personal observations and data from herbarium specimens.

CHLOROPHYLLUM MOLYBDITES (Meyer ex Fr.) Massee, Bull. Misc. Inform. 1898: 136.1898.

Pileus 4.5–15.5 cm broad, ovoid to obtuse when young and unopened, becoming convex to broadly convex upon opening, finally plano-convex to uplifted in age, disc sometimes distinctly raised following expansion; margin incurved prior to rupture of the partial veil, remaining incurved upon opening, then becoming decurved, infrequently plane in age, finely lacerate at first, becoming rimulose to rimose, finally splitting deeply, often faintly striate (more obvious in age); surface moist but not viscid when young, becoming dry; cuticle continuous in the young button stage, during enlargement remaining continuous on the disc but becoming concentrically to irregularly diffracted and forming flattened to uplifted scales which often rub off easily toward the margin, infrequently splitting radially, the disc becoming diffracted scaly to areolate scaly in age with the scales composed in part of the flesh; exposed flesh (the remainder of the pileus surface in later stages) appearing appressed fibrillose to appressed fibrillose scaly, frequently shaggy fibrillose scaly to minutely squarrose scaly toward the margin (especially when young), the scales easily rubbing off and formed primarily by aggregation of the upper layers of radially arranged flesh fibrils, rarely with small amounts of cuticle at the tips; cuticle color variable in young unopened carpophores, reddish brown ("russet" to "rood's brown" to "liver brown" to "warm sepia") to brown ("sayal brown" to "bister"), often variegated and spotted with pale to dark buff shades ("light ochraceous-buff" to "antimony yellow" or "pale pinkish buff" to "cinnamon-buff"),

FIG. 1. *Chlorophyllum molybdites*, × ⅓, *Sundberg 1228*.

occasionally spotted dull pinkish vinaceous ("light cinnamon-drab") to pinkish brown ("fawn color") to blackish purple ("dark livid brown" to "warm blackish brown"); disc and cuticular scales often assuming somewhat different shades of reddish brown ("natal brown" to "vandyke brown" to "argus brown") or brown ("brussels brown" to "prout's brown" to "cinnamon-brown" to "tawny-olive") to becoming pinkish brown ("wood brown" to rarely "avellaneous") with age; surface flesh white at first, rarely spotted pale pinkish ("pale cinnamon-pink") to dark pinkish vinaceous ("brownish vinaceous") in older but unopened buttons, some-times with pinkish vinaceous ("light grayish vinaceous" to "light russet-vinaceous" or "light cinnamon-drab" to "cinnamon-drab") tinges near the margin, becoming brownish pink ("vinaceous-buff") to pinkish brown ("wood brown") to light pinkish gray (near "light drab") in age, usually unchanging or darkening slightly on bruising, rarely staining "cinnamon" at first, then pale reddish brown ("cacao brown") and finally becoming brown ("verona brown"); tips of scales composed of flesh becoming brown (dark "wood brown" to "snuff brown" to "saccardo's um-ber") in age. Flesh (2–) 5–13 mm thick at the disc, soft but solid; white to off-white ("tilleul buff") to tinged pinkish gray ("light drab"), cream to buff ("cream-buff" to "pinkish buff" to "cinnamon-buff") near the stipe apex and lamellae, stain-ing pinkish ("buff-pink") to "light pinkish cinnamon" at first, then darkening to "cinnamon" to "orange-cinnamon," and finally becoming reddish brown ("vina-ceous-russet" to "rood's brown" to "verona brown") when bruised, infrequently staining pale orange ("salmon color" to "orange-buff") or brown ("sayal brown" to "snuff brown") at first, then becoming reddish brown. Taste mild. Odor not distinctive.

Lamellae free, remote from the stipe even when young, sometimes forking and more rarely anastomosing near the stipe apex; close; 6–18 mm broad; fragile; thin at the margin, but moderately thick near the pileus flesh; white in mass when young, often even when first expanded, becoming pale green ("pale glaucous green" to "yellowish glaucous" to "water green") to gray-green ("court gray" to "tea green" to "celadine green") when mature, tinged near gold to olive-gold ("honey yellow" to "isabella color") where beginning to dry out naturally; margin entire and finely white fimbriate at first, becoming irregularly discontinuous and dark brown to almost black in age.Lamellulae in two to three tiers.
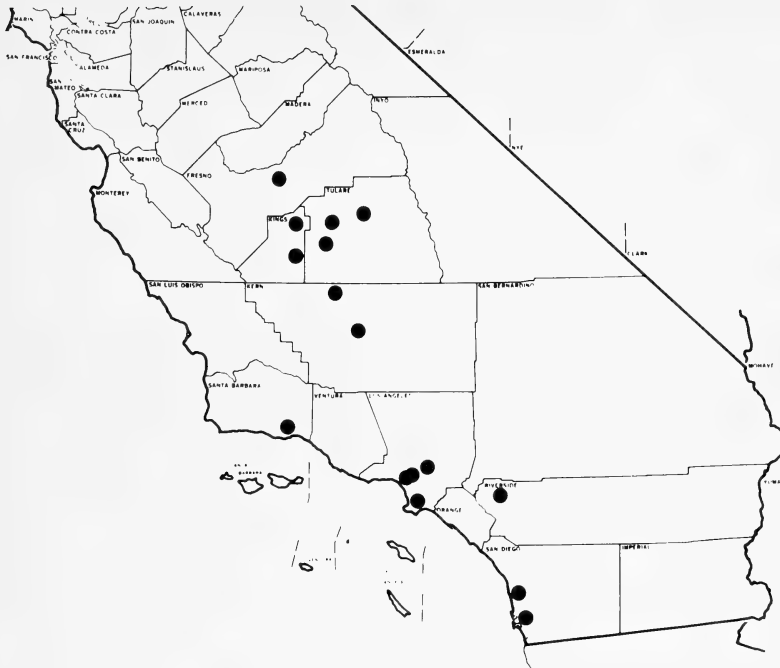
Fig. 2. Distribution of *Chlorophyllum molybdites* in California.

Stipe 5.7–12.0 cm long, 6–15 mm broad at the apex, equal to slightly enlarged below, rarely clavate; often but not always easily separable from the pileus; surface dry, silky to innately fibrillose throughout at first, sometimes appearing peronate-scaly above, areolate-splitting and shiny below in age, clothed at the base with a tightly appressed white mycelial growth; white to off-white ("tilleul buff") to rarely pale buff ("pinkish buff") above the annulus, sometimes streaked to tinted with pinkish vinaceous ("pale vinaceous-fawn" to "light russet vinaceous") to dark pinkish brown ("fawn color" to "army brown") to rarely dark pinkish gray ("benzo brown") shades, often superficially green ("water green" to "gnaphalium green") from spore deposits at maturity, staining buff ("cinnamon-buff"), then darkening to "cinnamon" to "vinaceous-cinnamon" when bruised; below the annulus white to near brownish pink ("avellaneous") and sometimes spotted with pinkish vinaceous ("pale brownish vinaceous") or purple-gray ("light brownish drab") at first, becoming pale to dark pinkish brown ("wood brown" to "fawn color" to "natal brown") to reddish brown ("cinnamon-brown" to "rood's brown" to "auburn" to "warm sepia") in age, whitish fibrils forming an overtone giving the darker colors a streaked appearance; stuffed, becoming hollow; pith fibrils white to off-white ("tilleul buff"); cortex "tilleul buff" to infrequently brownish pink ("vin-aceous-buff" to "avellaneous"), sometimes concolorous with the surface where ad-jacent to it, staining pale buff ("pinkish buff"), then buff ("cinnamon-buff" to "pinkish cinnamon") to "cinnamon," then pale orange ("orange-buff") to "orange-cinnamon," finally becoming pale to dark reddish brown ("vinaceous-tawny" to "russet" to "walnut brown" to "vandyke brown") where bruised.

Annulus superior to infrequently median, attached and sleeved above, flaring below, typically immovable when fresh, often becoming free and movable on drying, thick and solid, complex and having three frequently indistinct flanges;
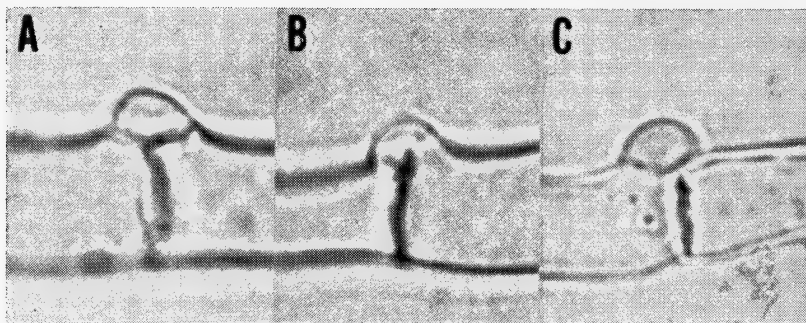
Fig. 3. Clamp connections from the pileus trama of *Chlorophyllum molybdites:* a, *Sundberg 1251;* b, c, *Sundberg 1229.* All approximately × 2,100.

upper surface white and often spotted with pinkish vinaceous ("pale vinaceous-fawn" to "light grayish vinaceous") to pinkish gray ("ecru drab") shades at first, becoming pinkish brown ("avellaneous" to "wood brown") in age, sometimes tinged green ("water green" to "gnaphalium green") from the spore deposit, undersurface brown ("snuff brown" to "prout's brown") to reddish brown (warm sepia") near the margin and white with infrequent pinkish vinaceous tinges elsewhere.

Spore deposit pale green ("pale glaucous green" to "deep lichen green" to "water green" to "corydalis green") to gray-green ("mineral gray" to "vetiver green" to "gnaphalium green" to "sage green" to "celadine green") to almost gray ("storm gray") when fresh, occasionally as light as "cream-buff," becoming slightly darker green ("tea green" to "andover green" to "lincoln green") on drying, fading in age to a shade of dark gold to brownish gold ("yellow ocher" to "mars yellow").

Spores (7.7–) 10.3–12.2 (–13.5) × (6.3–) 7.7–9.0 (–10.9) μ, ovoid to very short ellipsoid, apex truncate, infrequently at a slight angle, inequilateral in side view, smooth, hilar appendix present, apical pore present giving some a notched appearance, wall thick, aguttulate or uniguttulate, entire spore dark blue in cresyl blue, pale yellowish green to pale yellowish brown in KOH when viewed singly (color most obvious in wall), weakly to strongly dextrinoid (pale yellowish orange to reddish orange to reddish brown) when viewed singly in Melzer's reagent.

Basidia (24.2–) 29.4–44.8 (–61.5) × 9.0–12.9 (–14.1) μ, mostly 4-spored, occasionally 3- or 2- or 1-spored but not notably different in size, clavate, some with narrow elongate bases, often granulose, hyaline to rarely tinged pale yellow to pale yellowish brown in KOH, yellowish to pale to deep yellowish orange in mass and hyaline to pale yellowish when viewed singly in Melzer's reagent.

Cheilocystidia (18.0–) 21.9–47.4 (–62.4) × (9.5–) 10.3–25.5 μ, abundant, sometimes scattered in fascicles along the lamellae margin, arising as hyphal tips or branches, narrowly to broadly clavate to sphaeropedunculate to subsaccate, infrequently with angular to rostrate apices, rarely covered with an amorphous material, bases often narrow and elongate, walls thin to unevenly thickened and yellowish when viewed singly in KOH, hyaline to yellowish brown in mass and hyaline to pale yellowish to pale yellowish brown when viewed singly in KOH, concolorous in Melzer's reagent. Pleurocystidia absent.

Lamellae trama composed of loosely interwoven hyphae, hyaline in KOH, hyaline to pale yellowish in Melzer's reagent; oleiferous hyphae often present; subhymenium cellular, segments small, compact, concolorous with the trama proper.

Pileus trama composed of tightly or more often loosely interwoven hyphae, segments 5.1–15.4 μ wide, hypodermal segments usually shorter and broader than cuticular elements, sometimes swollen and enlarged, rarely almost globose, entire trama hyaline to infrequently yellowish to yellowish brown in KOH, pale yellow to pale yellowish orange in mass and hyaline to pale yellowish to pale yellowish orange

to rarely pale yellowish brown when viewed singly in Melzer's reagent (segments of the same hyphal strand may differ in color) ; oleiferous hyphae present, hyaline to pale yellowish to rarely pale yellowish green in KOH.

Cuticle scattered in patches due to diffraction caused by pileus expansion, composed of tightly and irregularly arranged more or less upright hypae and hyphal tips, appearing somewhat turf-like, longer hyphae or at least the apical portions frequently repent and forming a thin, often loosely arranged, appressed and interwoven layer above the upright elements; terminal segments usually not well differentiated, length extremely variable, (18–) 20.6–86.2 (–132.4) $\times$ (2.6–) 3.8–9.0 (–15.8) μ, often arising as hyphal branches, rarely ventricose to slightly enlarged above, very seldom clavate, apices usually rounded, infrequently tapered to mucronate or rostrate at the apex, walls irregularly flexuous, thin to unevenly thickened, especially in the upright segments, rarely encrusted, some appearing striated in KOH, infrequently with a fine sparse granular content; subterminal segments often with thickened walls; hyaline where thin to yellowish brown to rarely reddish brown where thick in mass and hyaline to pale yellowish to pale yellowish brown when viewed singly in KOH, pale yellowish orange to orange-brown to pale reddish brown in mass and hyaline to pale yellowish to pale to dark yellowish brown when viewed singly in Melzer's reagent.

Clamp connections always present in the pileus trama of both young and old specimens, often rare and never at every septum, seen at the base of some cheilocystidia in one collection, apparently lacking elsewhere.

A pale yellowish to pale yellowish brown pigment, which is soluble in water but not alcohol, diffuses from the tissue during sectioning preparation.

Habit and habitat: Scattered to gregarious in laws or more rarely in garden soils, usually arranged in fairy rings. July through September.

Specimens examined. Fresno Co.: *Sundberg, 1217, 1220, 1222 1246–1248, Thiers 20742.* Kern Co.: *Sundberg 1236, 1237, Thiers 20740.* Kings Co.: *Sundberg 1230–1232, 1234.* Los Angeles Co.: *Floyd* s. n., *Sloan,* in 1966, 1967, *Brubaker* s. n. Riverside Co.: *Smith* s. n. San Diego Co.: *McLean* s.n., *Miller* s. n. Santa Barbara Co.: *Walker* s. n. Tulare Co.: *Sundberg 1225, 1227–1229, 1243–1245, 1249–1251, Thiers 20741.*

DISCUSSION

Chlorophyllum molybdites differs from closely related taxa by its colord spores. It appears most similar to *Lepiota rachodes* (Vitt.) Quel., but lacks the palisade cuticle of pyriform cells foud in the latter. Its summer and early fall fruiting habit is also distinctive.

As indicated in Fig. 2, *C. molybdites* is apparently restricted to the southern part of California. It may possibly occur further north than present data indicates, especially in the Central Valley, since it has been reported from much more northerly latitudes elsewhere (Groves, 1962; Singer, 1948; 1962; Smith, 1954).

California material studied in the fresh condition appears to be *C. molybdites* var. *marginata* A. H. Smith, but the lamellae margins are white in the button stage rather than dark as indicated in the original description of the variety (Smith, 1949). However, the margins do darken to almost black as the carpophores mature.

The presence of clamp connections (fig. 3), also recently noted in

Arizona collections by C. Leathers (personal communication to H. D. Thiers), is of interest since Singer (1948; 1962), Smith (1949), and Smith (1954) all reported their absence. Preliminary anatomical examination of collections from other parts of the United States (Sundberg and H. D. Thiers, in preparation) has verified the presence of clamp connections in this species. This evidence indicates that they were probably overlooked by previous workers and their absence cannot be used, as had been by Singer (1948; 1962), in support of the generic segregation of *Chlorophyllum* from closely allied species of *Lepiota* sensu lato.

I wish to thank H. D. Thiers for guidance leading to and during this study and for his critical comments on the manuscript. The criticisms of K. Wells and G. Breckon were most appreciated. Financial support for field work was provided by the Department of Botany, University of California, Davis.

Note added in proof. Recently clamp connections were reported in *C. molybdites* from Tennessee and Israel (Heinemann, P. Bull. Jard. Bot. Etat 38:195–206. 1968) and from Africa and South America (Singer, R. Beih. Nova Hedwigia 29:1–405. 1969).

LITERATURE CITED

GROVES, J. W. 1962. Edible and poisonous mushrooms of Canada. Queen's Printer, Ottawa.
RIDGWAY, R. 1912. Color standards and color nomenclature. Washington, D. C.
SINGER, R. 1948. New and interesting species of basidiomycetes. II. Pap. Michigan Acad. Sci. 32:103–150.
————. 1962. The Agaricales in modern taxonomy. 2nd ed. J. Cramer, Weinheim.
SMITH, A. H. 1949. Mushrooms in their natural habitats. Sawyers, Portland.
SMITH, C. O. 1936. Lepiota morgani in Southern California. Mycologia 28:86.
SMITH, H. 1954. A revision of the Michigan species of Lepiota. Lloydia 17:307–328.
SUNDBERG, W. J. 1967. The family Lepiotaceae in California. Master's thesis. San Francisco State College.

POLYPHYLETIC ORIGIN OF TETRAPLOID POPULATIONS OF GUTIERREZIA SAROTHRAE (COMPOSITAE)

OTTO T. SOLBRIG

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The widespread western North American species *Gutierrezia sarothrae* (Compositae—Astereae) possesses two chromosomal races: a diploid ($n = 4$) race that is the most common, and a less common tetraploid ($n = 8$) race, that comprises approximately 20% of populations. Both races are morphologically very similar. Although the polyploids tend to have statsistically slightly larger pollen and stomata, there is no single character by which the two races can be separated (Solbrig, 1964). This is due to a great deal of variability in both the diploid and tetraploid forms. Neither can the two races be separated on the basis of geographical distribution since the tetraploid populations occur interspersed throughout the distribution of the species.

In a previous paper (Solbrig, 1964) I suggested that polploids may have arisen from diploids more than once. This would tend to explain their morphological diversity and geographical distribution. The major reason for making this suggestion, was that at any one locality where polyploids occurred, they tend to show the expected "gigas" characters in relation to the diploids of that area. However, the diploid populations of another region are not necessarily smaller. In the present paper further evidence in favor of the hypothesis of a polyphyletic origin of the polyploid populations is presented as a result of a numerical analysis of relationships among the populations.

Materials and Methods

The data collected in previous studies (Solbrig, 1960; 1964; 1965) were utilized in the present analysis. The OTU is the breeding population. The characters used are the mean value obtained after measuring 13 characters in 50 individual plants chosen at random in a population. For this study data from 15 diploid $(n = 4)$, 5 tetraploid $(n = 8)$ and 14 populations of unknown chromosome number of *G. sarothrae,* as well as 3 tetraploid $(n = 8)$, 1 hexaploid $(n = 12)$ and 1 of unknown chromosome number of *G. bracteata;* 1 diploid $(n = 4)$ population of *G. serotina* and 1 hexaploid $(n = 12)$ population of *G. serotina* and 1 hexaploid $(n = 12)$ population of *G. californica;* and 2 tetraploid populations of *G. microphala,* were utilized (table 1). The data were processed on an IBM 7090 Computer at the University of Michigan Computing Center.

Two numerical analyses were used. One, the Prim Network (Prim, 1957), is essentially a coefficient of similarity in a multidimensional space that produces a linear clustering of OTU's. The second is a program that produces a phylogenetic tree following the principle of parsimony, where species are derived from a given ancestor along the most parsimonious paths (Kluge and Farris, 1969; Wagner, 1961).

Results

Figure 1 depicts graphically the Prim Network that was obtained. It can be seen that the variability of the species follows three major lines. First, a line that is characterized by a tendency towards smaller heads with a reduced number of florets per head and that culminates in populations of *G. microcephala* that have only 1 ligulate and 1 tubular florets. Of the 16 populations in this line, 6 are diploid, 3 are tetraploid (including both populations of *G. microcephala*) and seven are of unknown chromosome number. Ten of the populations come from the southeast area of the distribution of these species, that is, the area comprised by Colorado, New Mexico, Oklahoma and Texas. The other six populations come from Utah, Wyoming, Kansas and South Dakota.

The second direction exhibited by the pattern of variation is toward an increase in head size with accompanying increase in the number of florets. Only three populations of *G. sarothrae* are involved, together
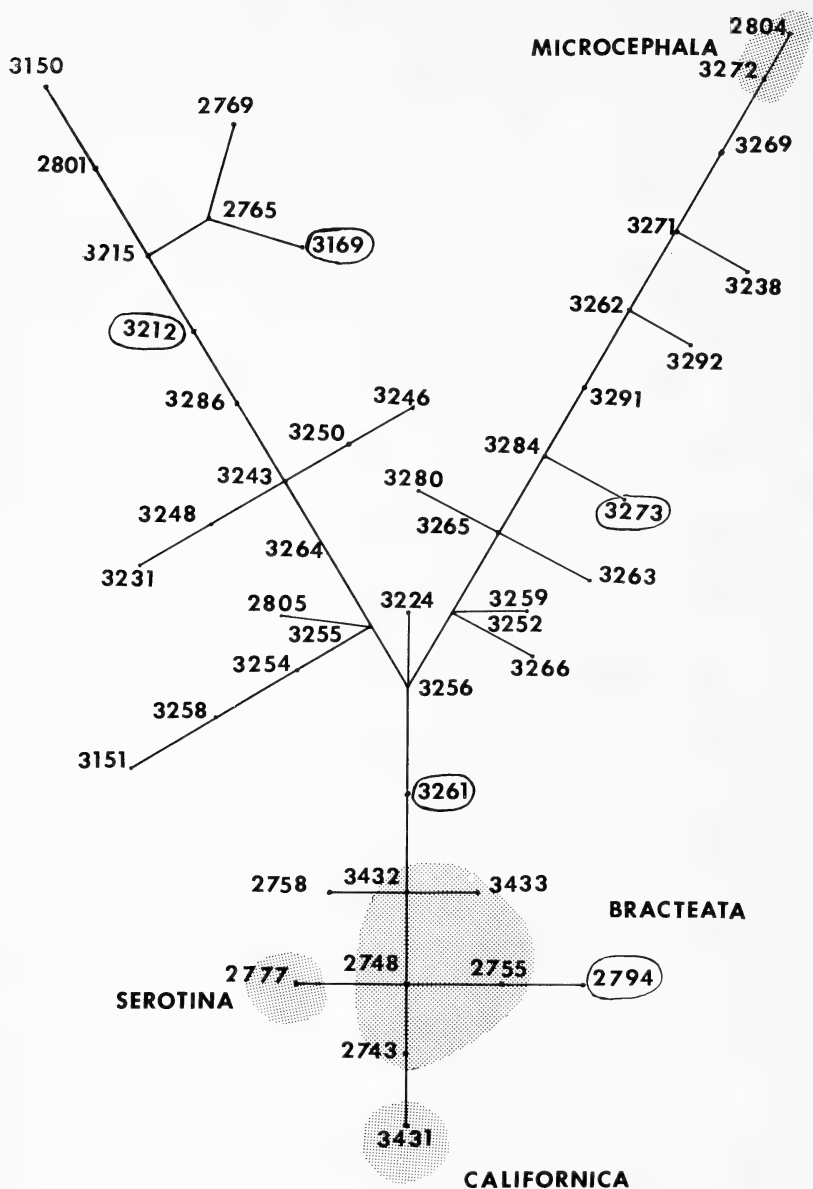
FIG. 1. Prim network of the populations studied. The lines separating any two populations represent the phenetic distances. The angles are arbitrary, and distances between populations other than along the drawn lines non-significant. All populations that are not shaded are *Gutierrezia sarothrae,* those encircled in a balloon are tetraploid with $n = 8$; all other *G. sarothrae* are either diploids or of unknown chromosome number (see table 1).

TABLE 1. LOCALITIES SAMPLED FOR THIS STUDY AND CHROMOSOME NUMBERS.
Collection numbers are those of the author and specimens are in the Gray Herbarium.

Gutierrezia bracteata. California: Cache Creek, *3432;* Arroyo del Puerto, *3433,* n = 8; Arroyo del Puerto, *2743,* n = 8; Pond Ranch, *2748;* Temblor Range, *2755.*
Gutierrezia californica. California: Point Bonita, *3431,* n = 12.
Gutierrezia microcephala. Arizona: Hyde Park, *2804;* New Mexico: White City, *3272.*
Gutierrezia sarothrae. Arizona: Payson, *2794,* n = 8; Ash Fork, *2801,* n = 4; Hyde Park, *2805,* n = 4. California: near Temecula, *2768,* n = 4; near Chula Vista; *2776,* n = 4; near Rancho Santa Fe, *2769,* n = 4. Colorado: Colorado National Monument, *3261,* n = 8; Colorado National Monument, *3262,* n = 4; near Salida, *3263;* near Fountain, *3264;* near Trinidad, *3265.* Idaho: near Dubois, *3254,* n = 4; near Pocatello, *3255.* Kansas: near Medicine Lodge, *3292,* n = 4. Montana: Glendive, *3248;* Sanders, *3250,* n = 4. Nebraska: Roscoe, *3224,* n = 4; near Chadron, *3231.* New Mexico: near jct. highways 285 and 286, *3169,* n = 8; near Glenwood, *3215;* near Las Vegas, *3266;* near Roswell, *3269,* n = 4. North Dakota: Dickinson, *3243;* Little Missouri R. and highway 85, *3246.* Oklahoma: near Bouse Jct., *3291.* South Dakota: near Rapid City, *3238.* Texas: near Van Horn, *3212,* n = 8; near White City, *3271,* n = 4; near Van Horn, *3273,* n = 8; near Alpine, *3280,* n = 4; near San Angelo, *3284;* near Abilene State Park, *3286,* n = 4. Utah: near Boulder, *3150,* n = 4; near jct. highways 24 and 6, *3151,* n = 4; near Ogden, *3256;* near Vernal, *3258,* n = 4; near Talmadge, *3259.*
Gutierrezia serotina. Arizona: Tucson, *2777,* n = 4.

with all the populations of *G. bracteata, G. californica* and *G. serotina* that were analyzed. Two of the three populations of *G. sarothrae* that exhibit this pattern of variation are tetraploid; in addition all populations of *G. bracteata* and *G. californica* are either tetraploid or hexaploid, so that of 10 populations involved, 2 are hexaploid, 5 are tetraploid, 2 are diploid and one is of unknown chromosome number. All but one of the populations grow in either Arizona or California. The exception is population *3261*, a tetraploid *G. sarothrae* from Grand Junction, Colorado.

The remaining 21 populations, all of them *G. sarothrae*, comprise what may be called "typical" *sarothrae*. Geographically they come from throughout the range of the species, including California and Texas. Chromosomally 8 populations are diploid, 2 tetraploid and eleven are of unknown ploidy level.

Figure 2 depicts the phylogeny produced by the Farris program. For purposes of this analysis, population *3256* of *G. sarothrae* which exhibits characters at the center of the species variability in the Prim Network was chosen arbitrarily as exhibiting the most primitive characters. Runs were made using other populations as primitive. This produced different shaped trees, but no variation in the basic relations of the populations to each other. According to the phylogenetic tree produced by this program, there are three evolutionary tendencies within *G. sarothrae* that follow roughly the lines of variation uncovered by the PRIM diagram: one is a tendency towards smaller heads with fewer flowers that culminates in *G. microcephala;* the other is a tendency towards larger heads that culminates in *G. bracteata* and *G. californica,* and the third is also
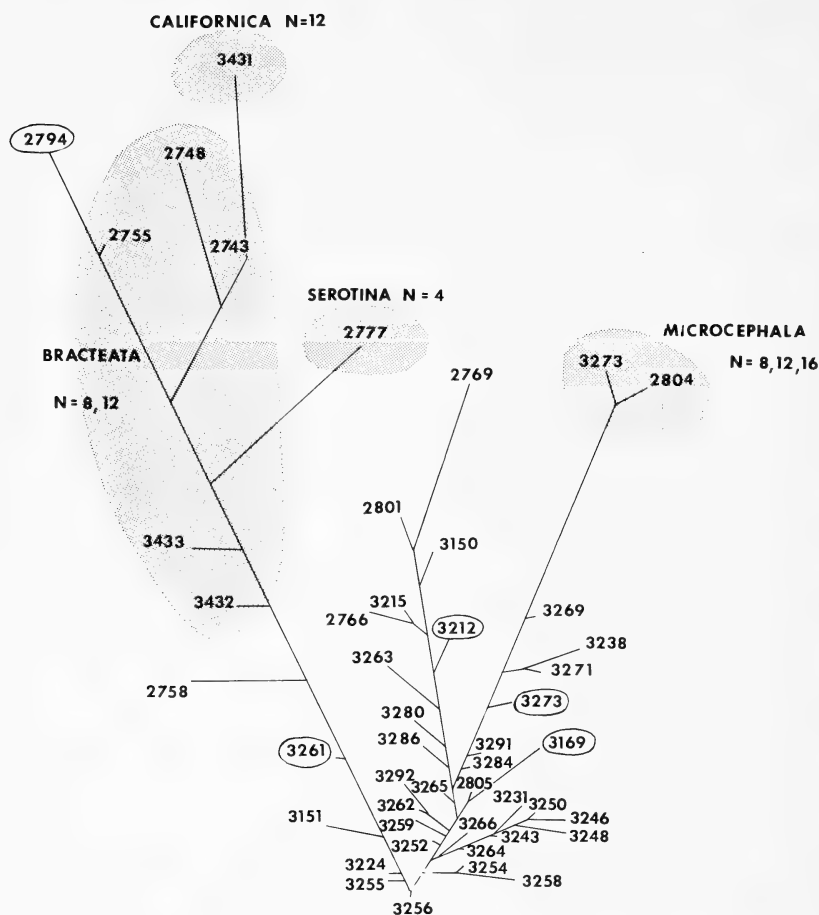
Fig. 2. Hypothetical phylogeny following the most parsimonious lines drawn by a computer following a program devised by J. A. Farris (Kluge, 1969). Non-shaded populations are *G. sarothrae;* those included in a balloon are tetraploids with n = 8; all other *G. sarothrae* are either diploid or of unknown chromosome number (see table 1).

a tendency towards larger plants with larger heads not connected to the previous one. *Gutierrezia californica* appears to be the most modified of the species analyzed; the line that culminates in *G. microcephala* follows. These numerical indices tend to confirm the taxonomic treatment with one exception: population *2794* from Arizona appears to be related both in its pattern of variation and in its hypothetical phylogenetic history to *G. bracteata,* and probably should be classified as such. Blake in the Flora of Arizona (Kearney and Peebles, 1942) classified the large headed Arizona populations as *G. californica* (= *G. bracteata*). This would extend the range of this species, previously considered by me (Solbrig,

1965) as restricted to California and Baja California. Of greater interest for our present discussion, is that polyploid populations are found in all three of the phylogenetic lines.

DISCUSSION

The present numerical analysis tends to confirm the hypothesis that tetraploid populations of *G. sarothrae* have arisen and become established in more than one instance. This would explain the geographical dispersion of the tetraploids, and also the fact that they cannot be separated as a group from diploids also taken as a whole. However, when tetraploid populations are compared to the diploid populations to which they are most closely related within each of the three major lines of variability, they show the expected "gigas" characteristics (fig. 1). This analysis permits us to obtain a reasonable idea of the evolutionary patterns within a species. From the "typical" or "modal" population it appears that a line with larger heads and more flowers developed in the southwest United States that eventually lead to the formation of three species: *G. serotina, G. bracteata* and *G. californica*. On the other hand, in the southeast part of the range, forms with narrower heads and fewer flowers were selected that lead to the formation of *G. microcephala*, a species that eventually became widespread over all of southern United States and northern Mexico. It is impossible to affirm that polyploidy provided the isolating barrier in these instances and aided the selective trends, but it appears to be a plausible hypothesis.

I wish to thank J. S. Farris and A. K. Kluge for assistance and for the loan of the program decks used.

LITERATURE CITED

KEARNEY, T. H., and R. H. PEEBLES. 1942. Flowering plants and ferns of Arizona. U. S. Gvt. Printing Office, Washington.

KLUGE, A. K. and J. S. FARRIS. 1969. Quantitative phyletics and the evolution of Anurans. Syst. Zool. 18:1–32.

PRIM, R. C., 1957. Shortest connection networks and some generalizations. Bell System Tech. J. 36:1389–1401.

SOLBRIG, O. T. 1960. Cytotaxonomic and evolutionary studies in the North American species of Gutierrezia (Compositae). Contr. Gray Herb. 188:1–63.

————. 1964. Infra-specific variation in the Gutierrezia sarothrae complex (Compositae-Astereae). Contr. Gray Herb. 193:67–115.

————. 1965. The California species of Gutierrezia (Compositae-Astereae). Madroño 18:75–84.

WAGNER, W. H. 1961. Problems in the classification of ferns. In Recent Advances in Botany 1:841–844.

XYLEM MONOTERPENES OF PINUS PONDEROSA, P. WASHOENSIS, AND P. JEFFREYI IN THE WARNER MOUNTAINS OF CALIFORNIA

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In the Warner Mountains of northeastern California, the subsection Ponderosae of the genus *Pinus* is represented by three species: ponderosa pine (*Pinus ponderosa* Laws.), Washoe pine (*P. washoensis* Mason & Stockwell), and Jeffrey pine (*P. jeffreyi* Grev. & Balf.). Washoe was initially reported to be confined to a small stand at Patterson Meadow at the Warners' southern end (Haller, 1961), but it will probably be greatly enlarged by more recent studies. Ponderosa is found quite extensively throughout the area. Jeffrey grows considerably less extensively than ponderosa but much more extensively than Washoe, though limited to the southern end of the Warners (Critchfield and Little, 1966). Botanically, the area is of interest because it lies on the northeastern fringe of the range of Jeffrey pine and contains one of the isolated stands of Washoe.

The monoterpene composition of the xylem resin of ponderosa is extremely variable, while that of the other pines is much less variable and can be somewhat stereotyped (Mirov, 1961; Smith, 1964; 1967). The composition of an average ponderosa pine from low elevation in the Warners is about 7% α-pinene, 25% β-pinene, 46% 3-carene, 10% myrcene, 9% limonene, 1% β-phellandrene, and 2% terpinolene. A normalized composition for average Washoe is 5% α-pinene, 10% β-pinene, 65% 3-carene, 15% myrcene, 1% limonene, 1% β-phellandrene, and 3% terpinolene and some trace components; Jeffrey pine is about 95% heptane, 2% nonane, and the remaining 3% divided among several of the monoterpenes.

Individual ponderosa pines have been found whose monoterpene composition falls within the average composition of Washoe. A few such trees have been found in low-elevation stands in the northern Warners and in stands in the central and northern Rocky Mountains. These ponderosa stands in the eastern portion of its range often are classified as *P. ponderosa* var. *scopulorum* Englem.

In 1965–66 a study was made of the monoterpene composition of the xylem resin of ponderosa or Washoe or both in three areas of the Warner Mountains (fig. 1) to determine a, range of stands which could be classified as Washoe on the basis of monoterpene composition, b, how often individual trees in ponderosa stands showed the full characteristics of Washoe monoterpenes, and c, the possibility of hybridization among the three species. Jeffrey pine was studied in the southern area where it grows with ponderosa or Washoe or both.
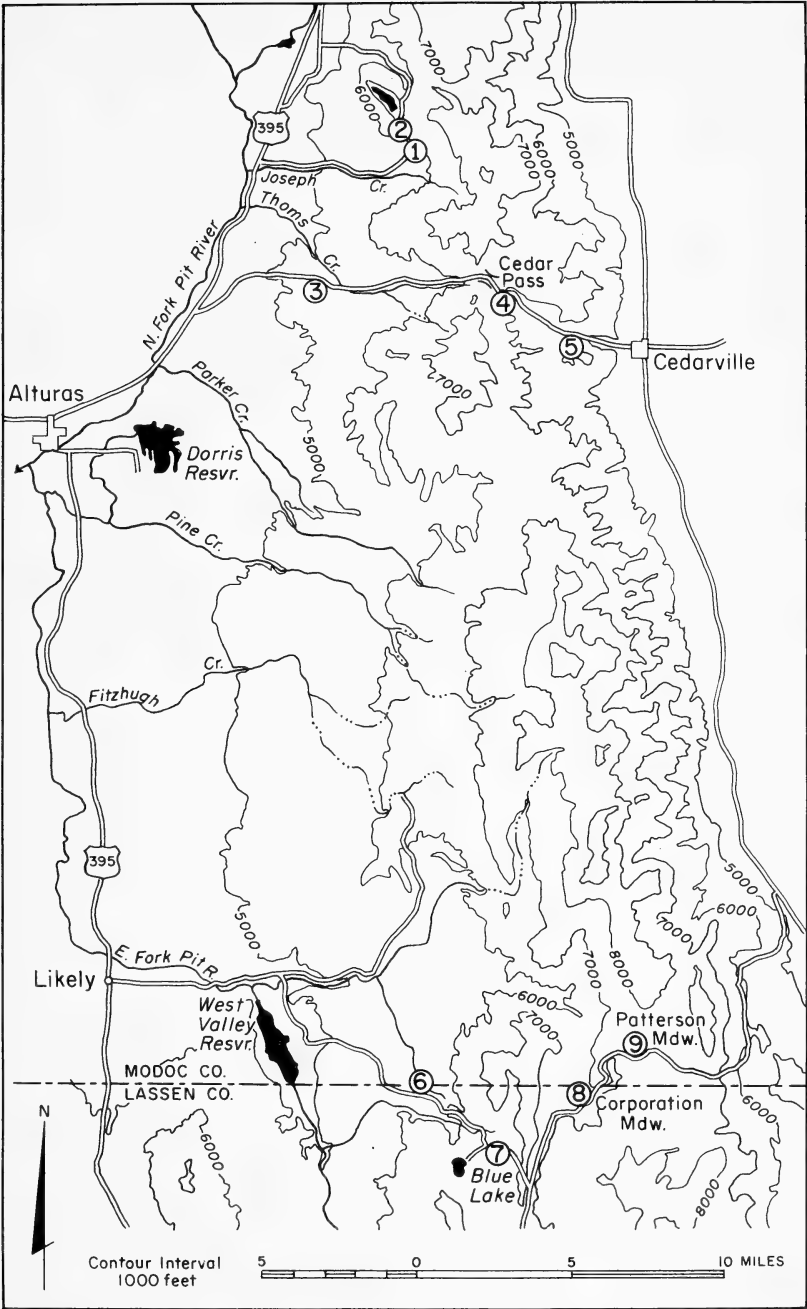
FIG. 1. Location of study plots (0) and their elevation in three areas near Alturas, Modoc Co., Calif.

TABLE 1. INDIVIDUAL TREES SELECTED FROM EACH PLOT TO SHOW CHARACTERISTIC MAJOR MONOTERPENE COMPOSITION OF WASHOE PINE IN PERCENT

Plot No.	α-pinene	β-pinene	3-carene	Myrcene	Limonene
1	7	1	69	17	Trace
	6	1	65	22	1
2	6	20	60	8	Trace
	6	14	62	12	1
3	7	4	69	13	1
	15	14	60	6	Trace
4	3	16	63	11	1
5	4	1	79	10	Trace
	10	2	74	8	Trace
	16	1	68	10	Trace
6	8	4	66	15	Trace
	3	6	71	15	Trace
	7	4	69	12	2
7	4	1	78	12	1
	6	3	69	15	Trace
	6	4	65	19	Trace
8	5	11	64	14	Trace
	6	8	65	16	Trace
	6	12	60	17	1
9	5	4	73	12	1
	5	2	78	9	—
	9	1	65	19	Trace

Two to four plots were selected at different elevations in the three areas. The elevation at each plot is as follows: plot 1, 5,500 ft.; plot 2, 5,700 ft.; plot 3, 5,000 ft.; plot 4, 6,000 ft.; plot 5, 5,000 ft.; plot 6, 5,800 ft.; plot 7, 7,000 ft.; plot 8, 6,800 ft.; and plot 9, 7,200 ft. About 20 trees per plot were tapped for resin at plots 1 to 8, inclusive. Except for the Jeffrey pines, no effort was made to describe the trees morphologically; they were selected simply on the basis of geography. Previous data gathered for the Patterson Meadow location of Washoe were included for a reference as the ninth plot.

I used previously described procedures for tapping the trees, preparing the samples for analysis, and analyzing the samples by gas chromatography (Smith, 1964). All results of analysis are based on the normalization of the monoterpene fraction of the xylem resin; i.e., each monoterpene is expressed as a percent of the total monoterpenes.

RESULTS

The frequency distribution of each of the five major components— α-pinene, β-pinene, 3-carene, myrcene, and limonene—in each of the nine plots is given in figure 2. Trees with the typical composition of Washoe pine were found in each location (table 1). The frequency of this type of tree seemed to shift markedly between 6,000 and 7,000 feet; plots below this zone (plots 1–6) can be classified as typical ponderosa stands, containing a scattering of trees which have monoterpene char-
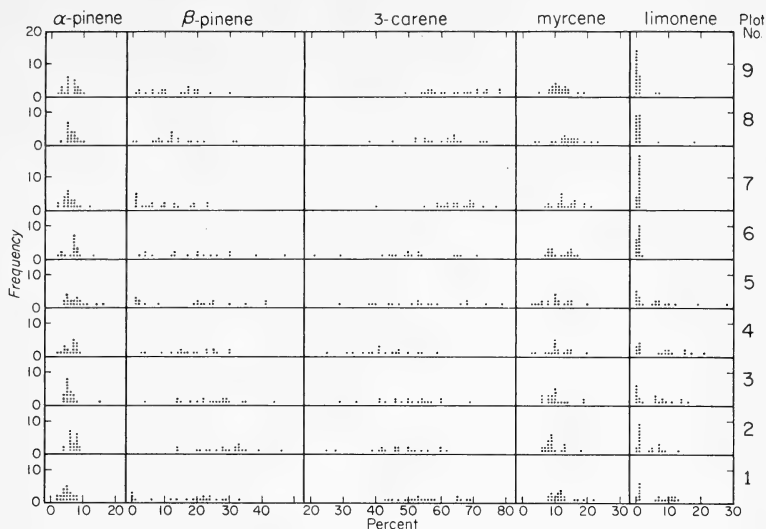
Fig. 2. Frequency distribution of the five major monoterpenes of Washoe and ponderosa pine from nine plots in the Warner Mountains, northeastern California.

acteristics of Washoe, comprising generally about 10% of the stand. Trees at higher elevation are typical Washoe; in these plots (7–9) an infrequent tree has the monoterpene characteristics of ponderosa pine, comprising generally about 10% of the stand. In addition to trees in low-elevation stands with all the monoterpene characteristics of Washoe, individual trees may be found which show at least one of the character-istics of Washoe; i.e., either > 60% 3-carene, < 20% β-pinene, or < 2% limonene. The occurence of these two types of trees suggests the possibility of both geographical and physiological mixing of ponderosa and Washoe.

This study also suggested that the previously defined range of Washoe in this area should be enlarged (Haller, 1961). If a criterion of > 60% 3-carene, < 20% β-pinene, and < 2% limonene is used for Washoe pine, 10% of the trees below the 6,000- to 7,000-foot zone fit this criterion and might be called Washoe; 38% of the trees above this zone do not fit this criterion and might be called either ponderosa or hybrids between ponderosa and Washoe. There is some evidence that plot 6, at about 5,800 feet, is near the transition zone, since the frequency dis-tribution of limonene for the trees in this plot (fig. 1) is typical of Washoe, while the 3-carene and β-pinene distributions are typical of ponderosa.

Limonene was of particular interest in this study. Except in a few instances it is lacking in trees from the typical Washoe plots; in all plots considered typically ponderosa in the Warners or the Sierra Nevada it may be absent or it may occur in an amount of from about 5 to 10%.
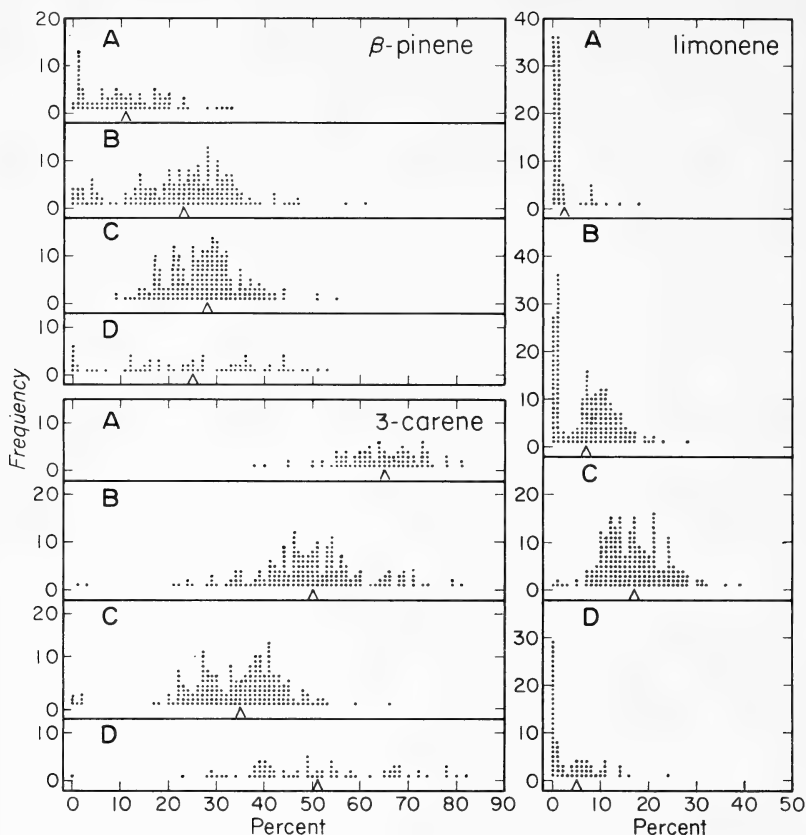
Fig. 3. Frequency distribution of β-pinene, limonene, and 3-carene from four sources: A, Washoe pine, B, low-elevation ponderosa in Warner Mts., C, ponderosa from central Sierra Nevada, D, var. *scopulorum* of ponderosa from Colorado. Wyoming, and Nebraska.

Only a few trees had between 1 and 5%.

The Jeffrey pines growing at plot 6 were found to be very similar to those in the Sierra Nevada, but the group included one tree that had a monoterpene composition highly suggestive of that of a hybrid between Jeffrey and Washoe. Its composition was 17% heptane, 2% nonane, 2% α-pinene, a trace of α-thujene, 4% β-pinene, 55% 3-carene, 6% myrcene, 11% limonene, and 3% terpinolene. The amounts of heptane and nonane are clear signs of Jeffrey pine. The low β-pinene, high 3-carene, and trace of α-thujene are the basis for believing the other parent is Washoe. However, the 11% limonene suggests that ponderosa could be the other parent. There is always the rather remote possibility of a three-way hybrid.

Hybrids have been artificially produced between Jeffrey and both ponderosa and Washoe (Liddicoet and Righter, 1960) but not without

TABLE 2. DIFFERENCES AMONG MEANS OF LIMONENE AND t-VALUES
OF FOUR SOURCES OF PONDEROSA OR WASHOE PINE

Comparison	$X_1 - X_2$	d.f.	t
Washoe vs. Warner, low elevation	5.2	272	5.10**
Washoe vs. Sierra Nevada	16.1	290	7.02**
Washoe vs. var. *scopulorum*	2.8	158	2.01*
Warner, low elevation vs. Sierra Nevada	10.9	388	4.52**
Warner, low elevation vs. var. *scopulorum*	2.4	258	2.88**
Sierra Nevada vs. var. *scopulorum*	12.3	274	5.20**

*= 95, and ** = 99% level of confidence for rejecting the null hypothesis.

difficulty (Critchfield and Little, 1966). Natural hybrids between Jeffrey and ponderosa have been found (Mirov, 1929), but natural hybrids between Jeffrey and Washoe have not been reported. The Jeffrey pines in the Warners are growing in a stand which chemically might be called ponderosa with a scattering of Washoe.

A frequency distribution of limonene, β-pinene, and 3-carene was made of four sources of ponderosa or Washoe pine (fig. 3): 1, typical Washoe sources (plots 7–9 plus data from Smith (1967)); 2, ponderosa at low elevations in the Warner Mountains (plots 1–6 plus previous data gathered near plot 1); 3, ponderosa from the central Sierra Nevada (Smith, 1966); and 4, ponderosa from Wyoming, Colorado, and Nebraska, where it is usually called var. *scopulorum* (Peloquin, 1964). This last grouping is a collection of trees from widely separate locations; but they do represent the whole region fairly well.

A null hypothesis was established that there was no difference in the limonene percentage among the various sources; a t-test of arc-sin transformed percentages shows that this null hypothesis can be rejected at the 95% or greater level of confidence in all comparisons among the four sources (table 2). However, from a visual inspection of the frequency distribution, it does appear that low-elevation ponderosa in the Warners is somewhat intermediate between central Sierra Nevada ponderosa and var. *scopulorum* but may be more closely related to var. *scopulorum*.

CONCLUSIONS

This study of xylem monoterpenes suggests: 1, that the range of Washoe pine in the southern Warner Mountains should be enlarged; 2, that some ponderosa stands have geographically mixed with Washoe stands; 3, that composition of the monoterpenes of the two species may overlap considerably; 4, that the two species hybridize naturally; 5, that Washoe is closely related to ponderosa, particularly to var. *scopulorum;* and 6, that low-elevation ponderosa in the Warners is intermediate between Washoe pine and ponderosa pine of the central Sierra Nevada of California.

LITERATURE CITED

CRITCHFIELD, W. B., and E. L. LITTLE,, JR. 1966. Geographic distribution of the pines of the world. U.S. D. A. Misc. Publ. 991.

HALLER, J. R. 1961. Some recent observations on ponderosa, Jeffrey and Washoe pine in northeastern California. Madroño 16:126-132.

LIDDICOET, A. R., and F. I. RIGHTER. 1960. Trees of the Eddy Arboretum. U.S. Forest Serv., Pacific SW Forest Range Exp. Sta. Misc. Pap. 43.

MIROV, N. T. 1929. Chemical analysis of the oleoresins as a means of distinguishing Jeffrey pine and western yellow pine. J. Forest. (Washington) 27:176–187.

————. 1961. Composition of gum turpentines of pines. Techn. Bull. U.S.D.A. 1239.

PELOGUIN, R. L. 1964. Geographic variation of the monoterpenes of Pinus ponderosa. Master's thesis, Stanford Univ.

SMITH, R. H. 1964. Variations in the monoterpenes of Pinus ponderosa Laws. Science 143:1337-1338.

————. 1966. The monoterpene composition of Pinus ponderosa xylem resin and of Dendroctonus brevicomis pitch tubes. Forest Sci. 12:63-68.

————. 1967. Variations in the monoterpene composition of the wood resin of Jeffrey, Washoe, Coulter, and Lodgepole pines. Forest Sci. 13:246-252.

STUDIEDS IN THE RHODOPHYLLOID FUNGI.
I. GENERIC CONCEPTS

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This paper is concerned with the Rhodophyllaceae in the sense of Singer (except *Clitopilus* and *Rhodocybe*).

In 1821 Elias Fries classified the rhodophylloid fungi into tribes which were distinguished by variations of the following features: 1, consistency of the carpophore, particularly of the stipe, 2, attachment of the lamellae, 3, shape of the pileus, and 4, nature of the pileal surface. In 1838 he further emphasized the nature of the pileal surface as a diagnostic feature, using it as well as other characteristics to divide the tribe *Entoloma* into three sections, and admitted species with flocculose pilei to tribe *Nolanea,* which previously had contained only mushrooms with glabrous pilei. In subsequent publications Fries no longer used the pileal surface in diagnostic characterizations but defined his tribes (which he now called subgenera) only on the basis of consistency of stipe, type of pileal margin, and attachment of lamellae. These three features have continued to be used by mycologists who have chosen to maintain the Friesian groupings, whether at the generic or subgeneric level. Unfortunately all three are variable, or hard to assess, or both. The difficulty of accurately defining taxa by such features has led some

contemporary mycologists to place all rhodophylloid fungi in a single genus, *Rhodophyllus* Quel., or *Entoloma* (Fr.) Kummer emend. Donk, characterized by pink, angular spores, subparallel lamellar trama, and attached lamellae.

This solution does indeed create a clearly defined genus for the rhodophylloid fungi, but it avoids the questions of what characteristics would be more satisfactory than those used by Fries to delineate subgeneric taxa. In recent years some efforts have been made to find such characters. Romagnesi (in Kühner and Romagnesi, 1953) and Hesler (1967) have emphasized microscopic characters more than macroscopic ones. Smith and Shaffer (1964) have suggested using diameter rather than consistency of the stipe; they define a fleshy-fibrous stipe as one with a diameter at the apex greater than 5 mm, and a cartilaginous stipe as one with the apex less than 5 mm broad. The probable value of urea as a chemotaxonomic aid in separating certain groups of the rhodophylloid fungi was shown by Tyler, et al. (1965).

The present study proposes the use of the anatomy and the general aspect of the pileal surface as important diagnostic characters, and correlates concentration of urea with various microscopic and macroscopic features.

Affinities and Characterization

The rhodophylloid fungi have pink to vinaceous spores that are angular in face, side, and end views, lamellar trama composed of subparallel hyphae, and lamellae that are variously attached but never distinctly free. These fungi are closely related to species of *Clitopilus* and of *Rhodocybe* which have spores that are angular in end view. In *Clitopilus,* the spores are longitudinally grooved or striate when seen in side or face view; in *Rhodocybe,* the spores are roughened to warty when seen in face or side view. Several other genera also have pink spores, but differ from the rhodophylloid genera in other ways. For example, the punctate-roughened spores of *Lepista* are not angular in any view. *Rhodotus* has smooth to echinulate spores, free lamellae, and divergent lamellar trama. *Volvariella, Chamaeota,* and *Pluteus* all possess smooth spores, convergent lamellar trama, and free gills; furthermore, *Volvariella* has a volva, *Chamaeota* an annulus.

Chromatographic Methods

One hundred mg of finely ground gill, pileus and stipe tissue was placed in a screw cap vial, along with 1.5 ml ethanol and agitated vigorously on a rotary shaking machine for approximately 24 hours. Fifty μl of clear supernatant of each extract was spotted one inch from the base of $9\frac{1}{4} \times 22\frac{1}{2}''$, oxalic-acid-washed Whatman No. 1 filter paper, together with reference spots of 5, 10 and 25 μg of urea respectively. The chromatogram was developed with a wash liquid composed of n-butanol-acetic acid-water (4:1:1) for approximately 18 hours. Four to five chromatograms were run simultaneously in each chromatographic

TABLE 1. UREA AS A CHEMOTAXONOMIC INDICATOR IN CERTAIN RHODOPHYLLOID FUNGI

Genera (sensu Dennis, et al.	Number of Species	Urea Concentrations
Claudopus	1 (2)*	5
Nolanea	5 (34)	5
Entoloma	7 (17)	0 - 2
Leptonia	5 (42)	0 - 0.3
*Figures in parentheses are number of collections.		

chamber located in a constant temperature room at 25°C. The chromatograms were dried at room temperature, marked to show the location of fluorescent spots and then sprayed with 2% p-dimethylaminobenzaldehyde in hydrochloric acid (Ehrlichs reagent, hereinafter referred to as PDAB). (Ehrlich's reagent: p-dimethylaminobenzaldehyde (PDAB), 6 grams; Ethanol, 95%, 229 ml; and Concentrated hydrochloric acid, 71 ml. If the spray is stored in a colored bottle and kept below room temperature, it should remain stable for extended periods.)

The Rf values were calculated for all unknown compounds and for three urea standards. The sizes and color intensities of yellow spots with the same mobility as the three standards were compared with the latter. Extracts rated 0-1 contained none to approximately 5 μg/spot; 2, around 10 μg; 4, about 25 μg and 5, more than 25 μg.

RESULTS

Although 77 compounds were detected in the 279 extracts examined, only those compounds forming a yellow chromophore at the same Rf value as those of the urea standards (0.50±0.06) are of chemotaxonomic concern in the present study. Ninety-five of the 279 collections analyzed in the above manner were identified to species by classical microscopic and macroscopic techniques. The placement of these species into genera (sensu Dennis, et al., 1960), together with data on their urea concentrations, are shown in Table 1.

The data in Table 2 include *Pouzaromyces* Pilát and a segregate of *Leptonia* (*L. sericella* species complex). The data further show that urea levels in all collections placed in *Nolanea* were consistently high, whereas those in *Leptonia* and *Entoloma* were much lower.

TABLE 2. UREA IN 279 COLLECTIONS OF RHODOPHYLLOID FUNGI

Genera		Urea Concentrations			
		0 - 1	2	4	5
Leptonia sericella species complex	15*	15	0	0	0
Pouzaromyces	2	0	1	0	1
Leptonia	86	63	15	3	5
Entoloma	66	40	23	2	1
Nolanea	108	0	0	1	107
Claudopus	2	0	0	0	2
Total	279				
*Number of collections examined.					

KEY TO THE GENERA

Stipe eccentric, lateral, or lacking . . . . *Claudopus*
Stipe central.
  Pileal surface in radial section a layer of repent, radially oriented hyphae.
    Urea concentration low (0 to +1, rarely +2) ; clamps usually present on 20%
      or more of the pileal cuticular hyphae; carpophores large and fleshy (pileal
      trama 3 mm or more at edge of umbo, apex of stipe 5 mm or more in
      diam. . . . . *Entoloma*
    Urea concentration high to very high (+4 to +5) ; clamps absent or if present,
      on less than 10% of the pileal cuticular hyphae; carpophores usually small
      or medium sized, and thin-fleshed (pileal trama 2 mm or less, apex of stipe
      less than 5 mm), but sometimes large and fleshy as in *Entoloma* . *Nolanea*
  Pileal surface in radial section an entangled to irregularly interwoven tricho-
    dermium, a palisade trichodermium, an ixotrichodermium, or a hymeniform
    layer (at least when young).
    Urea concentration high to very high (+4 to +5) ; pileus thin-fleshed, conic
      to campanulate, often with a papillate or cuspidate umbo, the cuticle often
      overlain by a colorless superficial layer or veil . . . . *Nolanea*
    Urea concentration low to medium (0 to +3) ; pileus varying in shape and
      thickness of flesh, but not conical with papillate or cuspidate umbo.
      Pileal cuticle a palisade trichodermium, or hymeniform, at least on the
        disc . . . . *Leptonia*
      Pileal cuticle an entangled to an irregularly interwoven trichodermium or an
        ixotrichodermium.
      Terminal cells of pileal cuticle averaging less than 8 μ wide . . *Entoloma*
      Terminal cells averaging 8 μ or more wide.
        Young, fresh carpophores entirely white to pale cinerous. *Alboleptonia*
        Carpophores not entirely white to pale cinereous.
        Cuticle at apex of stipe similar to pileal cuticle.
          Cuticular hyphae of the pileal disc 190–600 μ long, 5-10(-15)-septate,
            average length greater than 250 μ . . . . . *Pouzaromyces*
          Cuticular hyphae of the pileal disc up to but not exceeding 300 μ in
            length, (1-)3-5-septate, average length 225 μ or less . *Leptonia*
        Stipe and pileal cuticles not similar.
          Caulocystidia, if present, versiform but not indense clusters . *Leptonia*
          Caulocystidia obclavate to aculeate and in rosette-like clusters.
                                  Pouzaromyces

GENERA

CLAUDOPUS (W. G. Smith) Gill., emend Pat, Les Hyménomycètes
d'Europe, 113. 1887. Basionym: *Agaricus* subgenus *Claudopus* W. G.
Smith, Clavis Agaricinorum. Type species: *Agaricus byssisedus* Pers.
per Fr.

In members of this genus the carpophore often lacks a stipe; when
one is present, it is always lateral or eccentric. Also, the habit of the
carpophores of growing on the underside of logs or of shelving clumps
of moss has not been encountered in other fungi with pink, angular
spores. *Leptonia dichroa* and related lignicolous species have a tricholo-
matoid carpophore.

Extracts from only two collections of *Claudopus* were chromato-
grammed. Each possessed a high concentration of urea, but otherwise had
no distinctive Erlich-positive spots.

ENTOLOMA (Fr.) Kummer, Der Führer in die Pilzkunde, 23, 97. 1871. emend. Basionym: *Agaricus* tribus *Entoloma* Fr., Epicrisis, 143. 1838. Synonym: *Agaricus* subgenus *Entoloma* (Fr.) Rabenh., Deutschl. Krypt.-Fl. 1:508. 1844. Type species: *Agaricus prunuloides* Fr.

Pileus: glabrous, at times with a pruina of whitish or grayish fribrils, or with minute colorless squamules; surface dry, lubricous, or viscid; context 3 mm or more thick at the edge of the umbo. Stipe: 5 mm or more broad at the apex. Pileal cuticle: in radial section, either of repent hyphae, or an entangled to interwoven trichodermium, or an ixotricho-dermium; terminal cells long, thin, claviform, averaging less than 8.0 μ wide; hypoderm similar to the pileal cuticle. Clamp connections: on at least 20% or more of the septa of all pileal cuticular hyphae, long, thin, at times rare. Pigmentation: vacuolar, rarely externally incrusted. Urea concentration: low (0 to +1).

Deviations from one or another of these characteristics are encountered. For instance, some specimens have very few clamps on the pileal cuticular hyphae, but are recognizable as Entolomas by their fleshy, tricholomatoid carpophores with glabrous pileus and low urea content. In other specimens the pileus instead of being glabrous is covered with a pruina of whitish or grayish fibrils, or with minute colorless squamules, and in still others, externally incrusting pigment replaces vacuolar pigmentation. But in all of these instances, however, the specimen can be identified as an *Entoloma* by its fleshy carpophore, low urea content, and relatively abundant clamp connections.

NOLANEA (Fr.) Kummer, Der Führer in die Pilzkunde, 24, 95. 1871. emend. Basionym: *Agaricus* tribus *Nolanea* Fr., Syst. Mycol. 1:204. 1821. Type species: *Agaricus pascuus* Fr.

Pileus: convex to campanulate or conic, rarely depressed or umbili-cate, often umbonate, papillate, or cuspidate; surface glabrous, at times overlaid with a superficial veil, dry or lubricous; context 2(-5) mm or less thick at the center or at the edge of the umbo. Stipe: 4(-8) mm or less broad at the apex. Pileal cuticle: in radial section either of repent hyphae or an entangled to interwoven trichodermium; hypoderm often differentiated. Clamp connections: absent or if present, on less than 10% of the septa of all pileal cuticular hyphae, rarely more abundant. Pigmentation: vacuolar or etxernally incrusted. Urea Concentration: high (+4 to +5).

In occasional specimens the pileus is depressed to umbilicate, but more often, the carpophore is almost tricholomatoid in stature, and has clamps on more than 10% of the septa in the pileal surface. In both instances the fungus can be included in *Nolanea,* because the specimens also possess the distinctive combination of high urea content and repent pileal cuticle.

Nolanea can be distinguished from *Entoloma* by its pileal cuticle whose hyphae are well differentiated from those of the pileal trama, by the absence or rarity of clamp connections, the less fleshy carpophore,

and more reliably by the high urea concentration. *Leptonia, Pouzaromyces,* and the *Leptonia sericella* species complex all differ from *Nolanea* by virtue of the different structure of their pileal cuticle, and their low urea content.

POUZAROMYCES Pilát, Sborn. Národn. Mus. Praze 9B (2):60. 1953. Type species: *Agaricus fumosellus* Winter.

The species of this genus are distinguished by their dark brown to gray-brown tomentulose to densely scaly pilei, initially dark brown to gray-brown lamellae, and pruinose to densely scaly stipes that are concolorous with the pilei. Cheilocystidia are present on the lamellar edge. The pileal cuticle is composed of septate, entangled hyphae with dark brown vacuolar pigment and some externally incrusted pigment. The cuticle at the apex of the stipe is either similar to the pileal cuticle, or bears rosette-like clusters of long, obclavate to aculeate caulocystidia.

Pouzaromyces can be distinguished from *Entoloma, Nolanea,* the *Leptonia sericella* species complex, and most other Leptonias on the basis of color, and of the nature of the surface and cuticle of both pileus and stipe. Certain species of *Leptonia* (e.g., *L. subdysthales*) resemble *Pouzaromyces* in general appearance, especially as to color, but differ in the structure of the pileal cuticle, or the cuticle of the stipe, or both.

LEPTONIA (Fr.) Kummer, Der Führer in die Pilzkunde, 24, 96. 1871. emend. Basionym: *Agaricus* tribus *Leptonia* Fr., Syst. Mycol. 1:201. 1821. Synonyms: *Eccilia* (Fr.) Kummer, Der Fuhrer in die Pilzkunde, 23, 94. 1871. *Leptoniella* Earle, Bull. N. Y. Botan. Gard. 5.424. 1909. Type of species: *Agaricus euchrous* Pers. *per* Fries.

Pileus: tomentulose or punctate or squamose to squamulose, at least on the disc, at times silky-, matted-, or appressed-fibrillose. Pileal cuticle (in radial section and at least on the disc): an entangled trichodermium, hymeniform, or a palisade trichodermium; pilocystidia or cystidioid terminal cells 8μ or more in diameter. Clamp connections: present or absent. Pigmentation: vacuolar or rarely incrusted. Urea concentration: variable (0 to +3).

The species of *Leptonia* are characterized primarily by the nature of the pileal surface and the structure of the pileal cuticle. The surface is tomentulose or punctate or squamose to squamulose, at least on the disc, and the cuticle is an entangled trichodermium of agglutinated or non-agglutinated hyphae, or is hymeniform, or a palisade trichodermium. Pilocystidia or cystidioid terminal cells are 8μ or more in diameter, with vacuolar (rarely incrusted) pigment. The cuticle at the apex of the stipe is of repent hyphae, or bears scattered clusters of caulocystidia. Clamps may be present or absent. Most of the species have small to medium-sized, rather thin-fleshed carpophores, but there are some exceptions. A fleshy stature, or frequent clamp connections on the pileal cuticular hyphae, or both, relates some species of *Leptonia* (e.g., *L. jubata, L. dichroa, L. griseo-cyanea,* and *L. chalybaea*) to *Entoloma*. However,

the species of *Entoloma* differ in their smooth, glabrous pilei, the structure of their pileal cuticle, and the nature of their pilocystidia.

In *Leptonia,* urea concentration varies from 0 to $+3$. Of 86 collections examined, 78 had little or no urea (0 to $+1$). Eight collections, including 3 each of *L. dichroa* and *L. jubata,* showed a concentration of $+2$ to $+3$. All eight belong to sections of *Leptonia* that do not have a tomentulose pileal disc, thus there seems to be a correlation between urea concentration and the type of pileal surface, which may have significance at the sectional level.

One group of Leptonias, referred to previously as the *L. sericella* species complex, seems different enough from the remainder of the genus to warrant special attention. This group of species has been placed in a new genus, *Alboleptonia* (Largent and Benedict, 1970). This group is characterized by the entirely white to pale cinereous carpophore, the silky to appressed-fibrillose or minutely squamulose pileal surface consisting of an entangled trichodermium, the presence of a fugacious superficial veil, low urea concentration (0 to $+1$), and a set of unique Ehrlich-positive compounds. The few white Leptonias not included in *Alboleptonia* (*Leptonia albinella* and related species) have the pileal cuticle hymeniform, or consisting of a palisade trichodermium. Pallid or nearly white species of *Entoloma* differ in their glabrous, dry to viscid pilei, larger stature, abundant clamp connections, and dissimilar Ehrlich-positive compounds.

SUMMARY

As suggested by Tyler, et al. (1965), a study of the urea concentration in species of *Rhodophyllus* proved to be a useful chemotaxonomic aid in classifying these fungi. On the basis primarily of urea concentration, type of pileal surface, and structure of the pileal cuticle, plus the occasional use of other structural or macroscopic features, five genera can be delimited, as follows:

Claudopus. Stipe lacking, or present and lateral to eccentric; place of growth, on the underside of logs or on shelving clumps of moss.

Entoloma. Clamps long, thin, relatively abundant; pileal surface glabrous or frosted; pileal cuticle repent, or an interwoven trichodermium; pilocystidia less than 8μ broad; urea concentration low.

Nolanea. Clamps absent or rare; pileal surface glabrous, dry or lubri-

cous; pileal cuticle of repent hyphae; urea concentration high.

Pouzaromyces. Clamps absent or rare; pileal surface minutely tomentose to densely scaly; surface of stipe pruinose to densely scaly; pileal cuticle of septate, entangled hyphae with dark pigment; cheilocysidia present; apex of stipe with a distinct cuticle; urea concentration not determined.

Leptonia. Clamps usually absent, if present, thick and rather numerous; pileal surface appressed-fibrillose, tomentulose, punctate, or squamulose, at least on the disc; pileal cuticle hymeniform, a palisade trichodermium, an entangled trichodermium, or an intewoven layer of submoniliform hyphae; pilocystidia broad; urea concentration low to medium.

In addition to the above five genera, a distinctive group of species, the *Leptonia sericella* species complex (now *Alboleptonia* Largent & Benedict, 1970), can be characterized as follows: entire corpophore white to pale cinereous; clamps rarely present; pileal surface silky to minutely squamulose; pileal cuticle an entangled trichodermium with a fugacious superficial veil; several unique Ehrlich-positive compounds present.

LITERATURE CITED

DENNIS, R. W. G., P. D. ORTON, and F. B. HORA. 1960. New check list of British agarics and boleti. Trans. Brit. Mycol. Soc. 43. Suppl.

FRIES, E. M. 1821. Systema mycologicum. Vol. I. Ex Officina Berlingiana, Lund.

————. 1838. Epicrisis systematis mycologici. Gleerup, Lund.

HESLER, L. R. 1967. Entoloma in southeastern North America. Beih. Nova Hedwigia 23.

KÜHNER, R., and H. ROMAGNESI. 1953. Flore analytique des champignons supérieurs. Mason et Cie., Paris.

LARGENT, D. L. and R. G. BENEDICT. 1970. Studies in the rhodophylloid fungi II: Alboleptonia, a new genus. Mycologia 62:437–452.

SMITH, A. H., and R. L. SHAFFER. 1964. Keys to generat of higher fungi. Univ. Michigan Biol. Station, Ann Arbor.

TYLER, V. E., R. G. BENEDICT, and D. E. STUNTZ. 1965. Chemotaxonomic signficance of urea in the higher fungi. Lloydia 28:342-353.

A NATURALIZED CORTADERIA (GRAMINEAE) IN CALIFORNIA

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Munz (1968) recorded *Cortaderia selloana* (Schult.) Asch. & Graebn. as naturalized in San Francisco and the North Coast Ranges. He further referred to a heavy infestation of this species at Big Lagoon, Humboldt Co. From the Big Lagoon populations D. W. Cooper of Eureka sent me specimens, transplants, and seed from which plants were raised. All have proved identical with plants widely naturalized in northern North

Island, New Zealand. These are referred by Connor (1965) to *C. atacamensis* (Philippi) Pilger following the treatment of Chilean *Cortaderia* by Acevedo de Vargas (1959).

The two most recent revisions of *Cortaderia* for the section of the genus including *C. selloana, atacamensis,* and *rudiuscula* (Acevedo, 1959; Conert, 1961) are not in good agreement, and Conert does not cite Acevedo's paper. Acevedo (1959) truly describing *C. atacamensis* as "Hermosa Cortaderia," also referred to the confusion between it and *C. rudiuscula* Stapf emend. Acevedo; she distinguishes *C. atacamensis* from *C. rudiuscula* by such characters as floret size, awns of lemmata, branching habit and panicle color. Conert (1961) preferred the often used combination *C. quila* (Nees & Meyen) Stapf to *C. rudiuscula*. While I cannot be sure that all records of *C. rudiuscula* in the United States refer to the entity here reported as *C. atacamensis* (cf. Bailey, 1949; Chase, 1950), it is certainly true of the recent report from Marin Co., California (Howell, 1970; pers. comm.).

Some points of comparison between *C. selloana* and *C. atacamensis* are given in Table 1.

TABLE 1. COMPARISON BETWEEN CORTADERIA SELLOANA AND C. ATACAMENSIS.

	atacamensis	*selloana*
Leaf color	deep green	bluish green
Leaf blades	hairy towards base on abaxial surface	glabrous on abaxial surface
Leaf sheath	densely hairy	glabrous or faintly hairy
Panicle color	deep violet	white through to light violet
Panicle branches	flexuous	stiff
Lemma	acuminate or shortly awned or mucronate; the small awn is very fragile and breaks off easily	strongly awned
Sex form	female only	hermaphrodite and female
Flowering time	late summer	mid to late autumn
Chromosome no.	**2n = 108**	**2n = 72**

LITERATURE CITED

ACEVEDO DE VARGAS, R. 1959. Las especies de gramineas del genero Cortaderia en Chile. Bol. Mus. Nac. Hist. Nat. 27:205-246.
BAILEY, L. H. 1949. Manual of cultivated plants. Macmillan, New York.
CHASE, A. 1950. Manual of the grasses of the United States. U. S. D. A. Misc. Publ. 200.
CONERT, H. J. 1961. Die Systematik und Anatomie der Arundineae. J. Cramer, Weinheim.
CONNOR, H. E. 1965. Breeding systems in New Zealand grasses. V. New Zealand J. Bot. 3:17-25.
HOWELL, J. T. 1970. Marin flora. Ed. 2. Univ. Calif. Press, Berkeley.
MUNZ, P. A. 1968. Supplement to a California flora. Univ. Calif. Press, Berkeley.

MORPHOLOGY, CHROMOSOME NUMBER, AND FLAVONOID CHEMISTRY OF BIDENS CORDYLOCARPA (COMPOSITAE)

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Coreopsis cordylocarpa was described by Gray in 1887. For many years no one seems to have questioned that this species had an appropriate generic assignment. In his two comprehensive treatments of *Coreopsis,* Sherff (1936, 1955) does not even suggest that *C. cordylocarpa* might have been improperly placed. In his later years, however, he indicated a specimen in the Field Museum *(Cronquist 9779)* as the type of a new *Bidens* species which he proposed to name in honor of Arthur Cronquist. The name was never published, and Sherff later recognized the Cronquist specimen as belonging to *Coreopsis cordylocarpa,* and so annotated it.

My first encounter with this species in the field was in the state of Jalisco in the late summer of 1966, where I was collecting with T. Melchert and P. Sorensen. All three of us were somewhat familiar with members of the Coreopsidinae, and it seems significant that our first impression was that we were observing a species of *Bidens.* In view of this, along with the fact that Sherff had also at one time assigned this taxon to *Bidens,* a detailed study seemed indicated. The present paper gives the result of this study.

MATERIALS AND METHODS

For the cytological studies, floral buds were fixed in the field in chloroform: absolute ethyl alcohol: glacial acetic acid (4:3:1). The anthers were squashed in aceto-hematoxylin, and the chromosomes observed in dividing microsporocytes.

Leaves and flowers which were collected in the field and dried, served as one source of flavonoids for chromatographic analysis. Achenes were collected at the same time, and fresh material from plants grown in the greenhouse was also analyzed for flavonoid constituents. The floral tissues (ray floret corollas, disk floret corollas and adnate anthers, disk floret ovaries, and chaff) were analyzed separately and found to be chromatographically identical. The leaf profiles were also determined. The tissues were placed in 0.1% HCl in methanol for 24–48 hours. This extract was applied to Whatman 3MM chromatographic paper (46 × 57 cm sheets) and run in two dimensions by the descending method. The first solvent system was tertiary butyl alcohol: glacial acetic acid: distilled water (3:1:1 v/v); the second glacial acetic acid: distilled water (15:85 v/v). Drawings of these chromatograms are shown in Fig 5. In these figures each chalcone-aurone pair is designated by a single letter and represented as a single spot because they invariably occur together as a complex mixture.

Individual flavonoids were purified by repeated chromatography, and

TABLE 1.

IDENTIFICATION AND SPECIAL MAXIMA OF THE FLAVONOIDS OF C. CORDYLOCARPA

Spot Designation	Identity	MeOH	+AlCl₃	+AlCl₃/ HCl	+NaOMe	+NaOAc	+NaOAc/ H₃BO₃
				Absorption maxima in mμ			
Leaves							
6	quercetin-3-	359	432	404	413	381	381
	glycoside	295	330	365	330	325	295a
		265a	300a	300a	272	271	261
		255	274	267			
16	naringenin-7-	330	385	385	445	330	330
	glycoside	283	306	306	390a	283	283
					286		
Leaves and floral tissues							
A	coreopsin	383	505a	440	450	480a	510a
		295	450	320	380a	385	413
		260	318	272	285	288	345a
		245	275	250		255a	285
			250				
A	sulfurein	403	450	405	488	487	435
		340a	342	335a	345	405	337
		274	292	275	291	340a	288
		256	255a	257		278	259
						255	
F	marein	382	520a	420	452	383	393
		320a	429	332	340	325a	320
		263	332	272	285	265	270
			273	250	253		
F	maritimein	416	455	413	497	443	442
		330	328	325	348	365	328
		273	287	273	290a	259	282
		242	248a	243	261		245
Floral tissues							
X	butein-sulfure- tin mixture?	——	——	——	——	——	——

a–denotes a shoulder or inflection.

the compounds were finally analyzed spectrally, utilizing a Beckman DB-G Grating Spectrophotometer. Standard methods and diagnostic reagents were employed (Markham and Mabry, 1968; Jurd, 1962). The spectral properties of these compounds, together with their identifications, are given in Table 1.

RESULTS AND DISCUSSION

There are a combination of morphological features which serve to distinguish this species from other taxa in the genus *Coreopsis* found in

Fig. 1. Distribution of *C. cordylocarpa*.

Mexico. The (8)10-16 ray florets, club-shaped wingless achenes (fig. 3B), fruticose habit, relatively undifferentiated outer and inner involucral bracts (fig. 2B), and large (to 20 cm) pinnatisect, deltoid leaves (fig. 4A) are quite unique. Sherff (1955) treated *C. cordylocarpa* as a member of sect. *Coreopsis*. It is clearly a discordant element here, however, for all other species in this section are small annual or perennial herbs with dorsiventrally flattened, winged achenes. In fact, all species of *Coreopsis* which I have examined (primarily those from North America) have achenes which are variously flattened dorsiventrally. That Sherff placed *C. cordylocarpa* in the type section seems to indicate a lack of understanding of its affinities within the genus *Coreopsis*.

Certain morphological features of *C. cordylocarpa* are much more suggestive of some Mexican *Bidens* species than they are of any member of *Coreopsis*. Specifically, the outer and inner involucral bracts of *C. cordylocarpa* are quite similar in shape (fig. 2B), and differ primarily in color, the outer ones being dark green, whereas the inner are pale green to nearly white. These involucral characteristics are very similar to those encountered in many species of Mexican *Bidens*. In contrast, species of Mexican *Coreopsis* typically exhibit a highly dimorphic involucre with somewhat green and fleshy outer bracts which differ from the inner ones in shape, size, color, and texture (fig. 2A). Moreover, the elongate, club-shaped, terete, striate, and wingless achenes of *C. cordylocarpa* are similar in general shape and appearance to those of several species of *Bidens* from Mexico (fig. 3A, B). Certainly, the achenes of *C. cordylocarpa* in no way resemble the flat, winged fruits which are typical of all Mexican *Coreopsis*, and indeed of the genus as a whole (fig. 3B, C).

The chromosome number of *C. cordylocarpa* offers no clues as to its
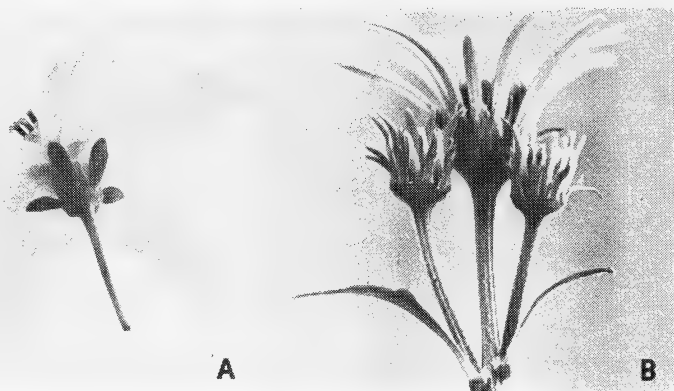
FIG. 2. Photographs of flloral heads. A, floral head of typical Mexican *Coreopsis* showing the highly dimorphic involucre; B, floral head of *C. cordylocarpa* showing the undifferentiated outer and inner involucral bracts.

generic affinities. A count of $2n = 146 \pm 2$ (fig. 4B) was determined in a large number of cells from *Melchert, Sorensen, & Crawford 6347A*. It must be emphasized that observations from several other populations *(Melchert, Sorensen, & Crawford 6354 & 6371; Carman 68-60)* revealed a chromosome complement of $2n = 146 \pm 6\text{-}8$. From these data, it appears justifiable to conclude that only one ploidy level exists in *C. cordylocarpa,* and that probably all populations have the same or nearly the same chromosome number. This high number, unique in the Coreopsidinae and one of the highest reported in the Compositae, is particularly interesting from an evolutionary point of view when considered together with the geographic distribution and ecology of the species. *Coreopsis cordylocarpa* is endemic to Jalisco, Mexico (fig. 1) and occurs only in or along the banks of shallow streams, indicating that it may be an old species, representing the only extant taxon of an otherwise extinct polyploid complex.

The flavonoid chemistry of *C. cordylocarpa* suggests a closer affinity to other Mexican species of *Bidens* than to any *Coreopsis* taxon. As shown in Fig. 5, the leaves and floral tissues are dominated by two chalcone-aurone pairs. Coreopsin-sulfurein (spot A) and marein-maritimein (spot F) are invariably present in large quantities in both leaves and flowers. In addition, the leaves (fig. 5, left) contain a flavonol (spot 6, quercetin-3-glycoside) and a flavanone (spot 16, naringenin-7-glycoside). The flowers also contain spot X (fig. 5, right), which appears to be a mixture of butein and sulfuretin, these being the aglycones of coreopsin and sulfurein respectively.

Chemical analysis of the leaves of other suffruticose or fruticose *Coreopsis* species from Mexico (members of sections *Electra, Anathysana,* and *Pseudo-Agarista*) has revealed the complete absence of coreopsin-sulfurein and marein-maritimein. These compounds are sometimes present in the floral tissues of certain of these species, but never
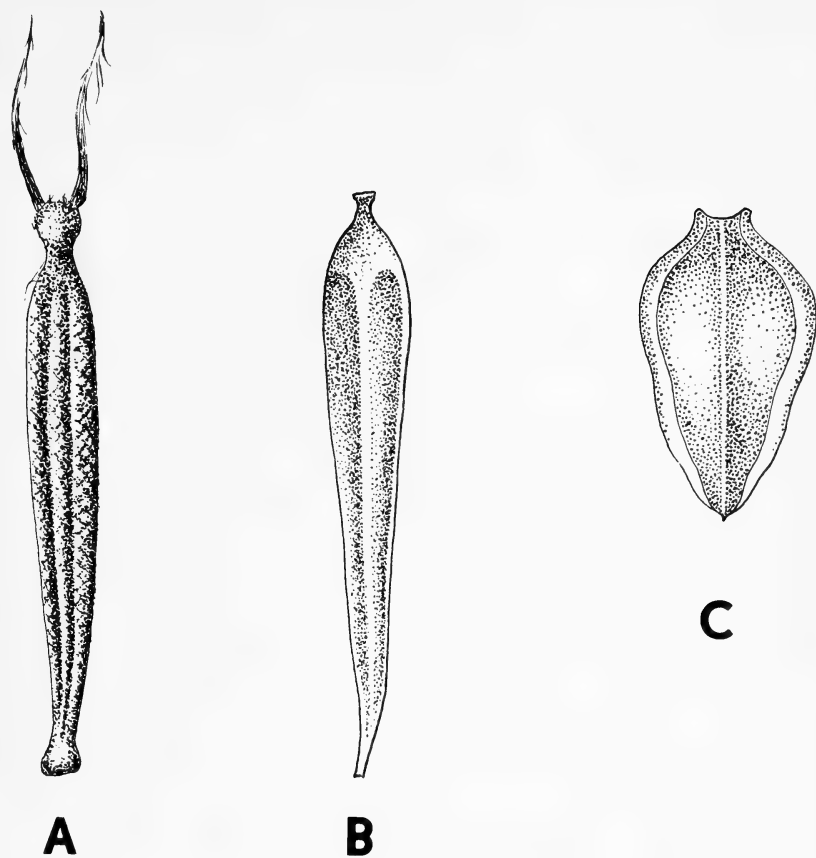
Fig. 3. Drawing of *Coreopsis* and *Bidens* achenes. A, achene of a typical Mexican *Bidens;* B, achene of *C. cordylocarpa;* C, achene of a typical Mexican *Coreopsis* (all × ca. 5).

in the leaves. It must be admitted that sufficient data are not available to make a meaningful statement concerning the distribution of these substances in the genus *Coreopsis* as a whole. However, it is instructive to compare the leaf profile of *C. cordylocarpa* to those of several species of *Bidens* from the United States and Mexico. The leaves of these taxa contain an unidentified chalcone-aurone pair which is chromatographically very similar (probably identical) to marein-maritimein. This evaluation is based upon conversations with T. E. Melchert and my observations of numerous chromatograms of the leaves of *Bidens* species. Although the chemical evidence is not conclusive, it certainly suggests that *C. corylocarpa* is much more similar to *Bidens* in its flavonoid chemistry than it is to *Coreopsis*.

Since the general morphology, as well as the preliminary chemical data, suggest that the affinities of *C. cordylocarpa* are with *Bidens* rather than with *Coreopsis,* the following new combination is proposed.

A **B**
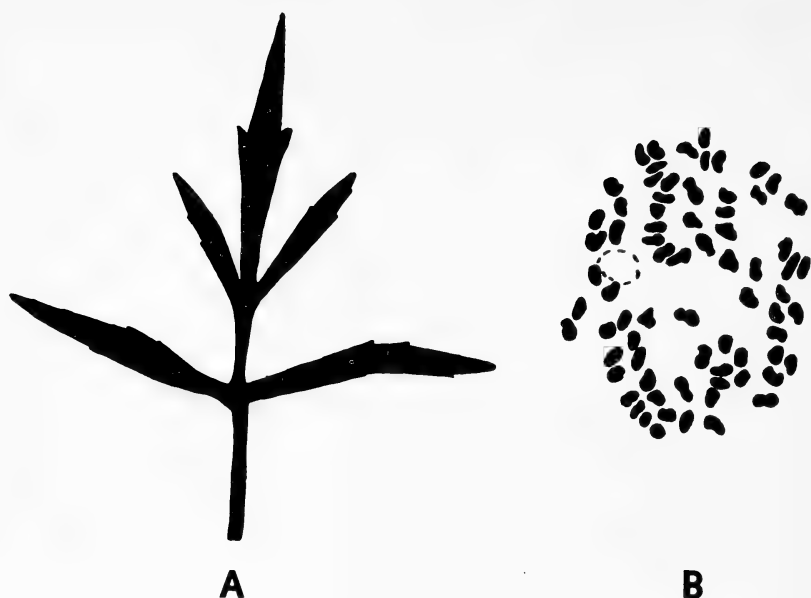
Fig. 4. A, silhouette of leaf of *C. cordylocarpa* (× ca. 1/2); B, meiotic chromosomes of *C. cordylocarpa*.

Bidens cordylocarpa (A. Gray) Crawford, comb. nov. *Coreopsis cordylocarpa* A. Gray, Proc. Amer. Acad. Arts 22:428. 1887. Fruticose, 0.5–2m tall, stems several from the base, red, hispid or with appressed hairs, becoming glabrous toward the base; leaves opposite, 10–20 cm long (including petiole), deltoid in general outline, pinnately divided, appressedly-pubescent on both surfaces; heads cymosely disposed, mostly 3-12 aggregated, peduncles 2–15 cm long, becoming densely pubescent near the involucre; heads 4–9 cm wide at anthesis; outer involucral bracts 6–10, lanceolate to narrowly so, hispid, 3–9 mm long; inner involucral bracts 8–12, lanceolate to narrowly ovate, hispid, 4–8 mm long; chaff narrowly lanceolate to linear, glabrous or sparsely hispid, 5–8 mm long at anthesis; ray florets 8–16, sometimes in a double whorl, neutral, ligule oblong to oblanceolate or linear, 0.6–4 cm long, 0.4–1.2 cm wide, entire or shallowly notched at the apex; disk florets 20–60, stigma hispid, shortly caudate; achenes club-shaped, essentially terete in cross section, glabrous, weakly striate, wingless, exaristate, and topped by a bald disk.

Representative specimens: MEXICO. Jalisco, bank of stream, 5200 ft. Sierra de San Estéban, *Barnes & Land 155* (F); banks of Río Blanco near Guadalajara, 5000 ft., *Pringle 11506* (F, MICH, MO, MSC, US); gravel along small stream 15 road mi N of Guadalajara, on road to San Cristóbal de la Barranca, 5100 ft., *Cronquist 9817* (F, MICH, MO, MSC, NY, TEX, US); in boulders and sand of stream bed leading into the barranca of the Río Blanco, ca. 8 mi N of Guadalajara, *Mel-*
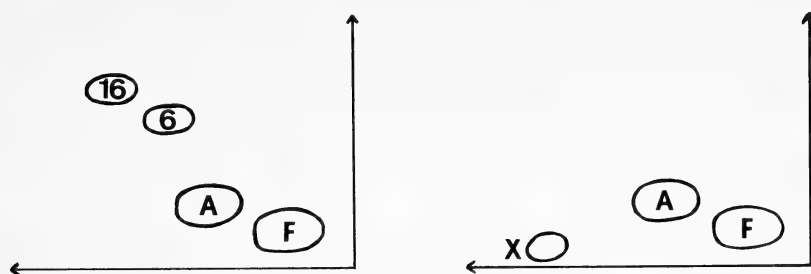
FIG. 5. Drawings of two dimensional chromatographic patterns of flavonoids in *C. cordylocarpa* (horizontal axis = tertiary butyl alcohol run; vertical axis = 15% acetic acid run) ; left, profile of leaves; right, profile of floral tissues.

chert, Sorensen, & Crawford 6354 (IA, RM) ; among boulders of swift stream, ca. 3 mi W of Cuaulta along road to Los Volcanes and Puerto Vallarta, *Melchert, Sorensen, & Crawford 6371* (IA, RM) ; among boulders of rocky stream bed 12.5–13 mi N of Zapopan, along dirt road to San Cristóbal de la Barranca, *Melchert, Sorensen, & Crawford 6347 A-B* (IA, RM) ; Hwy. 41, 7–8 mi N of Guadalajara, *Carman 68-60* (IA, RM).

LITERATURE CITED

JURD, L. 1962. Spectral properties of flavonoid compounds. *In* T. A. Geissman (Ed.). The chemistry of flavonoid compounds. Pergamon Press, Oxford & New York.
MARKHAM, K. R., and T. J. MABRY. 1968. A procedure for the ultraviolet spectral detection of ortho-dihydroxyl groups in flavonoids. Phytochemistry 7:1197-1200.
SHERFF, E. E. 1936. Revision of the genus Coreopsis. Fieldiana Bot. 11:277-475.
————. 1955. Coreopsis. *In* E. E. Sherff and E. J. Alexander. Compositae—Heliantheae—Coreopsidinae. North Amer. Fl. II. Pt. 2.

NOTES AND NEWS

NOTES ON THE FLORA OF THE PACIFIC NORTHWEST.—Extensive collections from Pend Oreille Co., Washington, were made by the author in connection with a floristic study (Layser, E. F. A floristic study of Pend Oreille County, Washington. M.S. thesis, State Univ. New York, College Forestry. 1969). Among the collections, certain ones seem worth special note.

Berteroa incana (L.) DC., a weedy European crucifer, was collected along the roadside in the northern part of Pend Oreille Co. (*Layser 1175*, WS) and previously

was known in the Pacific Northwest from British Columbia, Idaho, and Montana.

Carex sychocephala Carey, was reported by C. L. Hitchcock, et al. (Vascular plants of the Pacific Northwest, 5 vols., Univ. Washington Press. 1955–1969) from the Pacific Northwest from Montana, Kamloops, British Columbia, and Okanogan Co., Washington, and was noted as being "Seldom collected in our range." Since then it was found along a slough of the Pend Orielle River (*Layser 1201*, WS).

A hitherto undescribed form of *Crepis* was discovered at two different localities 10 miles apart. With respect to the polyploidy and apomictic induced polymorphic nature of this group, it is being treated as an anomalous form within a heteroploid complex (Babcock, E. B., and G. L. Stebbins. The American species of Crepis. Publ. Carnegie Inst. Wash. 504. 1938). The decision to recognize this form is based on its diverse morphology and its distribution.

CREPIS ATRABARBA Heller ssp. ORIGINALIS Babc. & Stebb. forma **pend-oreillensis** Layser, forma apm. nov. Caulis 3–5 dm alta; basalia folia linearis, 8–20 mm. longa, 2–6 mm lata, non pinnata vel rudimentaria; folia caulis linearis, dimidia supra; inflorescentia cymosa, axia centralis; capitulis 3–8; involucra 10–12 mm longa, tomentosa; flosculi 12–13; coma 7–8 mm longa; achenia viridula, 8 mm longa.

Material examined. Washington: Pend Oreille Co. Dry, rocky slopes in Dry Canyon, south of Cato Creek, Sec. 23, T37N, R37E, alt. 4000 ft., *E. F. Layser 894* (WS-holotype), June 1969; dry, shallow-soiled rocky slopes on Hall Mt., alt. 3500 ft., *E. F. Layser 830* (WS), June 8, 1969.

Geum rivale L. was known in Washington from one locality in Okanagon Co. (Thomson, J. W. Notes on the flora of the state of Washington. Rhodora 36:8–13. 1934). It has now been found in wet meadows in Pend Oreille Co. (*Layser 127*, WS).

Hieracium aurantiacum L. was noted by Hitchcock, et al. (op. cit.) to occur at Bremerton, Washington. The species is not uncommon along roadsides in the northern part of Pend Oreille Co. (*Layser 891*, NY, WS). This weedy species is rapidly becoming established in the Pacific Northwest.

Hieracium pratense Tausch, an aggressive European weed naturalized in eastern North America, has become established in the northern part of Pend Oreille Co. (*Layser 829*, NY, WS). This constitutes the first report of it from the Pacific Northwest, where it appears to have been introduced through erosion control seedlings of logging skid roads and road banks.

Mertensia platyphylla Heller was found in Pend Oreille Co. (*Layser 134*, F) and is the first report of this species east of the Cascades. The significance of this collection may involve more than a range extension, that is, a reassessment of the taxonomic affinities of *M. paniculata* (Ait.) G. Don. and *M. platyphylla* may be in order. Formerly these two species were thought to be allopatric. Evidence to the contrary not withstanding, this collection may provide support to the statement by Hitchcock (op. cit.) that *M. platyphylla* might better be considered a variety of *M. paniculata*.

Penstemon ellipticus Coult. & Fisch, is not uncommon in the northern part of Pend Oreille Co. and adjacent Stevens Co. on mountain peaks above 6000 ft. in elevation (*Layser 503, 867*, WS), and is an addition to Washington's flora.

Ranunculus longirostris Godr. was collected from Pend Oreille Co. (*Layser 80*, POM, WS) and is new for the state of Washington.

Sorbaria arborea Schneid, the cultivated false spirea, is occasionally found about old abandoned homesteads, where it reproduces and maintains itself by suckering (*Layser 1143*, WS).

Stellaria calycantha (Ledeb.) Bong. var. *calycantha* represents a new variety for Washington. It was collected in the northern part of Pend Oreille Co. (*Layser 310*, NY, WS). This variety is known from high latitudes in North America and was also reported from Oregon (Fernald, M. L., Gray's manual of botany. American Book Co., New York. 1950).—EARLE F. LAYSER, Department of Botany, Washington State University, Pullman 99163.

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EVIDENCE OF DIFFERENT ADAPTATIONS OF FLOWER COLOR VARIANTS OF ENCELIA FARINOSA (COMPOSITAE)

By Donald W. Kyhos

It has long been recognized that plants are extremely sensitive to their environments, particularly to moisture and edaphic factors. In natural undisturbed environments one of the most notable ways this remarkable sensitivity is revealed is by the general lack of hybrids between sympatric species which in disturbed habitats do produce hybrids and their various derivatives. A most lucid account of this well known phenomenon is provided by Anderson (1949). In most instances such sympatric species differ by several to many externally visible features and many differ also by a number of less obvious aspects, including physiological attributes.

In such cases where a relatively large number of genetically determined attributes differentiate ecologically distinct taxa, it seems likely that their differing ecologic adaptations will be correspondingly complex and hence difficult to analyze. On the other hand, with taxa that differ by one or at most a few genetically controlled features, the probability is much greater that their ecologic adaptations are simple and relatively easy to analyze.

Moreover, in the case of taxa that differ in many genetically based traits there appears to be little chance of obtaining evidence of the manner in which they differentiated. For example, whether geographic isolation was necessary for their divergence and their sympatry secondary, or whether it is possible that in some instances ecological differentiation initially resulted from a very few, or even a single heritable difference which permitted the occupation of new, closely adjacent sites well within effective pollination range of the original population.

Thus it is apparent that there are at least two substantial advantages in seeking populations to study that are ecologically distinct, but which have few genetic differences. First, it is more likely that their ecologic adaptation can be discerned and successfully analyzed and second, they are rather more likely to provide evidence of their mode of origin.

If a relatively simple heritable difference can bring about an altered ecologic adaptation in natural environments, then it should be possible to find populations at this initial stage of ecologic divergence when they differ by one, or at most, a very few heritable attributes, as appears to be the case in *Ricinus* in Peru (Harland, 1946) and *Spergula* in Europe (New, 1958; 1959) and perhaps in Australian Eucalyptus (Barber and Jackson, 1957).

Encelia farinosa Gray also appears to provide an excellent opportunity to study populations at such an early, but very significant stage of

divergence. Many populations of *Encelia farinosa* in the Sonoran Desert are polymorphic for a single conspicuous feature. In California, southern Nevada, Arizona, and adjacent Mexico, *Encelia farinosa* occurs as variety *farinosa*, in which the ray and disk florets are a bright yellow and it also occurs as *E. farinosa* var. *phenicodonta*, which differs only in that the disk florets are a rich brownish-purple. Populations may consist entirely of one or the other of these varieties, or may contain both intermixed. This seemingly trivial phenetic difference would not ordinarily lead one to suspect that it is an expression of a more fundamental biological difference. However, an examination of what proves to be a rather remarkable distribution pattern of these two varieties of *E. farinosa* strongly suggests that this apparently simple flower color difference has a high selective value itself, is part of a pleiotropic expression of genetic material which is adaptive in some other less obvious feature, or that this flower color character is genetically very closely linked with some other factor of high selective value that is not readily discernible. *Distribution pattern.*

Encelia farinosa is one of the dominant species of the Sonoran Desert, to which it is largely confined. It occurs in abundance from near the Cape region of Baja California, northward into the deserts of California, southern Nevada, southern Utah, Arizona, and Sonora, Mexico to Sinaloa (fig. 1). In the Cape region of Baja California, the southern-most populations of *E. farinosa* belong to var. *radians*, which occurs mainly in the tropical zone (Shreve and Wiggins, 1964). In the immediately adjacent deserts, *radians* is replaced by the very similar var. *phenicodonta*, which extends northward through the major portion of the Baja California peninsula to about San Felipe, Mexico. It is in this general region that the yellow disk flowered variety of *E. farinosa farinosa* appears and begins to replace *phenicodonta* in a most unusual pattern. In this more northern area of the Sonoran Desert, populations consisting entirely or predominantly of var. *phenicodonta* are largely confined to major river valleys. The yellow flowered populations of *E. farinosa* occupy much of the remainder of the northern Sonoran Desert, and are marginally sympatric with the brown disk flowered populations.

The writer first noticed this most unusual distribution pattern when making an approximately west to east transect across the Colorado River, near Blythe, California. While travelling south-eastward along the road from Rice, California toward Blythe, only yellow flowered *E.*

Fig. 1. *Distribution of Encelia farinosa.* The dotted line outlines the limits of the Sonoran Desert in northwest Mexico and the adjacent United States as defined by Shreve and Wiggins (1964). The shading denotes areas where *Encelia farinosa phenicodonta* occurs either in high concentrations or to the exclusion of *E. farinosa farinosa.* Five small disjunct *phenicodonta* localities are shown at about twice their proportionate size for clarity. *Encelia farinosa farinosa* occupies much of the remaining Sonoran Desert that is unshaded, as well as the area to the immediate north, included in this map.
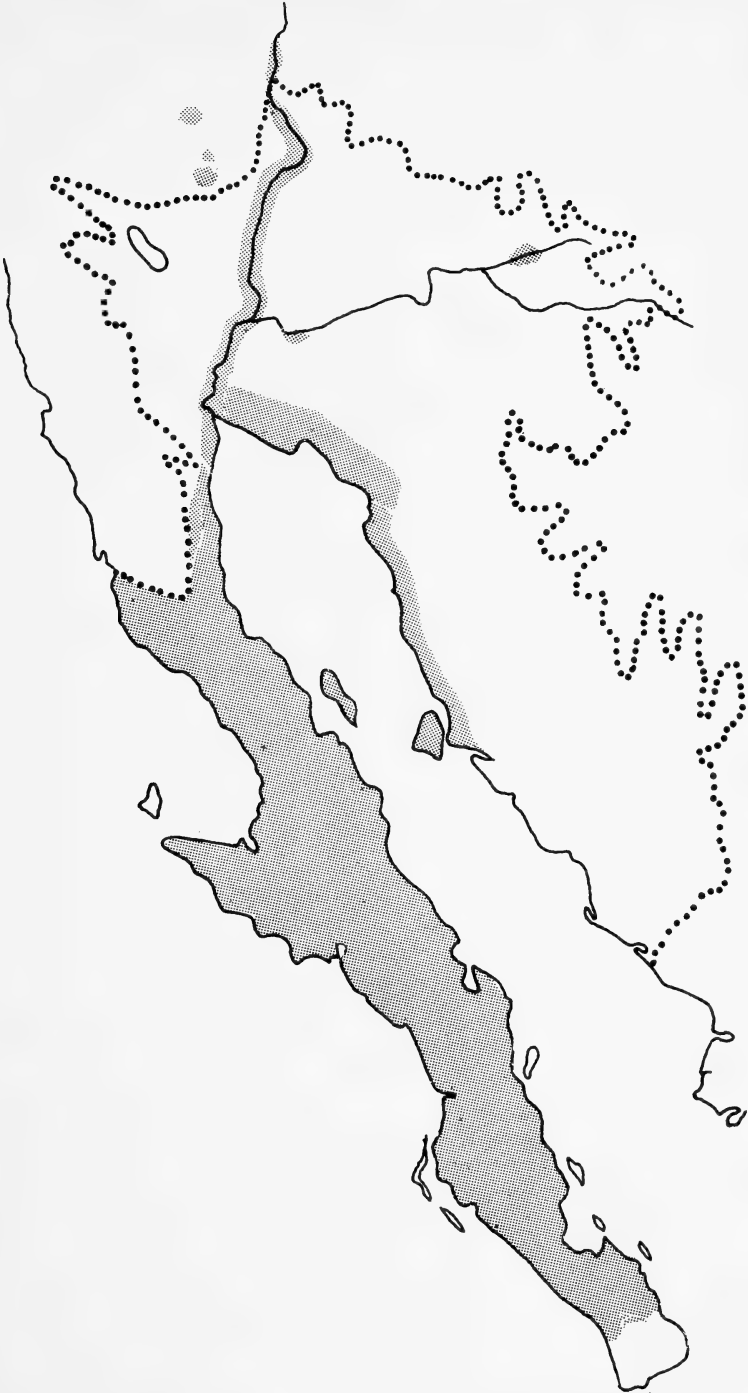
farinosa populations were initially encountered until a point approximately 26 miles from Blythe was reached (16 miles due west of the Colorado River). The next mile of *E. farinosa* populations included *phenicodonta* individuals at a frequency of 5 percent. In the next 6-mile interval approaching Blythe the frequency of *phenicodonta* individuals in the populations progressively increased to 38 percent, and upon approaching to within 9.3 miles of Blythe the frequency of *phenicodonta* plants in the population gradually increased to 70 percent. Within Blythe and its environs, intensive agricultural practices have essentially eliminated *E. farinosa,* however, upon crossing the Colorado River into Arizona, *E. farinosa* is once again abundant. Proceeding east from the Colorado River along U.S. Highway 60–70 for the first two miles only *phenicodonta* individuals are encountered and with each mile eastward the frequency of this taxon continually declines, until at 13 to 14 miles east of the Colorado River, *E. farinosa* populations consist of less than 7 percent *phenicodonta* plants. Still farther eastward only yellow flowered populations are encountered.

The well defined cline revealed by this initial transect suggested that *phenicodonta* individuals would probably be concentrated in other areas of the Colorado River valley to the north and south of Blythe, California. Much of the Colorado River valley to the south of Blythe is under intensive cultivation, and still farther south the few areas near the Colorado River that are readily accessible lack *E. farinosa.* This is also the case on both the Arizona and California sides of the Colorado River at Yuma. Somewhat to the north of Yuma, as the Picacho Recreation Area is approached from U. S. Hwy. 80, the clinal trend is again repeated, although less dramatically. In the area 8.1 miles north of Hwy. 80 on the road to the Picacho area, var. *phenicodonta* occurs in a frequency of less than 1.0 percent. At 11.7 miles north of the above locality the frequency climbs to 9.0 percent, and at the edge of the Colorado River the frequency reaches 15.0 percent.

Approximately 30 miles to the southwest of Yuma, near the confluence of the Rio Hardy and the Colorado River, in Mexico, a population sample of over 100 individuals includes only *phenicodonta* plants. Thirty-five miles to the south, near the mouth of the Rio Hardy, two closely adjacent samples, comprising 465 plants, average 90 percent *phenicodonta* individuals. Approximately 75 miles east of these three localities, along Mexico Hwy. 2, the frequency of *phenicodonta* drops to 4.7 percent and continues to decline still farther east from this point. Although the *E. farinosa* population samples in Mexico are few, they agree with the basic distribution pattern near Blythe. A sampling of *E. farinosa* along the Colorado River to the immediate north of Blythe, further confirms this clinal distribution pattern. In this area U. S. Hwy. 95 closely follows the course of the Colorado River for approximately 27 miles. An overall frequency of 84.8 percent *phenicodonta* individuals

occurs in the 27 mile interval. North of this area Hwy. 95 takes a north-westward course away from the Colorado River and it is at this point that the frequency of *phenicodonta* plants begins to decline and continues to decrease rapidly as one travels farther away from the Colorado River. If on the other hand, populations are sampled in an eastward direction, it is found that the frequency of *phenicodonta* plants increases as the Colorado River is approached and that they reach their highest incidence of 67.0 percent adjacent to the river in the Earp, California-Parker, Arizona area and to the north. Still farther north, with sampling along the road leading to the Chemehuevi Valley Indian Reservation, the pattern is repeated again. As the Colorado River is approached the proportion of *phenicodonta* in the populations progressively increases from zero (about 15 miles west of the river) to about 20 percent (within one or two hundred yards of the river). Twenty miles to the north in the Topock, Arizona area, a low incidence of 2.0 percent *phenicodonta* plants found at the river's edge quickly drops to zero within less than 0.2 miles from the river. Another 35 miles to the north, where Nevada State Highway 77 crosses the Colorado River, the pattern repeats, with *E. farinosa* populations within a quarter mile of the river containing approximately 20.0 percent *phenicodonta* individuals and with the frequency of these plants decreasing rapidly to zero at less than a mile from the river either in an eastward or westward direction.

In Arizona, other than along or relatively near the Colorado River valley, this writer has so far found only a single area where var. *phenicodonta* occurs in appreciable numbers. This locality is in south-central Arizona, in the Granite Reef Dam vicinity, about 10 miles northeast of Mesa, Arizona.

This site is most remarkable, since in a very small area it duplicates the pattern of distribution observed for the two varieties of *E. farinosa* in and around the much more extensive area of the Colorado River valley. Approaching this Granite Reef Dam locality from the south, one observes that within the interval of 2.2–0.4 miles from the margin of the canyon, the frequency of *phenicodonta* plants averages between 1.0 to 2.0 percent of the populations. In the interval between 0.4 miles south of the canyon and the canyon's south edge there is a progressive increase in *phenicodonta* individuals to 11.0 percent and in the next 0.2 mile interval, as one begins to descend into the canyon toward the Salt River, the frequency sharply increases to 37.0 percent and then to 62.0 percent within the next 0.3 miles. An even higher incidence of 88.4 percent *phenicodonta* plants is encountered at the base of the north wall of the canyon, essentially on the upper banks of the river.

While the association of var. *phenicodonta* with water courses is a prominent feature of its regional, as well as its local distribution pattern, it is apparent that relatively local concentrations of the variety are also found in another kind of habitat. The most notable of these occurs at the west base of the Granite Mountains, 0.2 miles south of the inter-

section of the road to Twentynine Palms with the road to Desert Center, California. This area is conspicuous because of the large sand dune that sprawls on the west slope of the Granite Mountains. Within and adjacent to a sandy wash that spills westward from these mountains, *E. farinosa phenicodonta* attains a frequency of 70.0 percent. Sampling to the immediate south of this locality reveals that this frequency rapidly drops to near zero within less than 5.0 miles, but again increases to about 17.0 percent in the populations at the southeast base of the Coxcomb Mountains. Continuing still farther south toward Desert Center this variety decreases to one percent or less of the populations. Approximately 15 miles north of the Granite Mountains locality, a concentration of *phenicodonta* attaining a frequency of about 20.0 percent occurs in the Iron Mountains. Another 33 miles to the north, approximately a 20.0 percent concentration of *phenicodonta* is found on the lower southeast-facing slope of Clipper Mountain, immediately northwest of Danby, California. In Arizona along U. S. Hwy. 80 at the summit of Mohawk Pass, immediately east of the town of Mohawk, var. *phenicodonta* locally makes up 54.0 percent of the population. Proceeding either east or west from this pass in the Mohawk Mountains, one descends and a rapid decrease in the frequency of *phenicodonta* plants occurs.

In Sonora, Mexico, where very little information on populations of *E. farinosa* is available, an examination of herbarium specimens suggests a most interesting geographic distribution of the two flower color forms of *E. farinosa*. Variety *phenicodonta* generally seems to occur abundantly only near the coast as far south as the latitude of Tiburon Island, and the yellow flowered populations appear to occupy largely the inland areas. Population samples are badly needed from this area of Mexico to establish if this suggested distribution pattern is correct.

Thus the data available from populations of *E. farinosa* indicate that *phenicodonta* is generally associated with major water courses or is largely confined to higher elevations of the California and Arizona deserts, and may be generally limited to the coastal area of the Sonoran Desert of Mexico.

INHERITANCE OF FLOWER COLOR

While a great deal yet remains to be learned about the inheritance of flower color in *E. farinosa,* some interesting observations from experimental crosses as well as natural populations shed some light on this important aspect. One of the first facts established was that when progeny are grown from *E. farinosa farinosa* and *phenicodonta,* where these taxa grow sympatrically in about equal proportions, both varieties can be obtained in the next generation from some of the plants belonging either to var. *farinosa* or *phenicodonta.* This progeny test clearly demonstrates that where the two varieties are sympatric they interbreed. This observation also suggests a simple inheritance for flower color. However,

an examination of natural populations reveals that there is the following additional complication. For while disk floret coloration as discussed above appears to be inherited in a relatively simple, perhaps single gene fashion, a survey of over 4000 individuals in natural populations shows a low incidence of individuals possessing brownish-purple anthers with corollas that are yellow or only slightly tinged with reddish-purple. However, this same sampling of plants has failed to reveal the reciprocal combination of yellow anthers and brownish-purple corollas in the disk florets. This observation seems to indicate that anther and corolla color are not determined by two independently segregating genetic factors, one for anther color and another for corolla color. Instead, it appears likely that one gentic factor produces yellow anthers and corollas, a second genetic factor produces brown anthers, with little or no effect on corolla color, and that a third factor produces brownish-purple anthers and corollas in the disk florets. This genetic scheme would explain the absence of plants with brownish-purple disk corollas and yellow anthers.

A similar inheritance pattern is seen in natural intergeneric hybrids between *E. farinosa* and *Geraea canescens*. Eleven such hybrids have been reported to date and of these, two had entirely brownish-purple disks. A third hybrid had yellow disk corollas and brownish-purple anthers, whereas the remaining eight hybrids had entirely yellow floral parts (Kyhos, 1967). *Geraea canescens* invariably has corollas and anthers that range in color from yellow to yellowish-orange, therefore the brownish-purple disk coloration in the intergeneric hybrid had to be inherited from *E. farinosa* in a dominant fashion. These observations reveal that the brownish-purple pigmentation of the disk corollas and anthers is transmitted to the hybrid in the same manner as in progeny of *E. farinosa*. It has not yet been possible by controlled crosses, however, to produce a large enough progeny in *E. farinosa* to fully examine the mode of inheritance of the three flower color forms. This is largely due to the difficulty of germinating the fruits of *E. farinosa* and the reluctance of this species to flower under greenhouse conditions.

Interspecific hybrids experimentally produced between *E. farinosa phenicodonta* and the yellow disk flowered *E. frutescens* further support an interpretation that flower color is probably inherited in a relatively simple way. These F_1 hybrids have all segregated into two classes: either they have had entirely yellow disk corollas and anthers, or these structures have been brownish-purple. Moreover, they have segregated in essentially equal frequencies with a Chi-square value conforming well to the 1:1 ratio expected in the test cross of a heterozygous dominant parent to a homozygous recessive one (see table 1).

Finally, controlled intraspecific crosses between individuals of *E. farinosa farinosa* and *phenicodonta* also indicate a relatively simple genetic basis for disk coloration, depending on which individuals are used as parents. So far in these crosses one of two things occurs. Either all the progeny are var. *phenicodonta* or the progeny segregate for the

TABLE 1. SEGREGATION OF DISK COLORATION IN F_1 HYBRIDS BETWEEN ENCELIA FRUTESCENS AND ENCELIA FARINOSA PHENICODONTA

	observed	expected	d	d^2		
Yellow disks	21	21	0	0		
					$X^2 = 0.0$	p = .99
Brownish-purple disks	21	21	0	0		

two varieties in a frequency that conforms well to a 1:1 ratio with the Chi-square test (table 2).

OBSERVATIONS ON POLLINATORS

Since disk floret color differentiates *E. farinosa farinosa* from *phenicodonta,* it was important to observe if natural pollinators distinguish between these two color forms and in so doing were perhaps responsible for the remarkable geographic distribution of these plant taxa. In line with this approach twelve populations were studied within and adjacent to the Colorado River valley, between Blythe and Needles, California. Six populations were in the area of sympatry of *farinosa* and *phenicodonta* and the remaining six were in areas occupied only by *farinosa,* between 10 to 14 miles removed from the Coloroda River. In all twelve populations it was found that pollen shed in both *farinosa* and *phenicodonta* begins about 9:00 a.m. and ceases in the early afternoon, with some day to day variation apparently depending on the weather. Pollen was shed somewhat earlier on warm sunny days than on cool cloudy days. Nevertheless, on any given day the two forms of *E. farinosa* always shed essentially synchronously, indicating that temporal factors apparently provide no reproductive isolation.

The remaining important aspect was whether different pollinators were attracted to the two flower color types. An examination of the six sympatric populations of *farinosa* and *phenicodonta* demonstrated a variety of flower visiting insects, including diptera, hymenoptera, lepidoptera, homoptera, and coleoptera. All of the species in each of these insect orders occurred on both varieties of *E. farinosa.* Morevover, they fly from individuals of each *E. farinosa* variety in a random fashion, with individual insects showing no preference for one flower color. The most important pollinator in each of these populations proved to be a small beetle, *Tanaops abdominalis* Le Conte, of the Malachiidae, which occurred in a frequency over 10 times greater than all of the other insect species combined. This beetle species moved from flower head to flower head, efficiently pushing among the disk florets, inadvertently picking up pollen along the way and then flying quickly and quite accurately to the next flowering head of *E. farinosa,* which might be either that of *farinosa* or *phenicodonta.*

TABLE 2. SEGREGATION OF DISK COLORATION IN PROGENY OF ENCELIA FARINOSA
FARINOSA × ENCELIA FARINOSA PHENICODONTA

	observed	expected	d	d^2		
Yellow disks	19	18	1	1		
					$X^2 = .111$	$p = >.70$
Brownish-purple disks	17	18	1	1		

DISCUSSION

Encelia farinosa phenicodonta has been recognized as a form or variety of *Encelia farinosa* Gray, for approximately fifty years (Blake, 1913: Johnston, 1924). Botanists who have dealt with these taxa apparently considered them to be simply flower color variants that differ only in this seemingly trivial aspect (Abrams and Ferris, 1960; Blake, 1913; Johnston, 1924; Munz, 1959; Shreve and Wiggins, 1964). However, closer scrutiny provides compelling evidence that these taxa have a much deeper and most intriguing biological significance. The distribution pattern of these taxa is quite remarkable and seemingly can only be interpreted as resulting from natural selection. It surely cannot be fortuitous that comparatively high frequencies of *phenicodonta* plants occur as a narrow, occasionally interrupted strand closely following the course of the Colorado River for approximately 260 miles north of the main body of this taxon (fig. 1). It seems even less likely that chance is a significant determinant in this remarkable distribution, when one notes that this 260 mile strand of *phenicodonta* is completely included within the range of *Encelia farinosa farinosa* and that these two taxa are sympatric along this entire 260 mile interval, and are known to interbreed with no evidence of reproductive isolation. In seeking an understanding of what selective forces may be operating to produce this striking distribution pattern, we perhaps can gain insight from the observation that the pattern along the Colorado River valley is dramatically repeated on a much smaller scale at Granite Reef Dam in east-central Arizona, near the city of Mesa. Both in the Colorado River valley and the Granite Reef Dam area of Arizona the populations of *Encelia farinosa* with the greatest proportion of *phenicodonta* plants occur closest to the water in these drainage systems, and as one travels away from the water course the frequency of *phenicodonta* individuals progressively declines until individuals of var. *farinosa* entirely replace *phenicodonta*. These observations suggest that in some manner water is important in determining the distribution of *E. farinosa farinosa* and *phenicodonta*. The apparent predominance of *phenicodonta* populations near the coast, with *farinosa* populations characterizing the more inland areas of Sonora, Mexico, again lends support to the idea that effective moisture is a crucial factor in the distribution of these two taxa. The credibility of this interpretation is further enhanced when it is recalled that the comparatively small

local concentrations of *phenicodonta* individuals, which occur away from water courses and large bodies of water, are found at higher elevations in the deserts of California and Arizona (e.g., at Mohawk Pass, Arizona, near Hwy. 80; and at Lobecks Pass near Hwy. 95, about 15 miles south of Needles, California; and in the Iron, Granite, Coxcomb Mts., and on Clipper Mt., all located in the Mohave Desert of California and its transition to the Colorado Desert to the south). These desert mountain ranges characteristically receive greater amounts of rainfall than the surrounding lower desert and thus in this regard would be similar to the habitats near water courses and large bodies of water.

It might be argued that the water course habitats, higher desert elevations, and coastal areas would provide cooler temperatures and thus temperature itself may be a critical factor in the distribution of these taxa. It is obvious that lower temperatures would tend to reduce transpiration and hence increase the amount of effective moisture. Thus it is important to separate the action of these two factors. An examination of maximum, minimum, and mean temperatures in the journal, *Climatologic Data,* through the ranges of these two taxa reveals no correlation with their distribution. If water stress is physiologically crucial in determining where these two taxa grow, it remains obscure how this factor is invariably associated with a seemingly unrelated characteristic such as disk flower coloration, except perhaps through pleiotropy or an extremely close genetic linkage.

On the other hand, the possibility cannot as yet be totally ruled out that flower color is itself adaptive. For example, it might be imagined that a pollinator preferring brownish-purple disks in *Encelia* is limited to areas of greater moisture in the desert, however no such evidence has yet been obtained. In fact, field observations support quite the opposite conclusion, namely, that the effective pollinators do not discriminate between *farinosa* and *phenicodonta* and progeny tests of these two taxa where they are sympatric bear this out.

While the selective factors which produce the remarkable distribution pattern of *farinosa* and *phenicodonta* are as yet unknown, some insight into the possible origin of these very similar taxa can be gained from what is known about the genetic basis of their differences. The available evidence indicates that these taxa are based on comparatively simple genetic differences. Brownish-purple disk floret coloration apparently can be inherited in a dominant, single gene fashion. Individuals of *phenicodonta* when crossed to var. *farinosa* either have produced progeny all with brownish-purple disks or in other crosses the progeny have segregated for brownish-purple and yellow disks in essentially equal frequencies. This rather simple situation becomes slightly more complicated, since many natural populations include a low frequency of individuals possessing yellow disk corollas associated with brownish-purple anthers. However, even with this additional aspect the genetic difference between these taxa appears to be quite simple, with disk

TABLE 3. LOCALITIES OF POPULATION SAMPLES

After each locality the letter t followed by a number indicates how many *Encelia farinosa farinosa* individuals occurred in the sample, whereas a number preceded by the letter p indicates how many *E. farinosa* phenicodonta individuals were in the sample.

ARIZONA. Near hwy 60–70, 2 mi E Colorado R., t-0, p-45; 1 mi farther E, t-10, p-240; 1 mi farther E, t-2, p-77; 1 mi farther E, t-17, p-122; 1 mi farther E, t-34, p-76; 1 mi farther E, t-33, p-251; 1 mi farther E, t-6, p-17; 1 mi farther E, t-30, p-14; 1 mi farther E, t-50, p-28; 1 mi farther E, t-28, p-3; 1 mi farther E, t-130, p-32; 1 mi farther E, t-157, p-16; 1 mi farther E, t-55, p-4, near hwy 80, 13.4 mi E jct with San Luis rd, t-96, p-4; 2 mi farther E, t-99, p-1, 1.7 mi farther E, t-337, p-6; 2.5 mi farther E, t-87, p-22, near hwy 80, 0.3 mi W Mohawk Pass summit, t-46, p-54; 1.1 mi E Mohawk Pass summit, t-170, p-30; hwy 80, 14 mi W jct with Theba rd, t-195, p-5; hwy 80, 15.9 mi W Buckeye, t-200, p-0; near hwy 80, 2.8 mi E jct with hwy 72, t-99, p-1; near hwy 80, 21 mi W jct with hwy 72, t-200, p-0; 9.3 mi N Wenden, t-200, p-0, rd to Dome, 6.3 mi N of hwy 80, t-94, p-11; 5.3 mi N of Tucson, t-200, p-0; 3-4 mi S Parker Dam, t-69, p-131; edge S rim Salt R. canyon at Granite Reef Dam, t-89; p-11; 0.8 mi farther S, t-98, p-2; 1.5-2 mi farther S, t-99, p-1; 2.2–2.7 mi farther S, t-152; p-3; 0.2 mi N, S rim Salt R. canyon, t-63, p-37; 0.3 mi farther N, t-38, p-62; N bank Salt R. at Granite Reef Dam, t-35, p-265.

CALIFORNIA. Hwy 60–70, 11.2 mi W Colorado R, t-110, p-24; near hwy 95, 8.4–33.4 mi N jct with hwy 60–70, t-106, p-384; at 34.6 mi N, above jct, t-48, p-532, and one plant with a light purple disk; at 46.5 mi N, above jct, t-48, p-4; Vidal Jct., t-39, p-1, 1 mi E Vidal Jct., t-16, p-7; 1 mi farther E, t-16, p-4; 0.8 mi farther E, t-172, p-28; from Earp to 7.4 mi N, t-17, p-35; Parker to 5 mi S, t-45, p-135; Vidal Jct. to 4 mi N, t-92, p-8; 1.5 mi farther N, t-99, p-1, 1.7 mi farther N, t-200, p-0; 1.2 mi farther N, t-290, p-10, 1 mi farther N, t-200, p-0, jct hwy 95 with rd to Chemehuevi Valley Indian Res., t-200, p-0; 4.8 mi farther E, t-100, p-0; 5.2 mi farther E, t-94, p-6; 4 mi farther E, t-49, p-1, 3.4 mi farther E, t-16, p-1, bank Colorado R. at Chemehuevi Indian Res., t-79, p-21; 4.3–5.5 mi W Colorado R. near hwy 66, t-100, p-0, W bank Colorado R. near hwy 66, t-98, p-2, 1.1 mi N Needles, t-99, p-1, S slope Clipper Mt. near Danby, t-182, p-38; hwy 95 at Lobecks Pass near jct with hwy 66, t-95, p-5, near rd from Blythe to Rice, 2 mi N Riverside Co. dump, t-30, p-70; 4.1 mi N, above, t-62, p-38, 3.5 mi farther N, t-190, p-10, 5.9 mi farther N, t-200, p-0; summit at S end Iron Mts., t-64, p-4; 0.4 mi farther W, t-26, p-0; 0.1 mi farther W, t-284, p-16; 0.5 mi N near summit Iron Mts., t-171, p-29; 0.5 mi S jct of rd to Desert Center and Twentynine Palms rd., t-44, p-173, 5.6 mi S of above, t-99, p-1; 8.3 mi farther S, t-83, p-17; 1 mi W of Desert Center, t-99, p-1; 0.1 mi N hwy 60–70, near rd to Twentynine Palms through Joshua Tree Nat. Mon., t-300, p-0; Morongo Wash, 2.6 mi N hwy 60–70, t-300, p-0; White Water Canyon, NW Palm Springs, t-400, p-2; 1 mi S, S border Anza-Borrego State Park near rd S2, t-200, p-0; Panamint Valley, 0.5 mi W Darwin Springs, t-200, p-0; 8.1 mi N hwy 80 near rd to Picacho Resort Area, t-107, p-1; 11.7 mi N, above, t-91, p-9; S bank Colorado R. at Picacho Resort Area, t-85, p-15.

MEXICO. 4–5 km S San Felipe, Baja California, t-0, p-100; 180 km N San Felipe, Baja California, t-0, p-100; 122 km N San Felipe, Baja California, t-19, p-142; 115 km N San Felipe, Baja California, t-24, p-280; Mexican hwy 2, 50 mi E San Luis, Sonora, t-100, p-5; Mexican hwy 2, 106 mi E San Luis, Sonora, t-96, p-4; Mexican hwy 2, 16 mi S Sonoyta, Sonora, t-98, p-2; 12.7 mi W Caborca, Sonora, t-22, p-123.

NEVADA. Near hwy 77, 0.3 mi W of Colorado R., t-90, p-23; 5.9 mi W, above, t-153, p-1.

corolla and anther coloration in the great majority of individuals match-
ing one another. Despite the relatively simple genetic basis for disk
floret coloration, this minor phenetic difference appears to be biologically
very important, perhaps in itself or possibly it is inextricably associated
with some factor that is crucial in determining where these taxa can
survive. In this situation the sympatric origin of one taxon from the
other appears quite feasible, with this simple genetic difference providing
the means by which a new or different habitat could be occupied,
resulting secondarily in allopatry of the two taxa in much of their
ranges, rather than allopatry being a necessary prerequisite for the
differentiation of these taxa.

The present distribution of *E. farinosa farinosa* and *phenicodonta*
suggests that the latter was previously more widespread, perhaps within
fairly recent times. *Phenicodonta* in the northern portions of the Sonoran
Desert not only occurs in high frequency, as a more or less continuous
strand, along the Colorado River valley, but it is found also as isolated
populations, some of which are quite small and far removed from the
great concentrations of *phenicodonta*. These scattered, well isolated pop-
ulations of *phenicodonta* may represent remnants of a once more
extensive distribution. The converse situation of scattered, well iso-
lated populations of *farinosa* in areas populated predominantly by
phenicodonta is unknown. This suggests that perhaps during a period
such as the hypsithermal, when comparatively warm, moist climates
may have extended farther north than today (Martin, 1963), *phenico-
donta* may also have occurred farther north than at present. With the
decline of the hypsithermal, *phenicodonta* may have retreated to the
south, leaving small isolated populations surviving in favorable local
sites as evidence of this former distribution, while *farinosa* came to
occupy most of the remainder of the Sonoran Desert, now untenable for
phenicodonta.

The relationships of *Encelia farinosa farinosa* and *phenicodonta* some-
what parallel those described for *Linanthus parryae* by Epling, Lewis,
and Ball (1960). In both *Linanthus* and *Encelia* different flower colors,
which have a relatively simple inheritance, seem to be indicative of
more deep-seated biological differences between individuals which ap-
parently interbreed freely. In each of these cases, the importance of these
distinct flower color differences as indicators of a crucial biological dif-
ference is revealed by the local and regional distribution patterns of
these flower color types. The distribution patterns in *Linanthus* and
Encelia appear to be the result of natural selection, but in neither case
is the nature of the selective forces known. However, the relatively
simple genetic differences of the individuals possessing these distinct
adaptations offer hope that their adaptations are commensurately simple
and hence ultimately can be understood.

SUMMARY

An unusual geographic distribution of *Encelia farinosa farinosa* and *E. farinosa phenicodonta* is presented as evidence that these taxa have a much greater biological significance than mere flower color variants. Crossing experiments indicate that the flower color differences of these taxa can be inherited in a single gene, dominant fashion. The association between flower color differences and the survival of these taxa in particular geographic areas remains unresolved.

LITERATURE CITED

ABRAMS, L., and FERRIS, R. S. 1960. Illustrated flora of the Pacific States. Stanford Univ. Press.

ANDERSON, E. 1949. Introgressive hybridization. Wiley and Sons., New York.

BARBER, H. N., and JACKSON, W. D. 1957. Natural selection in action in Eucalyptus. Nature 179:1267-1269.

BLAKE, S. F. 1913. A revision of Encelia and some related genera. Proc. Amer. Acad. Arts 49:362-641.

EPLING, C., LEWIS, H., and BALL, F. M. 1960. The breeding group and seed storage: a study in population dynamics. Evolution 14:238-255.

HARLAND, S. C. 1946. An alteration in gene frequency in *Ricinus communis* L. due to climatic conditions. Heredity 1:121-125.

JOHNSTON, I. M. 1924. Expedition of the California Academy of Sciences to the Gulf of California in 1921. The Botany (The Vascular Plants). Proc. Calif. Acad. Sci. IV. 12:951-1218.

KYHOS, D. W. 1967. Natural hybridization between Encelia and Geraea (Compositae) and some related experimental investigations. Madroño 19:33-43.

MARTIN, P. S. 1963. The Last 10,000 years. A fossil pollen record of the American Southwest. Univ. Arizona Press, Tucson.

MUNZ, P. A. 1959. A California flora. Univ. Calif. Press, Berkeley.

NEW, J. K. 1958. A population study of Spergula arvensis 1. Ann. Bot. (London) 22:457-477.

———. 1959. A population study of Spergula arvensis 2. Ann. Bot. (London) 23:23-33.

SHREVE, F., and WIGGINS, I. L. 1964. Vegetation and flora of the Sonoran Desert. Vol. 2. Stanford Univ. Press.

A NEW MYCOCALICIUM ON SCARRED SEQUOIA
IN CALIFORNIA

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Observations and collections have been made through many years of a discomycetous fungus that grows as a mat on an exudate from the surface of exposed heartwood of living specimens of the big tree, *Sequoiadendron giganteum* (Lindl.) Buchh., and the coast redwood, *Sequoia sempervirens* (Lamb.) Endl., in California. The fungus is never found on unscarred trees. It is present on the charred surface of burns and rarely on other large scars where there has been a flow of exudate from the wood.

The exudate flows down over the charred surface in spreading dark sheets or strands. It is watery in the fresh portion, becoming soft and sticky, then hard and brittle, lustrous Hessian Brown (R) to black on exposure and drying. The dried portion sometimes forms sheets up to 0.5 cm thick or balls up to 3 cm in diameter. In one instance the exudate streamed down over the burn for 5 m with the fungus growing over the lower 3 m of the area. The exudate usually issues from the more recently formed wood adjacent to the callus and not on the deeper parts of the burns.

Limited chemical examination of the dried exudate indicated that it is a very complex mixture of organic compounds, mostly water soluble, and very different from the resinous exudates from conifers such as pines and firs.

Surveys of fire-scarred specimens of the big tree were made in three areas:

	Exudate and fungus present	Exudate and fungus absent
Sequoia National Park (Giant Forest and Swanee Grove)	145	5
Yosemite National Park (Mariposa Grove)	35	5
Calaveras State Park (Calaveras Grove)	28	8
Total	208	18

Many fire-scarred trees of *Pinus, Abies,* and *Libocedrus* were examined in each of the above areas but no growth of the fungus was found.

The fungus has been found less often and less profuse in growth on the coast redwood than on the big tree of the Sierra Nevada. Flow of exudate onto scarred surfaces of the trees was found to be much more limited and growth of the fungus correspondingly less. For example, a survey of 63 fire-scarred trees in Big Basin Redwoods State Park, Santa Cruz Co., California, showed exudate present on 9, visible growth of the fungus on 3 with 1 showing mature apothecia, while 60 of the trees
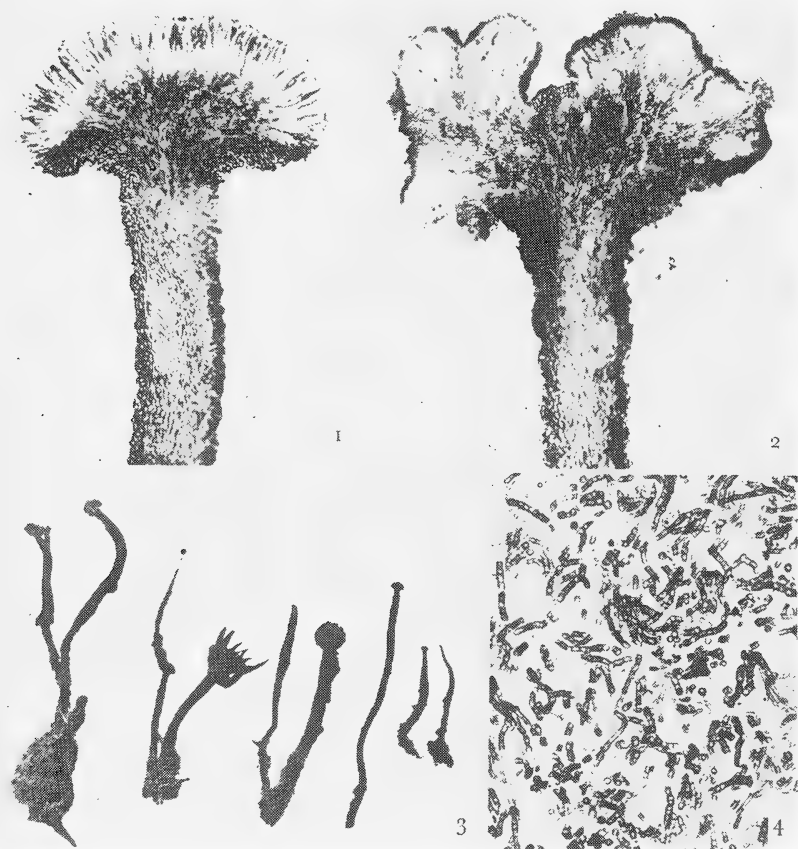
FIGS. 1–4. *Mycocalicium sequoiae:* 1, median section of apothecium (mazaedium lost in processing) ; 2, median section of lobulate apothecial head, $\times$ 82 ; 3, apothecia dissected from pseudostroma ; early stages right, proliferating secondary growth left, $\times$ 6 ; 4, microtome section of pseudostroma showing interlaced hyphae, $\times$ 82.

lacked any growth of the fungus. A search in the Cazadero Creek area in Sonoma Co. resulted in finding one tree with exudate and a growth of the fungus 5 $\times$ 3 cm in extent.

Approximately 100 fire-scarred trees were examined in Humboldt State Park, Humboldt Co., especially in the vicinity of Weott and Dyerville, and limited growth was found on 3 trees. Two of these occurrences were not on fire scars: scanty growth without fruting, forming a line of growth at the outer margin of the heartwood, where some exudate had appeared, was found on the cut end of a log from a recently felled tree. A second tree, at the roadside, had received a relatively large cut to remove the buttress next to the road. Quite copious exudate flowed from the cut and the fungus had formed a matted growth up to 3 cm thick; this showed some mature apothecia.

Besides scarcity of the exudate, another factor limiting growth of the fungus on the redwood is the growth of superficial molds over the surface of the discomycete mat. The molds frequently form floccose growths over the surface of the mat and apparently inhibit growth and fruiting of the discomycete. Such mold growths were seen in only a few instances on the fungus on the big tree. Growth of such superficial molds is undoubtedly favored by the relatively higher humidity surrounding those fire scars near the ground and commonly in deep shade in the fog-ridden belt occupied by the redwood. Corresponding sites on fire scars of big trees are surrounded through the long dry Sierran summer by less favorable environment for surface mold growth.

Description of the Fungus

Vegetative growth of the fungus varies from a floccose subiculum (very rare) to a mat-like pseudostroma (Vainio, 1890). The pseudostroma is resupinate and adherent to the charred surface. In extent of growth it varies greatly with moisture present. Examples were found where the pseudostromata covered a few cm^2, while some could be measured in m^2. The maximum development observed, on an extensive burn on a very large tree in Swanee Creek Grove, Sequoia National Park, measured 6 m at the ground perimeter and spread upward over the burn 0.5 to 1.5 m with tongues of growth extending upward for 2.4 m.

The pseudostroma is commonly 0.5 to 2 cm thick but may be up to 4.5 cm. It is composed of interlaced hyphae (fig. 4) which in younger growth near the edge are abundantly encrusted with crystals of calcium oxalate. The hyphae vary greatly in form and pigmentation. Those of younger portions appear hyaline under the microscope with thickened gelantinized walls. The walls do not stain—hence the spaced arrangement in the figure. In older portions the hyphae are mostly free of crystals, become amber to deep brown in color, and are frequently made up of torulose cells. The hyphae are 7-15 μ in diameter, with narrow lumina.

Stipitate apothecia develop in large numbers within the pseudostroma and grow to project above the surface of the mat (fig. 5). Stipes first appear as compact bundles of interlaced hyphae. As these elongate toward the surface of the pseudostroma, the outer cells of the cylindrical structure become thick-walled and dark in color. The stipes emerge through the surface of the pseudostroma as minute blackish columns with acute tips, giving the surface a distinctly setose character. There may be as many as 100 of these per cm^2. The stipes are 5-6 (4-8) mm long. Many remain as sterile pointed structures. In others, there is a branching of the hyphae within the tip and development of a palisade of hyphal elements to form the hymenium. The outer layer of blackened cells is reflexed to form the exciple (fig. 1), which surrounds a plane to convex hymenium. The surface of the hymenium is Chrysolite Green

Figs. 5–7. *Mycocalicium sequoiae;* 5, surface view of apothecia in nature; 6 mature apothecia from culture on wood block, vegetative growth scanty and floccose; 7, side view of apothecia in position in pseudostroma, × 15.

(R) and is farinose when dry due to the numerous green amorphous crystals attached to the surface. The apothecial heads are 0.5–1.5 mm in diameter. Stipes are frequently branched at various levels. Branching most commonly occurs near the tip, resulting in development of 2-20 contiguous convexities forming a lobulate head on a common stipe (fig. 2). Branching may occur at lower levels, each branch forming an apothecial head (fig. 7).

The stipitate apothecia are frequently found completely buried in the pseudostroma due to continued surface growth of the pseudostroma. These may show a second stipe developed as a proliferation through the hymenium of the first (fig. 3) or, more commonly, new stipes develop and grow through to the new surface.

Asci appear first near the center of the hymenial area and successively toward the margin as the surface expands and becomes more convex. The asci are inoperculate, cylindric-clavate, short stipitate, 50–70 $\times$ 6–10 μ, 8-spored, with the apical portion thick-walled. The walls of the asci stain blue with iodine. The spores are 1-celled, smooth, brown, uniseriate to biseriate in the ascus and 6–8 $\times$ 4–5 μ. Paraphyses are abundant, branched, colorless, with swollen tips 3–5 μ in diameter.

The walls and stipes of the asci gelatinize early, leaving the ascospores in linear groups of eight embedded in a gelatinous matrix and then extruded to the surface of the disk to form a mazaedium (Acharius, 1817). Acharius defined mazaedium as the superficial amorphous layer over the surface of the hymenium. Smith (1921), Dennis (1960), and Ainsworth (1961) define it as a type of fruit body or apothecium.

The production of asci is long-continued, new ones forming in areas where earlier ones have gelatinized and have been extruded to the surface.

No spermogonia were found as are described for some species of *Calicium* and related genera.

Cultural Studies

Germination tests showed a high percentage of viability in spores of material that had been held in a dry condition for as long as a year's time. Single ascospore cultures were grown on a number of common types of agar media and on extracts of *Sequoia* wood in agar. Maximum growth was a mycelial colony 2–5 mm in diameter at the end of 1 month at room temperature.

Blocks of heartwood of *Sequoiadendron giganteum* 15 cm long by 2.5 cm diameter and found by microscopic examination to be free of any fungus hyphae were soaked in water and sterilized by autoclaving in glass culture vessels with water to keep the lower ends of the blocks moist. Young colonies from single ascospores were placed on the end of the blocks. Such cultures were held at 10°C in dark, at room temperature in light and in dark, and in a daylight chamber at outdoor temperature. Growth occurred under all these conditions. It varied from light-brown floccose cushions to a delicate scarcely visible subiculum on the surface of portions of the blocks, the growth becoming darker with age. Least growth was in the chambers held at 10°C. Best growth was at outdoor temperature. Cultures held at room temperature showed an intermediate rate of growth. No marked difference was observed in vegetative growth in light and in darkness. No conidia were observed in any of the cultures.

Initial development of stipitate apothecia appeared in cultures in the outdoor chamber at the end of 4 months and these matured by the end

of 5 to 6 months (fig. 6). Cultures held at room temperature did not develop apothecia in either light or dark. Those held at 10°C for 5 months were sterile. Part of these were then moved to the outdoor chamber and apothecia developed after 3 additional months. Apothecia developed in culture chambers showed typical asci and spores. Vegetative growth was not the compact pseudostroma found in nature but at most a loose cottony felt (fig. 6).

MYCELIUM IN WOOD

Blocks of heartwood up to 5 cm thick were cut out from under burned areas in standing trees where the surface was covered by an extensive growth of the fungus. The wood appeared to be sound with no macroscopic evidence of decay. Microscopic examination of this wood showed occasional hyphae in the lumina of the wood cells, but there was no evidence of any appreciable destruction of the cell walls. The blocks of wood used for culturing the fungus were split and examined at intervals up to 1 year from the time the cultures were started, having been maintained in a moist condition. By the end of 3 months from the time of inoculation, hyphae were found within the cells throughout the length of the blocks. The hyphae ramified through the wood cells both longitudinally and transversely. The transverse hyphae commonly passed through pits and occasionally penetrated directly through the walls. Blocks that had been subjected to the action of the fungus for 1 year showed some discoloration, but no other evidence of change. Microscopic examination of these showed only slight corrosion of the cell walls. The evidence indicates that this fungus is capable of very slow digestion of wood when compared with the rate of action of other common wood-rotting fungi.

Field studies indicate that the fungus grows primarily on the exudate from the wood, this providing both the water and food material. Wood underlying areas bearing a heavy growth of the surface pseudostroma—which is certainly several years old—is sound in appearance and shows only very limited development of hyphae in the wood tissues. Kimmey and Lytle (1952) concur, saying, "Sterile black fructifications of an ascomycete were occasionally found growing in association with exudate from rift cracks in exposed heartwood but were not associated with decay."

CLASSIFICATION

The characters of the apothecium place this fungus in the Caliciaceae. This family is usually classified under the lichens and its members usually consist of a fungus-algal complex. Various authors have, however, described species under this family as lacking any algal component. They have frequently placed such species in the same genera with typical lichen species. Vainio (1890) established the genus *Mycocalicium* for species lacking gonidia and having one-celled, brown ascospores. Reinke

(1895) proposed the Protocaliciaceae as a sub-family under the Caliciaceae for those organisms that were non-lichen in nature and cited *Mycocalicium* and *Mycoconiocybe* as generic names for non-lichen members of the genera *Calicium* and *Coniocybe*. Vainio (1927) lists some seven genera of gonidia-free organisms under the Caliciaceae and gives descriptions for five species of *Mycocalicium*.

Various other workers have not accepted these proposals. Rehm (1896) lists seven genera and numerous species of this group of Discomycetes that do not have algal components. He states that the majority of the species in the family are true lichens and no generic distinction is made between the lichen and non-lichen members. He lists *Mycocalicium* as a synonym under *Calicium*. Schneider (1897) used the name *Mycocalicium* for typical lichens with one-celled ascospores as a distinction from *Calicium* with two-celled ascospores. The name was used in the same sense by Nearing (1962). Keissler (1938) lists all the gonidia-free segregates as synonyms under the regular lichen genera having gonidia, and discusses the difficulty of being able to know for certain that the lack of gonidia may not be merely a fortuitous circumstance. Arnaud (1931) presented the Caliciaceae as a complex of diverse elements drawn from the lichens, Sphaeriaceae, Perisporiaceae, Hysteriaceae, etc. It is very difficult to characterize clearly such a mixture. I prefer to consider the family as a more restricted group.

Clements and Shear (1931) divided the genera of the Caliciaceae into two groups: one saprophytic and non-lichen, the other forming typical lichen thalli with algae.

Studies, including the complete life cycle in pure culture, have proved that our fungus is not a lichen. The form of the apothecia, the manner of maturation, and the characteristics of the ascospores agree with those of the genus *Mycocalicium* as established by Vainio. Vegetative development and habitat are highly distinctive and lead to the conclusion that this is an underscribed species of *Mycocalicium*.

Mycocalicium sequoiae Bonar, sp. nov. Pars vegetativa corallina uvidaque ex subiculo hyphae intertextae vel ex pseudostromate expanso crassitudine usque ad 4.5 cm constans, in sinectute atrata rimosaque; apothecia super superficium extendentia; stipes teres, simplex vel ramosus, 4.8 mm longus; apice acuto demum capita turbinata diam. 0.5–1.5 mm formante; apothecia primaria demum pseudostromate obvoluta inde evolvent plura; asci inoperculati, cylindro-clavati, 8-spori, evanescentes, 50–70 $\times$ 6–10 μ, parietes iodino tingentes; gelatina sporaeque mazaedium in sicco crystalla irridia obtectae formantes; ascosporae 1-cellulae, ellipsoideae, fuscae, 6–8 $\times$ 4–5 μ, in asco uni-vel biseriatae; paraphyses ramosae; sporae asexuales deficientes.

Habitat. On exudate from exposed heartwood of living sequoias in California.

Holotype. On *Sequoiadendron giganteum,* Crescent Meadow, Sequoia

National Park, Tulare C.o, California, *Lee Bonar* (UC 1403569-holotype), July 1, 1935.

Collections studied. In addition to the holotype, 12 collections on *S. giganteum* from Calaveras, Mariposa, and Tulare counties, and 4 collections on *S. sempervirens* from Humboldt, Sonoma and Santa Cruz counties (all UC) were studied.

I am indebted to various persons for collections and aid in this study, especially to Doris Brenneman for help in the critical laboratory studies, to Rimo Bacigalupi for the Latin description, and to Victor Duran and A. A. Blaker for photographs.

LITERATURE CITED

ACHARIUS, E. 1817. Om de cryptogamiske vexter, som komma under nann af Calicioidea III. Kongl. Vetensk. Akad. Handl. 1817:220-244.

AINSWORTH, G. C., and G. E. BISBY. 1961. Dictionary of the fungi. Kew, England.

ARNAUD, G. 1931. Les Asterinees V. Etude sur les champignons parasites; Caliciacees, Hemispheriacees, etc. Ann. Epiphyt. 16:235-302.

CLEMENTS, F. C., and C. L. SHEAR. 1931. The genera of the fungi. New York.

DENNIS, R. W. G. 1960. British cup fungi. London.

KEISSLER, K. VON. 1938. Die Flechten: Caliciaceae. *In* Rab., Krypt. Fl. Deutschl., Oesterr. u.d. Schweiz. 9(1, 2):520-527.

KIMMEY, J. W., and P. C. LYTLE. 1952. Fungi associated with cull in redwood. Forest Sci. 1:104-110.

NEARING, G. G. 1962. The lichen book. Ashton, Maryland.

REHM, H. 1896. Ascomyceteen, Hysteriaceen und Discomyceteen. *In* Rab., Krypt. Fl. Deutschl., Oesterr. u. d. Schweiz. 1(3):382-414.

SCHNEIDER, A. 1897. A textbook of general lichenology. Binghamton, New York.

SMITH, A. 1921. Lichens. Cambridge.

REINKE, I. 1895. Abhandlungen über Flechten. Jahrb. Wiss. Bot. 28:39–150.

VAINIO, E. A. 1890. Etude sur le classification naturelle et la morphologie des lichens du Bresil. Act. Soc. Fauna Fl. Fenn. 7(2):1-256.

————. 1927. Lichenographia Fennica. III. Coniocarpae. Act. Soc. Fauna Fl. Fenn. 57:1-138.

NOTES AND NEWS

WALLACE ROY ERNST, 1928–1971.—Wallace Ernst, Curator of Botany in the Smithsonian Institution died of cancer in Washington, D.C., on October 8th, 1971, after an illness of about nine months. In addition to his Smithsonian curatorship, he held a professorship in absentia at the University of Kansas, and was for a number of years a valuable member of the editorial board of Madroño. Dr. Ernst was a recognized authority in the systematics of the Papaveraceae and an accomplished worker in the field of floral morphology. He received his first two degrees at the University of California at Los Angeles and his doctorate at Stanford University. An appreciation and biography will appear in Madroño in the near future.

—J. H. T.

THE GALIUM ANGUSTIFOLIUM COMPLEX (RUBIACEAE) OF CALIFORNIA AND BAJA CALIFORNIA

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Introduction

There are three groups of dioecious *Galium* species endemic to western North America, of which the *G. angustifolium* complex is the smallest, both in number of species and in its range. The other two were treated in earlier papers, as follows: the *G. multiflorum* complex of western United States, Sonora and Baja California (Ehrendorfer, 1956; 1961; Dempster, 1959; Dempster and Ehrendorfer, 1965); the fleshy-fruited polyploid complex of California, Oregon and Baja California (Dempster, 1958; 1962; Dempster and Stebbins, 1965; 1968). The imperfectly dioecious, or polygamous, group exemplified by *G. parishii* Hilend & Howell and *G. wrightii* Gray has not been comprehensively dealt with, although its relationship to the *G. multiflorum* group is obviously close and, quite likely, ancestral.

All four groups have four-leaved whorls, with the exception of *G. hardhamae* Demp. of the fleshy-fruited group, which has six leaves per whorl. The *G. angustifolium* complex, subject to the present paper, has important characters in common with the *G. multiflorum* group and the polygamous *G. parishii* group, notably the long straight specialized fruit hairs and the three-nerved leaves. Resemblance to the fleshy-fruited group is less marked, but is apparent in the rather extraordinary habit of reaching upward with greatly elongated stems which later become the slender woody scaffolds for subsequent herbaceous growth. Much of *G. angustifolium* Nutt. of the present group, and especially *G. nuttallii* Gray of the fleshy-fruited group exemplify this character.

The distribution of the present group, unlike that of the *G. multiflorum* complex, is not archipelagic, but resembles more that of the fleshy-fruited group in that it is largely continuous. Its occurrence (fig. 1) is chiefly in the southern coastal ranges, from the Sierra San Pedro Mártir of Baja California, northward into the Santa Lucia and Gabilan ranges of Monterey and San Benito counties. In Kern Co. it also occurs farther inland in the Tehachapi, Greenhorn, and Piute ranges, and at the southern end of the Sierra Nevada west of the crest. In the Mohave Desert it has been collected as far east as the Providence Mountains.

The *G. angustifolium* complex consists of one narrowly endemic, diploid, uniform species, *G. jepsonii*, one widely distributed polymorphic species on three ploidy levels, *G. angustifolium,* and one local hexaploid species, *G. johnstonii*, which apparently originated by hybridization from the other two. *Galium johnstonii* expresses its hybrid origin in
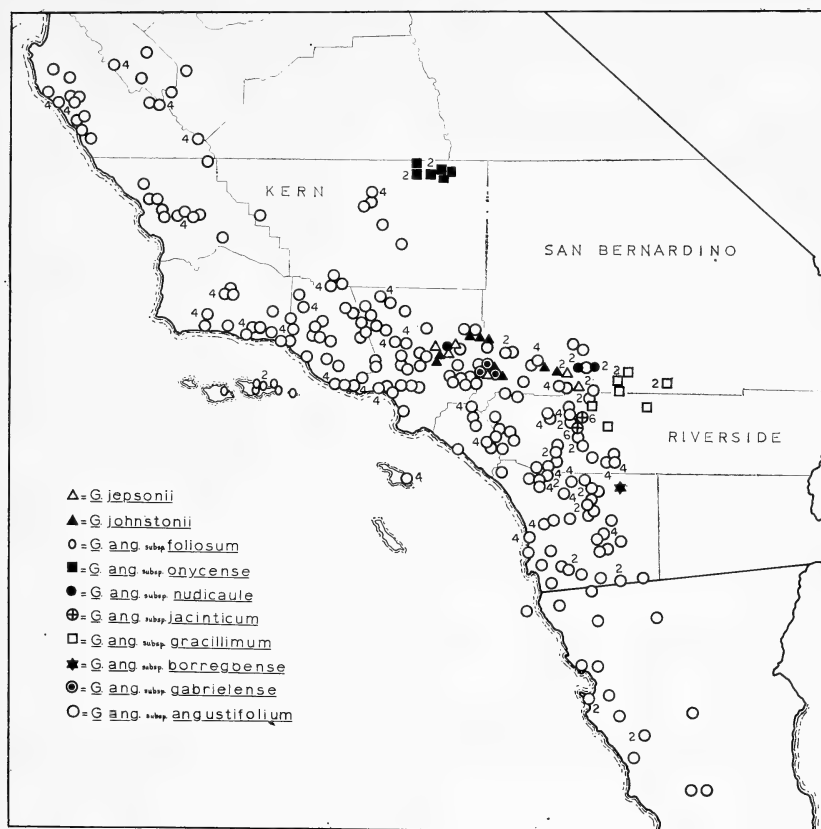
Fɪɢ. 1. Map showing entire distribution of the *G. angustifolium* complex. Numbers indicate actual chromosome counts divided by 11.

great variability within small populations, but seems to be genetically isolated from both parental species and is not taxonomically subdivisible. *Galium angustifolum*, on the other hand, is divisible into subspecies, of which the number recognized is limited chiefly by practical considerations. Unfortunately the diploids are not clearly separated from the tetraploids with respect to morphology and geography. Consequently we must content ourselves with describing as separate subspecies several of the forms which are morphologically uniform and geographically restricted, leaving the large remainder, both diploid and tetraploid, under ssp. *angustifolium*. Throughout this paper, all subspecies mentioned should be understood as belonging to *G. angustifolium*.

Were it not for the existence of the intermediate species *G. johnstonii,* there would scarcely be adequate reason to include *G. jepsonii* in the *G. angustifolium* complex. The concentration of leaves near the base of the plant, the truly campanulate corollas, and the short falcate ovary- and fruit-hairs all set *G. jepsonii* sharply apart. There is furthermore
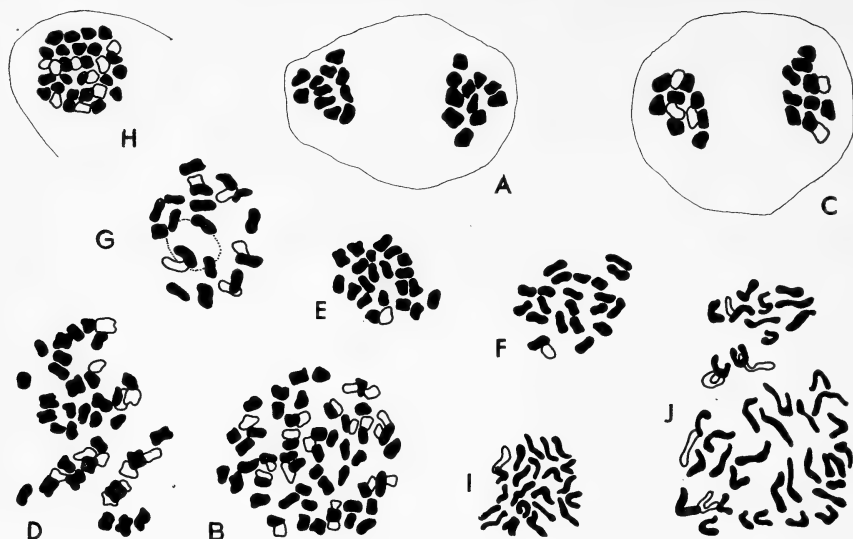
Fig. 2. Representative chromosome figures × 1700: A, *G. jepsonii*, meiotic, n = 11 *(4120)*; B, *G. johnstonii*, mitotic, **2n = 66** *(4118)*; C-J, *G. angustifolium*; C, ssp. *angustifolium*, meiotic, **n = 11** *(4128)*; D, ssp. *angustifolium*, mitotic, **2n = 44** *(4067)*; E, ssp. *foliosum*, mitotic, **2n = 22** *(4083)*; F, ssp. *onycense*, mitotic, **2n = 22** *(4207)*; G, ssp. *gracillimum*, mitotic, **2n = 22** *(4174)*; H, ssp. *jacinticum*, meiotic, 1 pole, **n = 33** *(4129)*; I, ssp. *nudicaule*, mitotic, **2n = 22** *(4147)*; J, ssp. *gabrielense*, mitotic, **2n = 44** *(4295)*.

no evidence that genes from *G. jepsonii* are present in any subspecies of *G. angustifolium*, nor that hybridization between the two species ever occurs on the diploid level. It is possible that *G. johnstonii* originated only once, perhaps from unreduced gametes of *G. jepsonii* and tetraploid *G. angustifolium*.

Any definition of the complex is therefore brief: plants perennial, dioecious, with 4 leaves to a node (i.e., 2 leaves and 2 stipular appendages, looking exactly alike); the generally narrow leaves obscurely 3-nerved, the marginal hairs spreading or apically directed; fruits with specialized hairs which are not uncinate.

The present group has gone a little farther with polyploidy than has the *G. multiflorum* complex, although not nearly so far as the fleshy-fruited group (Dempster and Stebbins, 1965; 1968). Of the species and subspecies here recognized, 5 are diploid, 1 tetraploid, 1 indistinguishably diploid and tetraploid, 2 hexaploid, and 1 unknown (fig. 2, table 1). The basic chromosome number is 11. The geographically isolated subspecies *foliosum* and *onycense* are both diploid. No comparable degree of isolation occurs within the fleshy-fruited group, although it is usual in the *G. multiflorum* complex.

The center of evolutionary activity appears to have been in the San Gabriel, San Bernardino, and San Jacinto Mountains, where the great

TABLE 1. CHROMOSOME COUNTS IN THE GALIUM ANGUSTIFOLIUM COMPLEX

(An asterisk after a collection number means that the count was about the number reported. All counts are from California, except the first two listed.)

G. *angustifolium* ssp. *angustifolium*. **2n = 22.** Baja California. Santo Tomas, *4229;* Punto Banda, *Hardham & Dempster 17,010**. Riverside Co.: *1890**; *4128;* *4131; 4134; 4177; 4178; 4239; 4241; 4245.* San Bernardino Co.: *4126; 4145**; *4149**. San Diego Co.: *4179; 4181**;*4182**; *4183; 4330; Bacigalupi 8282; Bacagalupi 8288; Bacigalupi 8371**. **2n = 44.** Kern Co.: *4208**; *4218.* Los Angeles Co.: *4114**; *4115**; *4116; 4117; 4169**; *4172**; *4190; 4191**; *4216; 4369**; *4731.* Monterey Co.: *4067; 4159; 4161**; *4193.* Orange Co.: *4352**; *4354**. Riverside Co.: *4137**; *4176**; *4249; 4258; 4276.* San Benito Co.: *4194**. San Bernardino Co.: *4141**; *4142; 4152; 4154**. San Diego Co.: *4189**; *4333; 4336**; *4340**; *4341**; *4347**; *Hardham & Dempster 17,013.* San Luis Obispo Co.: *Stebbins s. n.**. Santa Barbara Co.: *4163**; *4164**; *4166**; *4167.* Ventura Co.: *4111; 4113**; *4168**.

G. *angustifolium* ssp. *foliosum*. **2n = 22.** Santa Barbara Co.: *4083.*

G. *angustifolium* ssp. *gabrielense*. **2n = 44.** Los Angeles Co.: *4295.* San Bernardino Co.: *4294**.

G. *angustifolium* ssp. *gracillimum*. **2n = 22.** San Bernardino Co.: *4173; 4174.*

G. *angustifolium* ssp. *jacinticum*. **2n = 66.** Riverside Co.: *4129; 4130; 4244**; *4246**.

G. *angustifolium* ssp. *nudicaule*. **2n = 22.** Los Angeles Co.: *4123**; *4236.* San Bernardino Co.: *4147; 4150.*

G. *angustifolium* ssp. *onycense*. **2n = 22.** Kern Co.: *4206**; *4207.*

G. *jepsonii*. **2n = 22.** Los Angeles Co.: *4120; 4122.* San Bernardino Co.: *4143.*

G. *johnstonii*. **2n = 66.** Los Angeles Co.: *4118, 4121.*

majority of forms are to be found (fig. 3). Tetraploidy probably occurred repeatedly, involving ssp. *nudicaule* at least once to produce ssp. *gabrielense,* and perhaps once again in the production ultimately of hexaploid ssp. *jacinticum.* Other tetraploids, probably not involving either *G. jepsonii* or ssp. *nudicaule,* produced the taller forms of ssp. *angustifolium* which spread northward and westward, remaining regionally sympatric with the diploid form in San Diego Co. and the San Jacinto and San Bernardino Mountains, and occupying alone the northern and western remainder of the range, including the lower altitudes of the San Gabriel Mountains. The desert diploid ssp. *gracillimum* probably originated from the tall southern diploid by selection for the desert habitat. Subspecies *onycense,* on the other hand, is probably much more ancient in its isolation, and had not obviously contributed to any polyploid. The diploid island race ssp. *foliosum* is probably also very ancient, and may or may not have been involved in the production of the mainland tetraploids.

Again, in this group, for the third time, we find hispid polyploids with no visible hispid diploid progenitors. In the *G. multiflorum* complex (Dempster and Ehrendorfer, 1965) we observed two very hispid tetraploids, *G. hilendiae* Dempster & Ehrend. and *G. munzii* Hilend & Howell, the former related to diploid *G. multiflorum* Kell. and the latter to diploid *G. magnifolium* Dempster, both lacking any obvious, adequately hispid diploid ancestor. In the fleshy-fruited group (Dempster
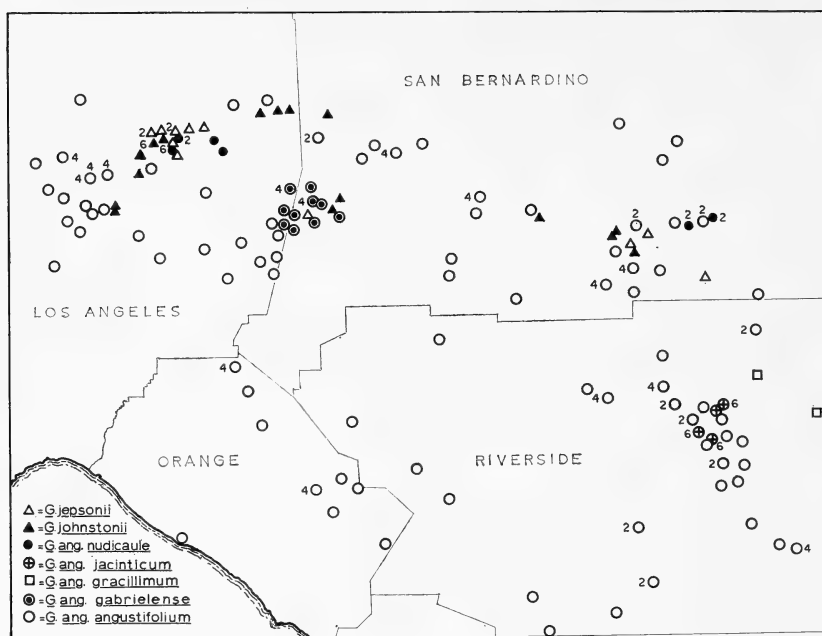
and Stebbins, 1965; 1968), the hispidity of some of *G. bolanderi* Gray and *G. andrewsii* Gray ssp. *gatense* (Dempster) Dempster & Stebbins cannot be adequately explained by assuming hybridization between existing diploids. In the present group, the hispid tetraploid forms of ssp. *angustifolium*, as well as the hispid tetraploid ssp. *gabrielense*, cannot be explained with reference to existing diploids. One may postulate the extinction of one hairy diploid ancestor, but it strains credulity to suppose that only the hairy diploids have become extinct in all three of our dioecious West American species groups. One is left to wonder whether some additive genetic mechanism may not be at work to cause greater hairiness in some polyploids than was expressed in their diploid ancestors.

Morphology

Habit is of some taxonomic importance. Low tufted forms, lacking woody stems above ground (fig. 4A-C), characterize *G. jepsonii*, ssp. *nudicaule*, usually ssp. *gabrielense*, and sometimes ssp. *angustifolium*. Taller forms with perennial scaffold stems (fig. 4D), as in much of ssp. *angustifolium*, may grow as high as 100 cm.

Stems in this genus are 4-sided, i.e., basically square in cross section. The angles are, however, more or less thickened and broadened by ex-
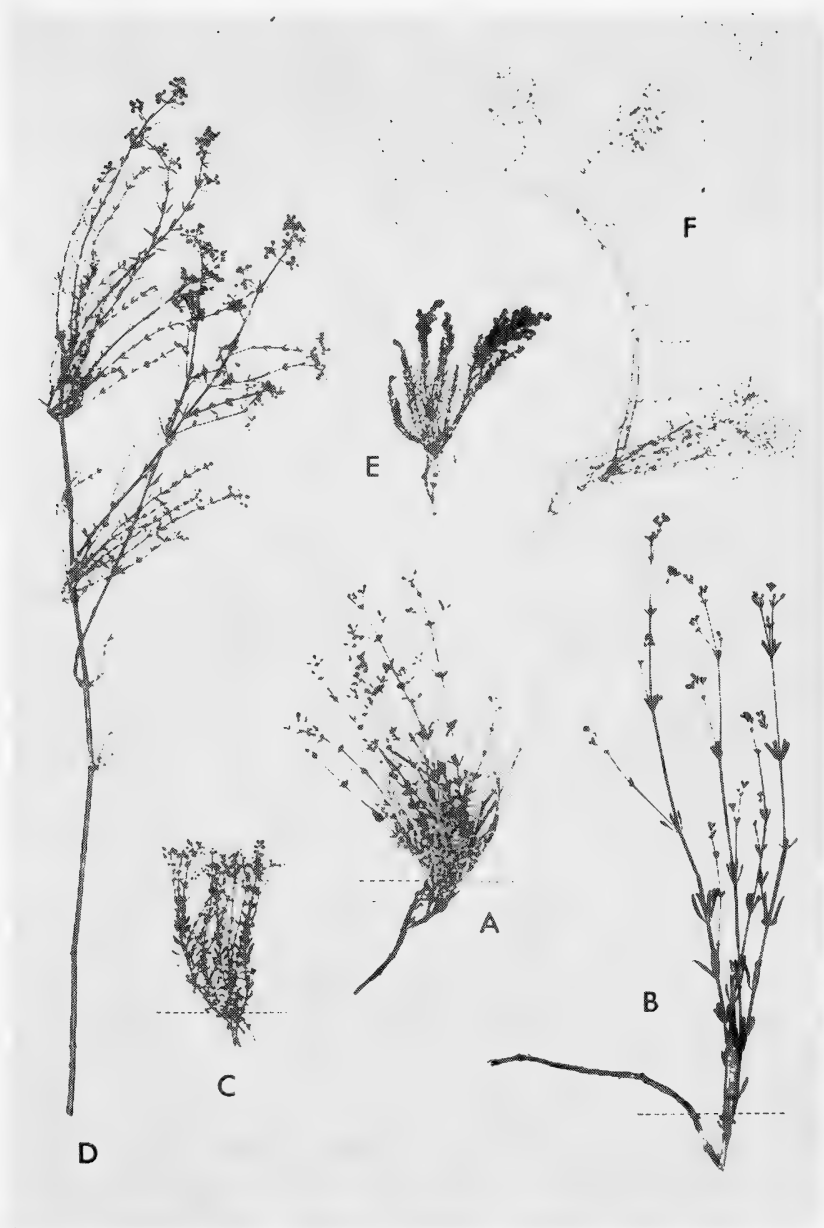
Fig. 4 Some representative habits × ⅓. In A, B, and C, ground level is indicated by dotted lines; D, E, and F are fragments broken off well above ground level. A, *G. jepsonii,* Cloudburst Summit *(4235);* B, *G. johnstonii,* Chilao Recreation Area *(4234);* C-F, *G. angustifolium:* C, ssp. *nudicaule,* Cloudburst Summit *(4236);* D, ssp. *angustifolium,* Little Thomas Mountain *(4347);* E, ssp. *foliosum,* Santa Rosa Island *(Niehaus 459);* F, ssp. *gracillimum,* 49 Palms Canyon *(4174).*
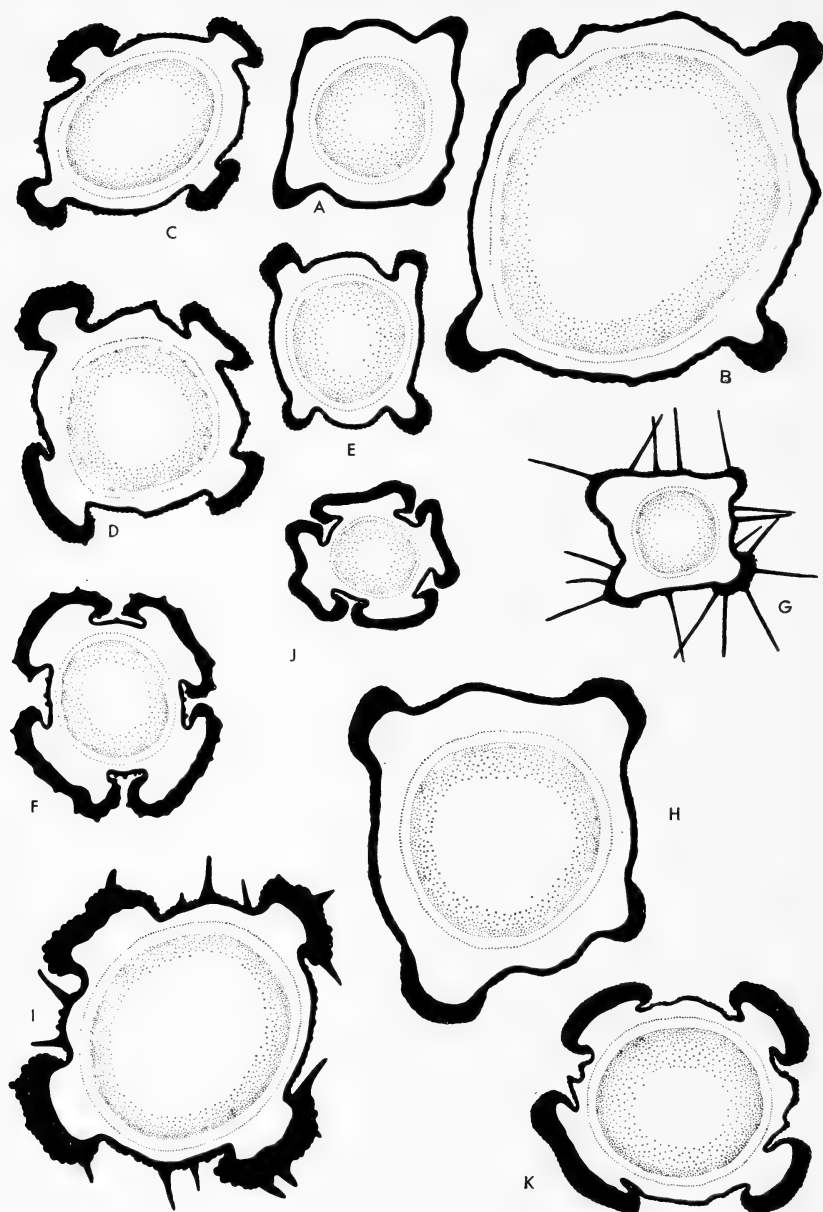
Fig. 5. Stem cross sections, × 24, to show comparative development of the angles. Collenchyma tissue with epidermis shown in black; stippled areas represent xylem, dotted circles endodermis. Size differences, although partially dependent on age of stems, are nonetheless of some taxonomic importance. A, *G. jepsonii*, San Gabriel Mountains *(4235);* B, *G. johnstonii* north side San Gabriel Mountains *(4156);* C-K, *G. angustifolium;* C, ssp. *nudicaule,* San Bernardino Mountains *(4147);* D, ssp.
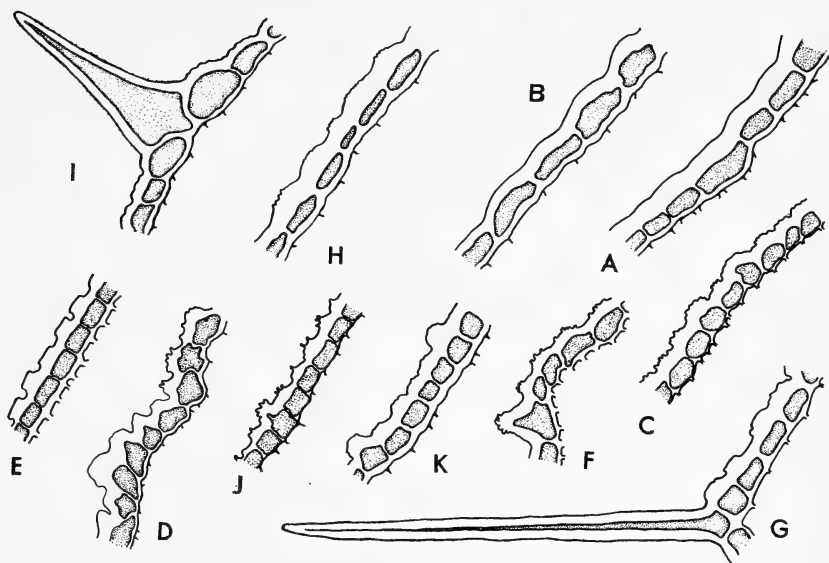
Fɪɢ. 6. Details of epidermis from the sides (not angles) of the stem cross sections in
Fɪɢ. 5: A, *G. jepsonii;* B, *G. johnstonii;* C–K, *G. angustifolium:* C, ssp. *nudicaule;*
D, ssp. *gracillimum;* E, I, ssp. *angustifolium;* F, ssp. *onycense;* G, ssp. *gabrielense;*
H, ssp. *jacinticum;* J, ssp. *borregoense;* K, ssp. *foliosum.* All × 140.

trusion of the cortex and addition of collenchyma. Such enlargement of
the angles occurs in varying degrees in the different species and sub-
species of this group (fig. 5). It is least developed in *G. jepsonii* (fig.
5A), and has been carried to such an extreme in young stems of ssp.
borregoense (fig. 5J) and ssp. *onycense* (fig. 5F) that the angles appear
as sides and the nearly covered sides appear as mere longitudinal
fissures. Subsequent growth in width of the stems causes the sides to
emerge into visibility.

Stems are chiefly glabrous, but in ssp. *gabrielense* (fig. 5G) and in
much of the tetraploid material of ssp. *angustifolium* (fig. 5I) they are
well supplied with hairs. Stems of ssp. *nudicaule* (fig. 5C), and others
to a less noticeable degree, are papillose, the papillae consisting of soli-
tary enlarged epidermal cells. Figure 6 shows details of the epidermis
of the sides (not angles) of the stems illustrated in fig. 5.

All plants of the *G. angustifolium* complex apparently have stomata
on both leaf surfaces. All leaves have 3 nerves, although the 3-nerved
condition is not very obvious, and the lateral nerves, even when seen in

gracillimum, Black Rock Spring (*Cole 989,* POM); E, ssp. *angustifolium,* diploid
form from Rincon Springs, San Diego Co. *(4339);* F, ssp. *onycense,* east of Onyx
(1432); G, ssp. *gabrielense,* Ontario Peak *(Johnston 1616,* UC) ; H, ssp. *jacinticum*
(4244, type) ; I, ssp. *angustifolium,* hairy tetraploid form from Del Mar *(4347);*
J, ssp. *borregoense,* Palm Canyon *(4375);* K, ssp. *foliosum,* Santa Cruz Island *(Elli-
son s.n.,* UC).
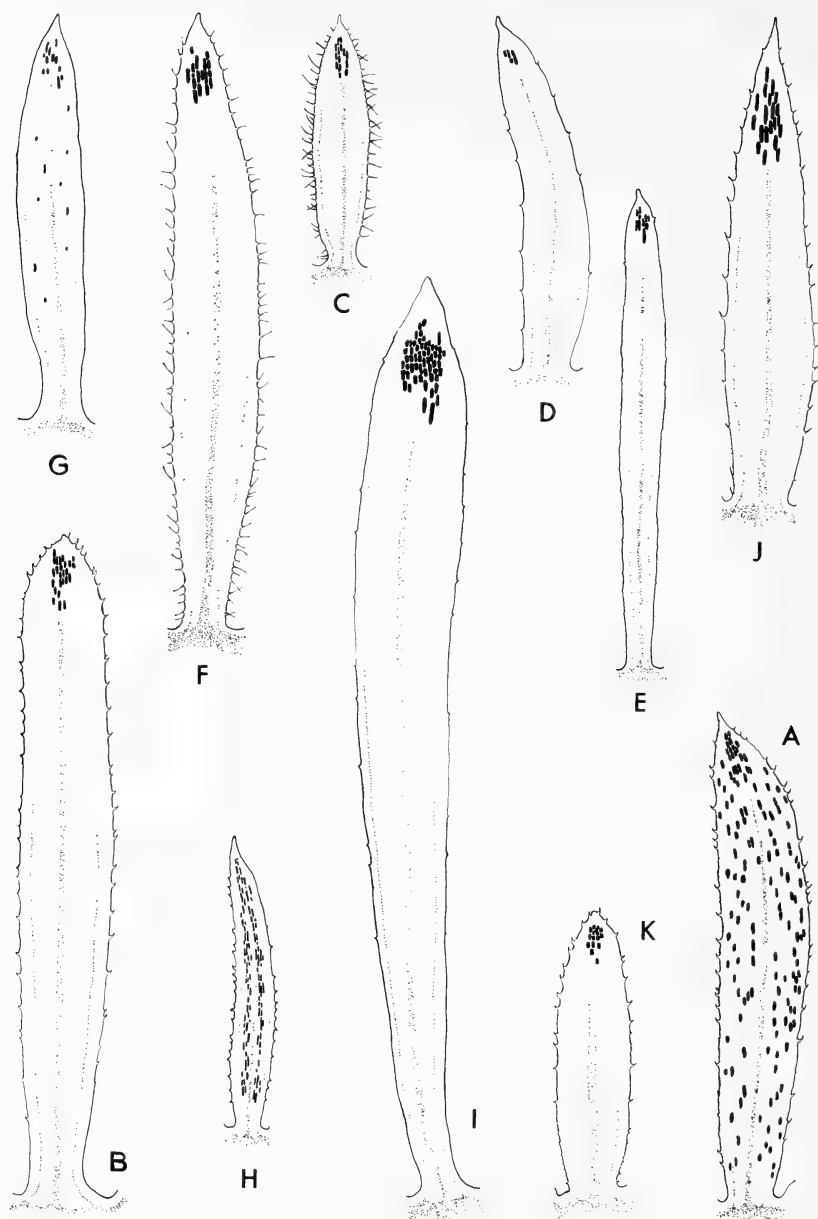
Fig. 7. Leaves × 7, cleared and stained to show principal veins, distribution of secretory cells, and features of the leaf margins. All surface hairs have been omitted. A, *G. jepsonii*, Cloudburst Summit *(4235)*; B, *G. johnstonii*, Chilao Recreation Area *(4234)*; C-K, *G. angustifolium*; C, ssp. *gabrielense*, San Antonio Mountains *(Raven 11,232*, CAS, JEPS) ; D, ssp. *foliosum*, Anacapa Island *(Hoffmann s.n.*, CAS) ; E, ssp. *angustifolium*, Catalina Island *(Fosberg S4354*, SMU, UC) ; F, ssp.

cleared and stained leaves, are sometimes tenuous, or even interrupted in very small leaves, as in ssp. *foliosum.*

Leaves (fig. 7), except the lowest, are for the most part strapshaped. Surface hairs are usual, and at least a few marginal hairs are nearly always present. Hairs vary considerably in length and stoutness, but are always either spreading or apically directed (fig. 9), never basally directed as in some members of the fleshy-fruited group.

The presence and distribution of secretory cells on the under side of the leaves is an important taxonomic character. These cells, of unknown function, have been observed in *Galium* species having 4-leaved whorls both in Europe (Nicolas, 1929) and in North America (Dempster and Ehrendorfer, 1965; Dempster and Stebbins, 1968). They are most commonly found clustered just below the leaf apex (fig. 7B-G, I-K) but are sometimes distributed over the entire lower surface, as in *G. jepsonii* (fig. 7A) and sometimes ssp. *angustifolium.* In ssp. *gracillimum* (fig. 7H) they occur in 2 bands at either side of the midrib. Table 2 summarizes our observations of this feature in the *G. angustifolium* complex, and shows that there is a considerable degree of taxonomic consistency with respect to this character.

Corollas of *G. angustifolium* are in general rotate, in conformity with the Linnaean description of the genus (fig. 8C-J). Old corollas especially, however, may be a little cupped at the base, so that they need to be cut before they will lie flat. The occurrence of truly campanulate corollas in *G. jepsonii* (fig. 8A) and its derivative *G. johnstonii* (fig. 8B) adds another to an increasing list of *Galium* species known to have this contra-diagnostic character (see discussion, Dempster and Ehrendorfer, 1965; Dempster, 1968).

The occurrence of hispid corollas in conjunction with glabrous or relatively glabrous herbage is also of interest. This character occurs not only in the present group, but also in the *G. multiflorum* complex, where it is diagnostic of the two species *G. matthewsii* Gray and *G. magnifolium* Dempster. It is apparent that hispid corollas may be produced in either of two ways: 1, by genes for general hairiness, the commoner situation, wherein the corolla hairs are commensurate in size and abundance with those on stems and leaves; and 2, by a separate gene or genes, as in *G. angustifolum* ssp. *nudicaule* (fig. 8F), *onycense* (fig. 8D), *gabrielense* (fig. 8H), *borregoense* (fig. 8G) and *jacinticum* (fig. 8J). In the latter circumstance, the corolla hairs are usually long, stout, abundant, and conspicuous, often quite disproportionately to those, if any, on stems and leaves. Since hairs occur only on the outside of the corollas, they are especially noticeable before the buds open. This character is apparent even to the naked eye, and is therefore very useful

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angustifolium, Castle Peak *(4067); G,* ssp. *borregoense,* Palm Canyon *(4375); H,* ssp. *gracillimum,* type locality *(Cole 989,* POM) ; I, ssp. *jacinticum,* Fulmor Lake *(4129); J,* ssp. *onycense,* Spanish Needle Creek *(Twisselmann 10,911,* CAS, JEPS) ; K, ssp. *nudicaule,* Cloudburst Summit *(4236).*
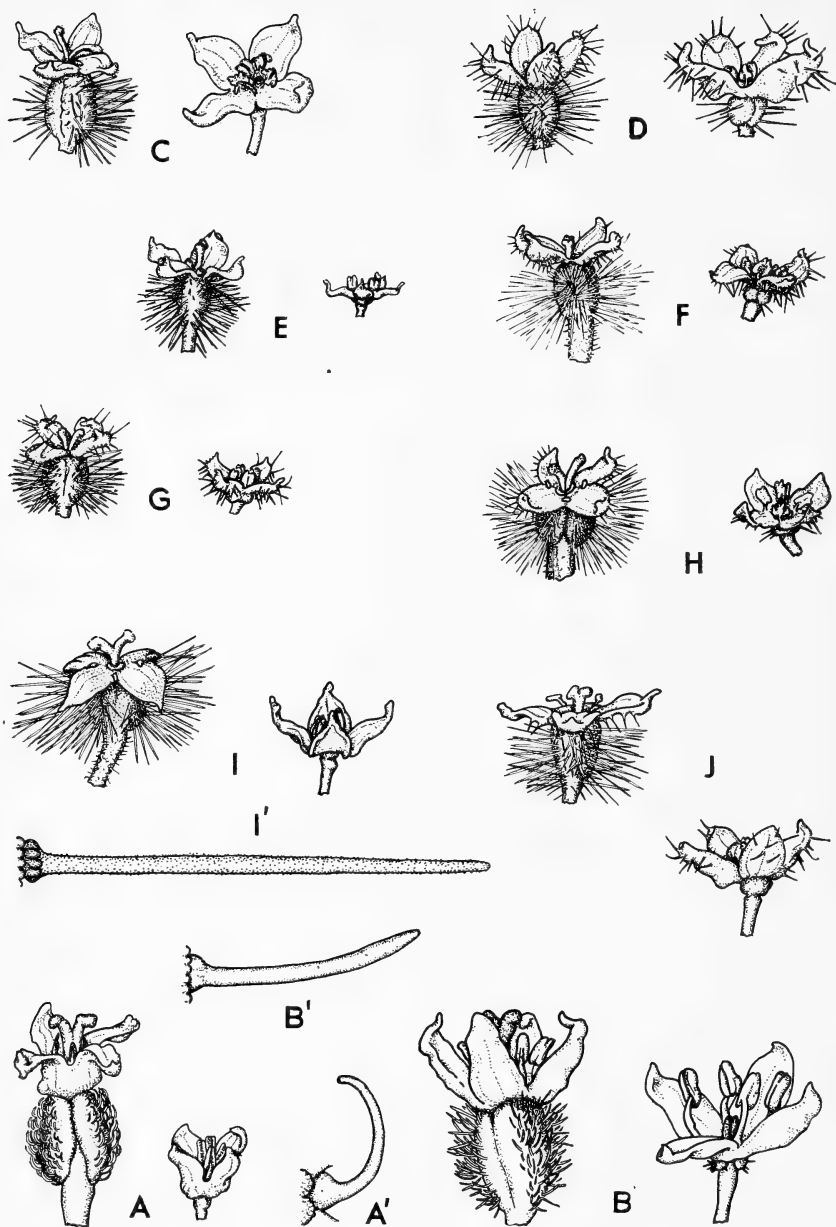
Fig. 8. Pistillate and staminate flowers, × 6: A, *G. jepsonii*, Cloudburst Summit (4235). B, *G. johnstonii*, Big Pines (4156). C-J, *G. angustifolium*: C, ssp. *foliosum*,

TABLE 2. DISTRIBUTION OF SECRETORY CELLS ON THE LOWER SURFACE OF THE LEAVES (FIG. 7)

Taxon	Number of individuals with secretory cells			
	clustered below leaf apex (subapical)	subapical plus a few scattered	mostly scattered over entire surface	none seen
G. angustifolium				
ssp. *angustifolium*	15	8	11	13
ssp. *borregoense*	1	1		
ssp. *foliosum*	5 (few)			4
ssp. *gabrielense*	6			2
ssp. *gracillimum*			9 (2 ranks)	1
ssp. *jacinticum*	2	2		1
ssp. *nudicaule*	3	1		1
ssp. *onycense*	5			5
G. *jepsonii*			7	
G. *johnstonii*	8			

in identification. Its presence also provides a valuable clue to the origin of the polyploid sspp. *gabrielense* and *jacinticum*.

All races and subspecies of *G. angustifolium,* like all members of the *G. multiflorum* complex and of the polygamous *G. parishii* group, are characterized by long straight spreading hairs on ovaries and fruits (fig. 8I'). *Galium jepsonii,* however, has short, upwardly curved hairs (fig. 8A'), and those of *G. johnstonii* are variably intermediate with respect to both length and curvature (fig. 8B').

Anacapa Island (*Howell 3792,* CAS, POM) ; D, ssp. *onycense,* Spanish Needle Creek (*Twisselmann 10,924, 10,911,* CAS, JEPS) ; E. ssp. *gracillimum,* Snow Creek Canyon (*Wolf 3648,* RSA, UC), Black Rock Spring (*Cole 990,* POM) ; F, ssp. *nudicaule,* Cloudburst Summit (*4236); G,* ssp. *borregoense,* Palm Canyon (*Munz & Hitchcock 11,339,* POM, *Dempster 4375*) ; H, ssp. *gabrielense,* Sunset Trail, *Johnston s.n.,* POM), San Antonio Canyon (*Roos 400,* POM) ; I, ssp. *angustifolium,* Del Mar (*4347),* Sespe Creek (*4111); J,* ssp. *jacinticum* (type, *4244*). Position of corolla lobes depends considerably on the developmental stage. Size of corollas, although it varies with the individual, is nevertheless significant taxonomically. A', B', I', ovary hairs × 40, to show relative size, shape and position: A', *G. jepsonii;* B', *G. johnstonii;* I', *G. angustifolium.*

KEY TO THE SPECIES AND SUBSPECIES

Fruiting pedicels 1–4 times as long as fruits; upper nodes much longer than the lower, the leaves often congested toward base of plant; fruits appearing longer than wide, the hairs shorter than the fruit body; corollas usually more or less cupped or campanulate.

  Plants low, generally less than 16 cm high; corollas cleft about halfway, the lobes little spreading; secretory cells evenly distributed; diploid   *G. jepsonii*

  Plants tall, generally over 18 cm high; corollas deeply cleft, spreading; secretory cells subapical; hexaploid . . . . *G. johnstonii*

Fruiting pedicels usually shorter than fruits; nodes approximately equal, the leaves not congested toward base of plant; fruits, with hairs, appearing spherical, the hairs usually as long as fruit body; corollas rotate . .*G. angustifolium*

  Corollas usually hispid (not always in ssp. *jacinticum*).

    Stems glabrous or nearly so.

      Inflorescences narrow, relatively few-flowered, the branching little compounded.

        Plants 6–16 cm high; leaves mostly 2–10 mm long; San Gabriel and San Bernardino mountains; diploid . . . . ssp. *nudicaule*

        Plants 17–35 cm high; leaves 11–26 mm long; San Jacinto Mountains; hexaploid . . . . ssp. *jacinticum*

      Inflorescences pyramidal, many-flowered, compoundly branched; plants 35–50 cm high; Borrego Desert . . . . ssp. *borregoense*

    Stems not glabrous.

      Stems merely scabrous, the hairs few and shorter than those on the leaves; angles of stems much thickened, often nearly concealing the faces; northeastern Kern Co.; diploid   . . . . ssp. *onycense*

      Stems hispid, the hairs usually abundant and long like those on the leaves; angles of stems narrow; vicinity of San Antonio Canyon, Los Angeles and San Bernardino counties; tetraploid   . . . . . ssp. *gabrielense*

  Corollas usually glabrous, or not more hispid than stems and leaves.

    Internodes of scaffold stems short, often shorter than the leaves; plants generally glabrous, the leaves very slender, often crowded; northern group of Channel Islands . . . . ssp. *foliosum*

    Internodes of scaffold stems long, generally much longer than the leaves, the leaves thus never crowded; not in northern Channel Islands.

      Plants tall and very slender, essentially glabrous; flowers, fruits and leaves diminutive, the latter early deciduous; deserts, San Bernardino and Riverside counties . . . . ssp. *gracillimum*

      Plants stouter, tall or sometimes lower and tufted, glabrous to often canescent; flowers, fruits, and leaves larger, the latter not soon deciduous; widespread in hills and mountains, but not in the deserts.

ssp. *angustifolium*

GALIUM JEPSONII Hilend & Howell, Leafl. W. Bot. 1:135. 1934. Based on *G. angustifolium* var. *subglabrum* Jepson, Manual Fl. Pl. Calif. 962. 1925. Type from Whitewater Basin, *Wilder 1113* (UC), undoubtedly from San Bernardino Co.

Plants low (fig. 4A), the erect glabrous stems commonly 8–16 cm high, arising in small clumps from widely spreading slender rhizomes or small woody base; leaves congested at the lower third or half of the stem, the upper portion having conspicuously elongated nodes and reduced leaves (fig. 4A), internodes of the lower, leafy portion ½ to as long as leaves, internodes of the upper portion 2–5 times as long as leaves; leaves 6–15
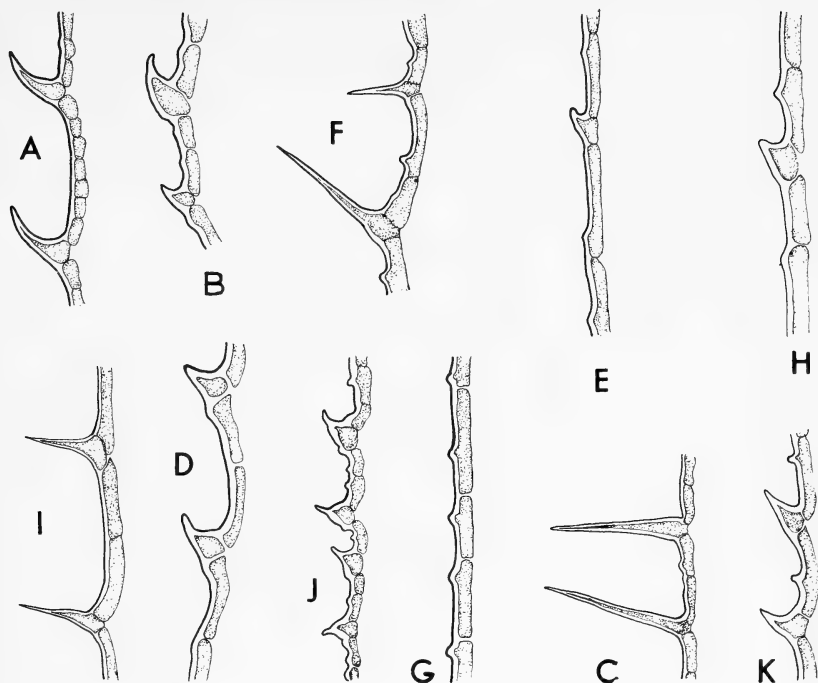
FIG. 9. Details of margins of the leaves in FIG. 7: A, *G. jepsonii;* B, *G. johnstonii;* C-K, *G. angustifolium;* C, ssp. *gabrielense;* D, ssp. *foliosum;* E, F, ssp. *angustifolium;* G, ssp. *borregoense;* H, ssp. *jacinticum;* I, ssp. *onycense;* J, ssp. *gracillimum;* K, ssp. *nudicaule.* All × 45.

mm long, thick, broadly linear, often a little falcate, the insertion broad, the apex narrowed rather suddenly to an obtuse, apiculate or sometimes acute, but not pungent, apex; leaf surfaces glabrous, the margins set with many short, rather stout, apically directed hairs; secretory cells scattered over the lower surface of the leaves; inflorescences lax, strict, relatively few-flowered, the short branches far apart, little compounded and strongly ascending; corollas glabrous, greenish, becoming cream-color and usually tipped with pink, campanulate, cleft about half-way, the tube somewhat fleshy, the lobes erect or scarcely spreading; ovaries of pistillate flowers not obviously hairy, but set with two tufts of ascending falcate hairs much shorter than the width of the ovary; fruits relatively few, the carpels 1¾ mm long, the upwardly curved hairs much shorter, the pedicels 1 to 4 times as long; **2n = 22.**

Openly wooded slopes, sandy granite soil, in mixed forest with *Pinus ponderosa.* San Gabriel and San Bernardino mountains, Los Angeles and San Bernardino counties, at 6400 to 7800 feet.

This heretofore little known and seldom collected diploid species is actually abundant at high elevations in the San Gabriel and San Bernardino mountains. Although inconspicuous and unprepossessing, it is un-

usual in several ways. Its relationship to *G. angustifolium* is apparent only by such general common characters as dioecy, 4-leaved whorls, 3-nerved leaves and dry fruits with specialized hairs. A fairly close relationship is further indicated by the highly probable assumption that the two species hybridized to produce *G. johnstonii. Galium jepsonii* has, however, certain extraordinary characters which distinguish it sharply from *G. angustifolium,* namely the fleshy campanulate corollas (fig. 8A), the short ascending falcate hairs of the ovaries and fruits (fig. 8A'), and the habit of sudden stem elongation above a congested leafy plant base. All of these characters, otherwise unique in the group, reappear commonly in individuals of the hexaploid *G. johnstonii* and nowhere else. The evenly distributed secretory cells are also diagnostic (fig. 7A), but this character also occurs sporadically in ssp. *angustifolium.*

Representative collections. Los Angeles Co.: San Gabriel Mountains, *Bacigalupi 6422* (JEPS), *Ewan 8415* (NO), *8438* (NO). San Bernardino Co.: San Antonio Mountains, *Johnston 6612* (CAS); San Bernardino Mountains, Jenks Lake, *4143*.

Galium johnstonii Dempster & Stebbins, nom. et stat. nov. Based on *G. angustifolium* var. *pinetorum* Munz & Johnston, Bull. Torrey Club 49:357. 1922. Type from Sierra Madre Mountains, Los Angeles Co., *Davidson* (UC). Not *G. pinetorum* Ehrend, Osterr. Akad. Wiss., Math.-Naturwiss, Kl., Sitzungsber., Abt. 1, Biol. 169:410. 1960.

Plants moderately tall (fig. 4B), the new shoots 18–38 cm high from a woody base, or sometimes arising from persistent woody stems up to 20 cm long; stems glabrous, the internodes generally longer than the leaves (except sometimes the lowest), the upper internodes often greatly elongated (2 to 5 times as long as leaves); leaves often somewhat thick, mostly narrowly linear, often a little falcate, 14–30 mm long, with broad insertion and obtuse or usually acute apex, the margins set with short, rather stout, apically directed hairs, the surfaces glabrous or set with minute curved hairs; secretory cells subapical; inflorescences very lax, few-flowered, racemosely or somewhat cymosely few-branched, the short branches ascending-divaricate; corollas relatively large, 3–5 mm across, glabrous, green, becoming pale yellow, rotate to flaring-campanulate with lobes much longer than tube; ovaries often longer than wide, set with few to many upward-curving or straight and spreading hairs, shorter than the length of the ovary, or sometimes as long; fruits relatively large, the body $2\frac{1}{2}$–3 mm long, the hairs spreading, usually shorter than the body, the pedicels commonly 1–3 times as long. **2n = 66.**

In open mixed forest, on lightly shaded slopes, at 5100 to 7300 feet; granitic sand. San Gabriel and San Bernardino Mountains, Los Angeles and San Bernardino counties.

This hexaploid species is so clearly intermediate between ssp. *angustifolium* and *G. jepsonii* as to leave little doubt as to its hybrid origin (table 3; fig. 10). Although the altitudinal range of *G. johnstonii* is a
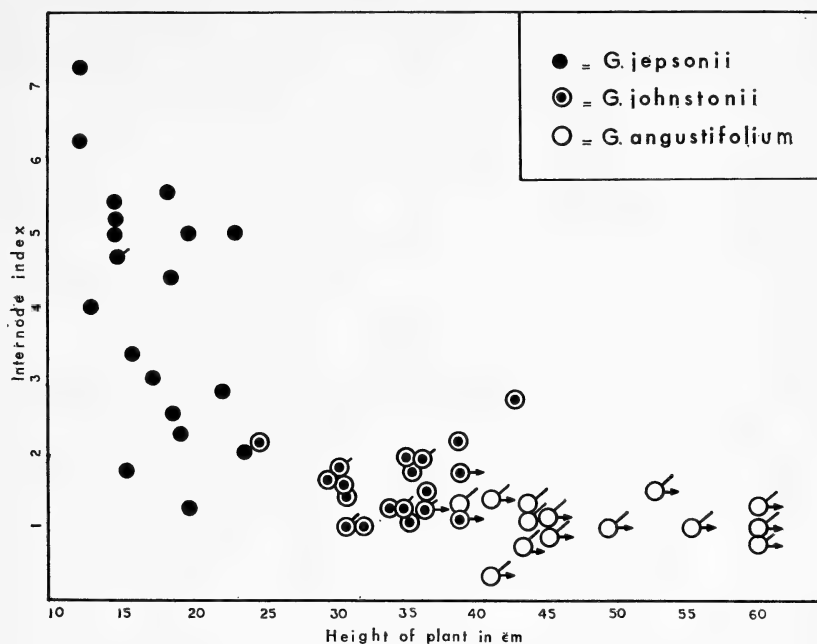
FIG. 10. Scatter diagram to show intermediacy of *G. johnstonii* between *G. jepsonii* and *G. angustifolium*. The internode index, derived from current year's shoots, was obtained by dividing the length of the internode ⅓ of the distance from the top, by the length of the internode ¼ of the distance from the bottom. A low figure indicates little difference, a high figure much difference. Arrow indicates that plant was taller than the measurement obtained. Long oblique line indicates ovarian hairs longer than ovary width, short line hairs about as long, no line hairs shorter than ovary width. All suitable pistillate plants were measured, from the San Gabriel Mountains only.

little lower than that of *G. jepsonii,* their ranges largely overlap, and the two species have been collected together twice by us (*4120 & 4121, 4233 & 4234*) and once by *Howe* (*45,584,* UC). We have not found either species growing with *G. angustifolium,* although they are regionally sympatric and their altitudinal ranges are not mutually exclusive.

Galium johnstonii is recognized first by its habit (fig. 4B), which is very lax, few-flowered, few-leaved and moderately low, and often demonstrates some gigantism in leaves, flowers and fruits. Closer examination will disclose the flaring campanulate corollas or, failing that, the short and often falcate ascending hairs of ovaries or fruits. The plants are too large to be confused with *G. jepsonii,* and the corollas much more like those of *G. angustifolium.* A solitary staminate individual may sometimes be mistaken for *G. angustifolium,* but pistillate individuals are unmistakable by virtue of their long pedicals and the short hairs on ovaries or fruits (fig. 8B').

TABLE 3. SOME COMPARISONS, SHOWING INTERMEDIATE POSITION OF GALIUM
JOHNSTONII BETWEEN G. JEPSONII AND G. ANGUSTIFOLIUM SSP. ANGUSTIFOLIUM
IN THE SAME GENERAL AREA

jepsonii	*johnstonii*	*angustifolium*
Plants low, 8–16 cm	Plants intermediate, 18–38 cm	Plants tall, 15–90 cm
Plants not woody above ground	Plants woody at base, or only a little above	Plants woody well above ground
Leaves congested near base of plant, the lower internodes much shorter than the leaves (internode/leaf index 0.2–*0.5*–1.0), the upper internodes much longer (index 1.1–*2.5*–5.2).	Intermediate: lower internodes, index 0.7–*1.3*–2.0; upper internodes, index 1.9–*2.6*–4.3.	Internodes about equal; lower internodes, index 1.0–*1.8*–2.7; upper internodes, index 1.3–*1.9*–3.3.
Second index/first index = 5	Second index/first index = 2	Second index/first index = 1+
Secretory cells subapical and scattered	Secretory cells subapical	Secretory cells mostly subapical
Flowers and fruits few	Flowers and fruits intermediate, never abundant	Flowers and fruits abundant
Corollas campanulate, the lobes not usually spreading	Corollas usually broadly flaring-campanulate	Corollas rotate
Pedicels 1–4 times as long as fruits	Pedicels 1–3 times as long as fruits	Pedicels shorter than fruits
Ovary hairs short, falcate, ascending	Ovary hairs intermediate in length, erect or spreading, straight or falcate	Ovary hairs long, straight, spreading
Altitudinal range: Los Angeles Co., 6400–7800 ft.; San Bernardino Co., 7000–7700 ft.	Altitudinal range: Los Angeles Co., 5320–7300 ft.; San Bernardino Co., 5000–7000 ft.	Altitudinal range: Los Angeles Co., 1000–5600 ft.; San Bernardino Co., 1500–7600 ft.

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray. Plants growing tall
by means of slender woody scaffold stems, or low and tufted from a
woody base; internodes subequal; inflorescences diffuse and many-flow-
ered, or sometimes few-flowered, the pedicels on pistillate plants usually
much shorter than ovaries; secretory cells usually subapical, but some-
times scattered; corollas rotate; ovaries and fruits appearing round, the
hairs usually abundant and as long as the diameter of the fruit.

Hilly and mountainous areas, in places where roots are sheltered from
heat and drought. From Sierra San Pedro Mártir, Baja California, north
to the Santa Lucia and Gabilan ranges of Monterey and San Benito
counties; eastward in Kern Co. to the west slopes of the Sierra Nevada,
and in San Bernardino Co. to the Providence Mountains.

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray, Fl. N. Amer. 2:22. 1841, ssp. ANGUSTIFOLIUM, as a synonym, Bot. Calif. 1:285. 1876. Type from "San Francisco? *Douglas!*", the locality certainly erroneous. *G. trichocarpum* Nutt., l. c., type from "St. Diego," *Nuttall* (PHIL). Not *G. trichocarpum* DC. *G. siccatum* Wight, Zoe 5:54. 1900. Type from Del Mar, San Diego Co., *T. Brandegee* (CAS). *G. angustifolium* var. *siccatum* (Wight) Hilend & Howell, Leafl. W. Bot. 1:135. 1934. *G. angustifolium* var. *bernardinum* Hilend & Howell op. cit. 134. Type from near Cactus Flats, San Bernardino Mountains, *Hilend 475* (CAS). *G. angustifolium* var. *diffusum* Hilend & Howell l. c. in part. Type from Saragosa Springs, upper Holcomb Valley, San Bernardino Mountains, *Hilend 533* (CAS). *G. angustifolium* var. *typicum* Hilend & Howell op. cit. 154. 1935.

Plants (15) 30–60 (100) cm high, the fertile branches arising singly or in tufts from the nodes of slender, woody, erect or arching scaffold stems (fig. 4D) or less commonly tufted from near the ground; stems glabrous to hispid, the internodes commonly 2–7 cm long, generally much longer than the leaves, at least on scaffold stems; leaves glabrous to canescent, 5–27 mm long, filiform to strap-shaped, tapered or abruptly acute at apex, the margins usually set with hairs of several sizes pointed in different directions; inflorescences usually profuse, but sometimes reduced, the flowers and fruits usually very abundant; corollas cream colored to greenish yellow, never conspicuously more hispid than the leaves and stems; $2n = 22, 44$.

Cliffs, canyons, and hillsides, in protection of trees, shrubs, or rocks, at 50 to 8200 feet; granite, shale, or sandstone. Sierra San Pedro Mártir, and northward in the Coast Ranges to Monterey and San Benito counties; Tehachapi and Greenhorn Mountains; Santa Catalina Island.

After subtraction of seven subspecies, what remains to ssp. *angustifolium* is still complex. The diploid form is the only form in Baja California and southern San Diego Co. Thence, northward through Riverside and southwestern San Bernardino counties, it is interfingered and interspersed with tetraploid forms. From Orange Co. northward into Monterey and San Benito counties, and in central Kern Co., apparently all of the populations are tetraploid.

The diploid form is readily defined: plants fairly tall, stems and corollas glabrous or nearly so, leaves only sparsely hairy and of small to moderate size. The tetraploids, on the other hand, are variable, being very tall or quite low and compact, glabrous or canescent on stems, leaves and corollas, and the leaves are sometimes considerably larger than in the diploids. All canescent plants are tetraploid, but most tetraploid plants are not canescent. Many tetraploids are recognizable by oversized leaves and flowers, but most of them do not exhibit this quality. Many tetraploid individuals are, in fact, indistinguishable from diploids, and it is

therefore impractical to separate the two races taxonomically, especially in consideration of their overlapping ranges.

Subspecies *angustifolium* remains, therefore, highly variable, particularly as to the included tetraploids. Among the latter can occasionally be recognized something of the low compact habit and narrow inflorescence of ssp. *nudicaule*, as for instance in San Diego Co., *Bacigalupi 3915*, suggesting introgression from that subspecies. The possibility of introgression from ssp. *foliosum* in Ventura Co. is discussed below under that subspecies. The canescence of much of the tetraploid material has no counterpart in any known diploid, a situation apparently homologous with that in *G. bolanderi* Gray, of the fleshy-fruited group.

The following names were reduced to synonymy for the reasons given: *G. siccatum* Wight, although striking in appearance, cannot be maintained as a separate taxon, because the canescent character which distinguishes it occurs sporadically throughout the tetraploid portion of the range, and because even at the type locality we find the population variable with regard to this character (*4347*). Variety *diffusum* Hilend & Howell comes close to our ssp. *gracillimum*, under which see discussion. Variety *bernardinum* Hilend & Howell is a rather low compact form without geographic unity, being based on quantitative characterse which appear here and there throughout the range.

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray ssp. **borregoense** Dempster & Stebbins, ssp. nov. A ssp. gracillimi simile, sed corollis hispidis, caulium angulis crassis (latera simulantibus), cellulis secretoriis subapicalibus discedit.

Type from Palm Canyon, Borrego Valley, San Diego Co., California, *Munz & Hitchcock 11,339* (POM 172789).

Similar to ssp. *gracillimum*, but corollas hispid with long hairs, leaves larger, more glabrous, and apparently not fugacious, the stem angles greatly expanded, presenting more surface than the sides except in older stems (fig. 5J); secretory cells mostly subapical; presumably diploid (stomata 33μ).

Only two collections are known: *4375* (staminate) and the type (pistillate), both from lower Palm Canyon, San Diego Co., where it is rare. The number of morphological differences, together with its isolated locality, south of the Santa Rosa Mountains in the Colorado Desert, dictate its separation from ssp. *gracillimum* of the Mohave Desert. Plants of the Palm Springs area, Riverside Co., lie between the two localities, i.e., south of the Little San Bernardino Mountains, but north of the Santa Rosa-San Jacinto mountain barrier, and although their location in the Colorado Desert rather than the Mohave suggests their inclusion with ssp. *borregoense*, they belong morphologically with ssp. *gracillimum*. Of the 5 collections from the Palm Springs area, one (*Spencer 1476*, POM), however, has hispid corollas, but its stems lack the exaggerated angle development found in ssp. *borregoense*.

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray ssp. **foliosum** (Hilend & Howell) Dempster & Stebbins, comb. nov. *G. angustifolium* var. *foliosum* Hilend & Howell, Leafl. W. Bot. 1:134. 1934. Type from Anacapa Island, *Howell 3792* (CAS).

Generally congested subshrubs (fig. 4E) 30–60 cm high, the internodes commonly 2–15 mm long, but those on scaffold stems occasionally longer (to 55 mm); the closely set nodes prominent after leaf-fall; stems glabrous, the angles much thickened, often nearly obscuring the faces in slender upper stems (fig. 5K); leaves narrowly linear, 3–11(17) mm long, often longer than internodes, nearly glabrous on the surfaces, the margins smooth, with few stout regularly spaced subequal apically directed hairs; flowers and fruits small, abundant, congested in complex amorphous inflorescences; corollas glabrous or obscurely hispid; $2n = 22$.

Exposed rocky slopes, 100 to 200 feet. Santa Cruz, Santa Rosa, and Anacapa Islands. Doubtfully on the mainland in Ventura Co. (see below).

This subspecies, like *G. californicum* H. & A. ssp. *miguelense* (Greene) Dempster & Stebbins, may derive its congested character in part directly from the windy island habitat. However, both the congested sub-shrubby habit and the small slender leaves are pretty consistent in *G. angusti-folium* of the northern group of Channel Islands, in sharp contrast to *G. angustifolium* of the southern group, and it seems extremely likely, therefore, that they are genetically determined. Moreover, we have seen the plants growing in fairly sheltered places on Santa Cruz Island without diminution of these characters, and material transplanted to Contra Costa Co. remained in character *(4083).*

Several collections from the Ventura Co. mainland resemble ssp. *foliosum* in varying degrees. It may be that true ssp. *foliosum* does occur there, but careful examination of the specimens casts much doubt upon this supposition. Subspecies *foliosum* is diploid, at least on Santa Cruz Island, and the cytologically known collections of ssp. *angustifolium* northwestward from San Bernardino Co. are tetraploid. Mainland material resembling ssp. *foliosum* is, however, of unknown chromosome number, and measurement of stomata gave no clue, since the overlap in size of stomata of diploids and tetraploids is too great (ssp. *foliosum* 32–38–41μ; tetraploid ssp. *angustifolium* 34–40–48μ). Study of marginal leaf-hairs seems significant, however, since in this respect the island material is rather uniform: the hairs, unlike those on mainland material, are of uniform size, evenly spaced, and rather stout for their length, the leaf margins being otherwise smooth. Mainland material has marginal hairs of several sizes, irregularly interspersed, and they are relatively slender. One collection allegedly from the mainland does indeed include material that appears to be ssp. *foliosum*. This is a sheet of four specimens, two apparently ssp. *foliosum* and two resembling the mainland forms, collected by T. S. Brandegee allegedly at Ventura in July, 1885 (CAS). The handwriting on the label appears to be that of Alice East-

wood rather than T. S. Brandegee, and there is a possibility that the two specimens of ssp. *foliosum* in fact came from Santa Cruz Island. It must be remarked, however, that since plants resembling ssp. *foliosum* are found only in Ventura Co., they may well be indicative of introgression from island material, either by way of seed or pollen transportation.

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray ssp. **gabrielense** (Munz & Johnston) Dempster & Stebbins, comb. nov. *G. gabrielense* Munz & Johnston, Bull. Torrey Club 51:299. 1924. Type from ridge east of Ontario Peak, San Bernardino Co., *Munz 6078* (POM). *G. siccatum* var. *anotinum* Jepson, Manual Fl. Pl. Calif. 962. 1925. Type from Mt. San Antonio, *Peirson 215* (JEPS).

Plants usually low, 6–20 (36) cm high, tufted from a woody base; stems hispid, the internodes a little shorter than to twice as long as the leaves; inflorescences narrow, relatively few-flowered, the branchlets short, ascending, little compounded; leaves 2–14 mm long, linear to sometimes oblong or elliptical, more or less hispid with short, rather stout hairs, the apex more or less acute; corollas yellowish or often red, hispid externally with few to many bristles, longer than those on stems and leaves; fruit body about $1\frac{1}{2}$–2 mm long, the pedicel $\frac{1}{4}$–$1\frac{1}{2}$ times as long, the hairs luxuriant, about as long as fruit body or longer; **2n = 44.**

Dry rocky or sandy granite slopes and ridges, in open forest or high chaparral, at 4000 to 8700 feet. Vicinity of San Antonio Canyon, Los Angeles and San Bernardino counties; upper San Gabriel Canyon, Los Angeles Co.

Aside from being tetraploid and hairy-stemmed, much of the material of ssp. *gabrielense* differs little from ssp. *nudicaule* (table 4; fig. 11). As might be predicted, however, the tetraploid subspecies is much more variable. Nevertheless, the plants do not usually exceed 20 cm in height, the leaves and stems are usually very hairy, and the hispid corollas, as with ssp. *nudicaule,* are diagnostic. Subspecies *angustifolium* as found in the wash near Claremont at the mouth of San Antonio Canyon presents a marked contrast, being much taller, with glabrous stems and corollas and profuse inflorescence. There is, however, some evidence of introgression, at least from ssp. *angustifolium* into ssp. *gabrielense,* and intermediates can be cited, e.g. *4295* (4x), *Hardham 14,288* (JEPS), *Johnston s.n.* from Cascade Canyon (POM).

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray ssp. **gracillimum** Dempster & Stebbins, ssp. nov. *G. angustifolium* var. *diffusum* Hilend & Howell, Leafl. W. Bot. 1:134. 1934, in large part, but not as to type.

Caules glabri; inflorescentiae laxae; folia gracilia saepe ephemera; flores fructusque parvuli; cellulae secretoriae in ordinibus duobus dispositae.
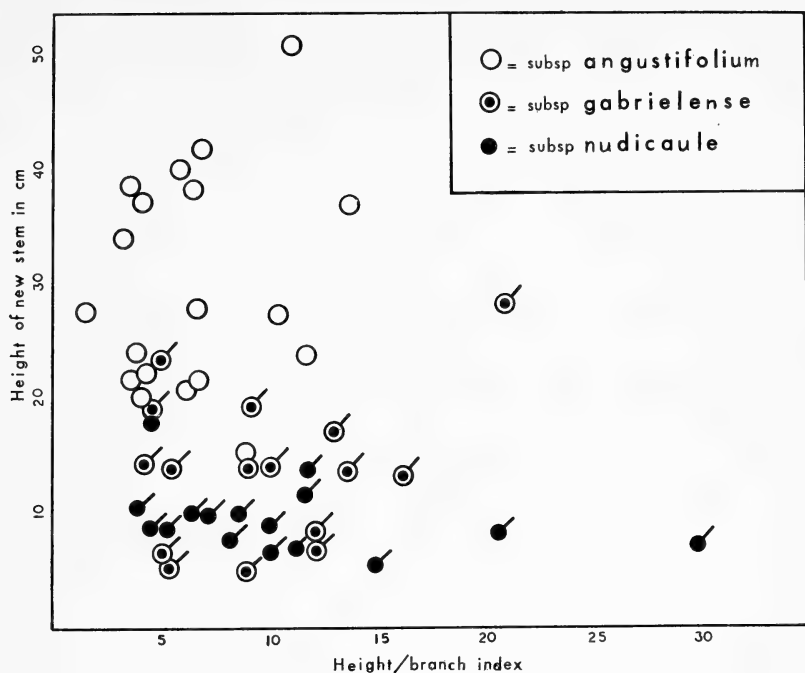
Fig. 11. Scatter diagram to show intermediacy of ssp. *gabrielense* between ssp. *nudicaule* and ssp. *angustifolium* of the same general area. Height/branch index was obtained by dividing length of shoot by the length of the longest branch of the inflorescence. Height in this instance refers only to current year's herbaceous growth. Oblique line indicates hispid corollas.

Type from Black Rock near Warren's Well, Little San Bernardino Mountains, San Bernardino Co., *Epling & Robison s.n.,* June 25, 1933 (DS, RSA, UC 574879-holotype).

Plants very slender throughout (fig. 4F), commonly 40 cm long from the persistent woody stems; stems glabrous, the internodes commonly 2 to 3 times as long as leaves; leaves small, 4–15(18) mm long, very narrowly linear to slightly oblanceolate, scabrous, somewhat ephemeral; secretory cells usually in two longitudinal bands each side of the midrib (fig. 7J); inflorescence very openly paniculate, the flowers and fruits rather abundant but very small; pedicels usually shorter than (to 3 times as long as) ovaries, but branchlets long and flowers thus not congested; corollas generally glabrous, but rarely hispid, about $1\frac{1}{2}$–2 mm across, yellowish or tinged with pink; fruits less than 2 mm long, the hairs $\frac{1}{2}$–$\frac{3}{4}$ as long; $2n = 22.$

Among granite rocks and boulders in partially shaded places in canyons and at northern base of rocky outcrops, 400 to 4800 feet. Providence and Little San Bernardino Mountains and east side of San Jacinto Mountains, San Bernardino and Riverside counties.

TABLE 4. SOME COMPARATIVE CHARACTERS OF THREE SUBSPECIES OF
GALIUM ANGUSTIFOLIUM

Subspecies *nudicaule* is represented by 20 individuals from Cloudburst Summit *(4123, 4236)* in the San Gabriel Mts; ssp. *gabrielense* is represented by 18, including all suitable plants from all pertinent collections; and ssp. *angustifolium* is represented by 19 from known or suspected diploid collections, chiefly from Swartout Valley and the San Bernardino Mts. In most of the characters measured, ssp. *gabrielense* is closer to ssp. *nudicaule* than to ssp. *angustifolium,* despite the deliberate inclusion of aberrant individuals from peripheral areas, suspected of introgression from ssp. *angustifolium.* For explanation of internode index and branch index see legends for Figs. 10 and 11, respectively.

	nudicaule	*gabrielense*	*angustifolium*
Height of new wood in cm	6–*9.3*–19	5–*11.8*–19.5	15–*31*–54
Leaf length in cm	0.3–*0.5*–1	0.4–*0.8*–1.4	0.8–*1.1*–1.6
Internode index	2.1–*4.6*–6.7	2–*4*–7	5.1–*7.7*–14.3
Branch index	2–*3.6*–7.4	1.3–*3.4*–6.6	1.6–*3.3*–5.8
Height/longest branch	4–*10*–30	4.3–*9.1*–21.5	2.2–*6.5*–14.6
Corollas	All hispid	All hispid	18 glabrous 1 pubescent
Stems	All papillose	15 hispid 3 glabrous	All glabrous

This diploid and definitely deserticolous subspecies is readily recognized by its slender open habit and strikingly small leaves, flowers, and fruits. All of these diagnostic characters remained unchanged from one winter to another under cultivation in Contra Costa Co. where, however, the plants did not survive the second winter.

The relationship of ssp. *gracillimum* to var. *diffusum* Hilend & Howell must be considered. Hilend & Howell (1935) included in their variety all of ssp. *gracillimum* and a great deal besides, being guided apparently by similarity in the habit and general appearance of the plants. We prefer, however, to limit ssp. *gracillimum* to plants of the oases and granite outcroppings in the true desert. The type of var. *diffusum* (Saragosa Spring, Holcomb Valley, San Bernardino Mountains, *Hilend 533,* CAS) can unfortunately not be included. Although it nearly resembles our desert plant, the flowers and leaves are slightly larger, and the latter are not caducous. Furthermore, the habitat is completely different, namely forested terrain in the San Bernardino Mountains at 7500 feet altitude. We therefore refer it to ssp. *angustifolium.*

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray ssp. **jacinticum** Dempster & Stebbins, ssp. nov. Altitudine plantae totae moderata (17–35 cm), foliis magnis (11–26 mm), inflorescentiis parvis, corollis plerumque hispidis.

Type from Black Mountain road, 0.9 mile above junction of road to

TABLE 5. SOME COMPARATIVE CHARACTERS OF THREE SUBSPECIES OF
GALIUM ANGUSTIFOLIUM

	nudicaule	*jacincticum*	*angustifolium**
Length of shoot of current year in cm	6–*9.3*–19	12.5–*18.4*–25.5	16.5–*32.5*–45
Length of leaf in cm	0.3–*0.5*–1	1.4–*1.7*–2.7	0.6–*1*–2
Corollas	20 hispid	13 hispid 8 sparingly hispid 1 glabrous	19 glabrous

*From the San Jacinto Mountains. If the plants had been measured from the ground, including the woody stems, the result would have been a great increase in the first figure for ssp. *angustifolium,* and almost no changes in the corresponding figure for the other two subspecies.

Pine Wood, San Jacinto Mountains, Riverside Co., *Dempster & Stebbins 4244* (JEPS-54620).

Plants moderately low, commonly 17–35 cm, the leaves relatively large; stems glabrous, the internodes about as long as the leaves; leaves 11–26 mm long, strap-shaped, abruptly narrowed at apex, glabrous or very shortly hairy on the surfaces, the apically directed marginal hairs longer; inflorescences relatively simple, narrow and few-flowered; corollas usually hispid, the hairs much longer than those on the leaves. **2n = 66.**

In partial shade in open mixed forest, 4200 to 6500 feet. West side of the San Jacinto Mountains.

This narrow endemic, found only in the Lake Fulmor-Black Mountain area of the San Jacinto Mountains is, however, not uncommon there. It is readily distinguished from diploid ssp. *angustifolium* of the same general area by its almost invariably hispid corollas, its relatively low habit, large leaves, and sparse inflorescences. The tetraploid plants of the northern San Jacinto Mountains, although the majority (5:2) have some bristles on their corollas, and the leaves tend to be large, are unlike ssp. *jacincticum* in being tall and woody. Tetraploids of the Santa Rosa Mountains to the south also have mostly somewhat hispid or pubescent corollas and are, in addition, low and largely lacking woody stems. They differ from ssp. *jacincticum,* however, in their consitently small leaves.

The hispid corollas, low non-woody habit, and sparse inflorescences, all suggest ssp. *nudicaule* as one of the progenitors of both ssp. *jacincticum* (table 5) and the tetraploids of these mountains, which are, however, tall. We are unable to account for the large leaves of ssp. *jacincticum* except to note that large leaves are often associated with polyploidy, as for instance in the tetraploids of central San Diego Co. and elsewhere, and in hexaploid *G. johnstonii.*

Representative collections. Riverside Co., San Jacinto Mountains: Fulmor Lake, *4129;* Alandale Pines, *4130;* Black Mountain Road, *4246.*

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray ssp. **nudicaule** Dempster & Stebbins, ssp. nov. A ssp. gabrielensi simile sed foliorum pilis brevioribus, caulibus papillosis omnino glabris differt.

Type from Cloudburst Summit, Angeles Crest Highway, Los Angeles Co., at 7020 feet, *Dempster & Stebbins 4236* (JEPS-54621).

Plants low, 6–16 cm high (fig. 4C); stems glabrous, more or less papillose, the internodes a little shorter than to twice as long as leaves; leaves 2–10(15) mm long, linear, or the shortest sometimes oblong or elliptical, more or less hispid with short hairs, the apex more or less acute; inflorescences narrow, relatively few-flowered, the branchlets short, ascending, little compounded; corollas usually red, often very dark but sometimes yellow, hispid externally with few to many slender bristles, which are longer than those on the leaves; fruit body about $1\frac{1}{2}$–2 mm long, the pedicel $\frac{1}{4}$–$1\frac{1}{2}$ times as long, the hairs luxuriant, about as long as fruit body or longer; $2n = 22$.

Steep sandy east- and south-facing slopes, in very open mixed forest; granite soil. Central San Gabriel and eastern San Bernardino mountains, at 6700 to 8200 feet.

The two well-separated populations of the central San Gabriel Mountains and the eastern San Bernardinos respectively have diverged somewhat in their evolution, but scarcely enough to merit separate names. Plants from the San Bernardino Mountains are considerably less hairy on corollas, leaves, and ovaries, the stems a little more elongated and scarcely papillose. There is no indication that the San Gabriel plants hybridize with either *G. jepsonii* on the same ploidy level (although they grow very near together at Cloudburst Summit, for instance) or with ssp. *angustifolium,* which in Los Angeles Co. seems to be all tetraploid. In the San Bernardino Mountains, however, where diploid ssp. *angustifolium* occurs, it is possible that introgression from that source may account for the fewer hairs, slightly greater stem elongation, and more apically directed leaf hairs or ssp. *nudicaule.* There is some evidence also of introgression in the other direction, or of hybridization with chromosome doubling, since two of our tetraploid collections of ssp. *angustifolium* from the San Bernardino Mountains (*4152* and *4154*) include plants with truly hispid corollas.

Representative collections. Los Angeles Co., San Gabriel Mountains: Mt. Waterman, *Ewan 10,028* (CAS, NO); Mt. Islip, *Fosberg & Ewan 4915* (NO). San Bernardino Co., San Bernardino Mountains: Cienega Seca Creek, *4147, 4150.*

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray ssp. **onycense** Dempster & Stebbins, comb. nov. *G. angustifolium* var. *onycense* Dempster, Brittonia 10:189. 1958. Type from hill above Onyx Ranch, near Onyx, Kern Co., *Dempster, Bacigalupi, & Robbins 1015A* (JEPS).

Plants grayish-green, slender, 12–30 (commonly 15–18) cm tall from the woody base; stems scabridulous or very shortly hispid, the hairs few,

very short and spreading; angles of stems very broad, often largely concealing the true faces (fig. 5F); internodes 2–2½ times as long as leaves, or a little longer in the inflorescence; leaves commonly 5–10(14) mm long, lanceolate, tapered gradually to an acute apex, the lower surface commonly glabrous, the upper surface and margins sparsely short-bristly, the hairs somewhat apically directed; inflorescence not narrow, the branchlets somewhat elongated; corollas hispid, usually pink; ovary and fruit hairs luxurious, longer than fruit body; $2n = 22$.

Growing from under and between large granite rocks and outcrops, with scattered Digger Pine and oaks, not common. Between Fay Creek and the crest of the Sierra Nevada in northern Kern Co., 3000 to 7200 feet.

This diploid subspecies is closest to ssp. *nudicaule,* but the plants are more lax, the inflorescences fuller and more open, the stems scabridulous, the leaves more acute and less hairy. It appears to have diverged in its evolution as a result of isolation and of selection for a more rigorous summer climate.

Representative collections. Kern Co.: Fay Creek, *Howell & True 41,811* (CAS, JEPS); near Onyx, *Voegelin 147, 131* (both UC), Dempster, Bacigalupi, & Robbins 1015B (JEPS); Spanish Needle Creek, *Twisselmann 10,911, 10,923, 10,924, 12,153* (all CAS, JEPS); west of Walker Pass, *1431.*

LITERATURE CITED

DEMPSTER, L. T. 1958. New names and combination in the genus Galium. Brittonia 10:181–192.
———. 1959. A re-evaluation of Galium multiflorum and related taxa. Brittonia 11:105–122.
———. 1962. A new species of Galium in California. Madroño 16:166–168.
———. 1968. Galium correllii (Rubiaceae), a new species from Val Verde County, Texas. Sida 3:249–251.
———., and F. EHRENDORFER. 1965. Evolution of the Galium multiflorum complex in western North America. II. Critical taxonomic revision. Brittonia 17:289–334.
———., and G. L. STEBBINS. 1965. The fleshy-fruited Galium species of California (Rubiaceae). I. Cytological findings and some taxonomic conclusions. Madroño 18:105–113.
———., and G. L. STEBBINS. 1968. A cytotaxonomic revision of the fleshy-fruited Galium species of California (Rubiaceae). Univ. Calif. Publ. Bot. 46.
EHRENDORFER, F. 1956. Survey of the Galium multiflorum complex in western North America. Contr. Dudley Herb. 5:1–36.
———. 1961. Evolution of the Galium multiflorum complex in western North America. I. Diploids and polyploids in this dioecious group. Madroño 16:109–122.
HILEND, M., and J. T. HOWELL. 1934. Preliminary studies in the genus Galium in Southern California. Leafl. W. Bot. 1:134–137.
———. 1935. The genus Galium in Southern California. Leafl. W. Bot. 1:145–168.
NICOLAS, G. 1929. Remarques sur l'epiderme des feuilles de quelques Galium. Bull. Soc. Hist. Nat. Toulouse 58:45–56.

A NEW TETRAPLOID SUBSPECIES OF LASTHENIA (COMPOSITAE) FROM OREGON

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The single perennial species of *Lasthenia* (Compositae: Helenieae) is the variable, rather local *L. macrantha* (Gray) Greene of California and southwestern Oregon. Recently I have recognized two subspecies of *L. macrantha:* ssp. *bakeri* (J. T. Howell) Ornduff, restricted to the closed-cone pinelands of California, and ssp. *macrantha,* which ranges along exposed areas of the immediate coast from Curry Co., Oregon, southward to San Luis Osbispo Co., California (Ornduff, 1966). The Oregon populations of this species (previously referred to ssp. *macrantha*) are tetraploid ($n = 16$) and the California populations are hexaploid ($n = 24$). I have stated without further explanation that "In cultivation these tetraploid races are easily separable from the hexaploids on the basis of head size and growth habit, but these differences are not always evident in wild plants" (Ornduff, 1966, p. 22).

Cultivated plants of the tetraploids tend to be lower and have smaller heads and leaves than the hexaploids. The tetraploids also form small dense mats by means of rhizomatous growth, whereas the hexaploids generally do not. In addition, flowering of tetraploids occurs only in the summer, whereas the hexaploids tend to be less seasonal in their flowering behavior. However, the phenotypic plasticity of wild plants (particularly of the hexaploids) in response to variations in edaphic, seasonal, or other local conditions is great. When this plasticity is superimposed upon the considerable interpopulation genetic variability of both the tetraploids and hexaploids, any taxonomic separation of these two chromosomal entities seemed impractical despite the striking differences between them in cultivation. Subsequent morphological studies of herbarium specimens collected from wild populations in California and Oregon have provided a number of fairly reliable characteristics by which field-collected plants of the tetraploids can be distinguished from the hexaploids. As a consequence, I am now giving the tetraploids subspecific recognition.

LASTHENIA MACRANTHA (Gray) Greene ssp. **prisca** Ornduff ssp. nov. Type. "Very abundant on Cape Blanco, Curry Co., Ore.," *L. F. Henderson 11400* ORE, PH, UC 446955-holotype), July 16, 1929.

Phyllaria corollae que radii ligulatae 11 vel pauciores; corollae radii lignulatae circa 7.5 mm longae; pedunculi circa 5–6 cm longi; par primum foliorum infra capitulum utrumque circa 1.3 cm longum, plerumque minor quam 3 mm latum; internodium primum infra par primum foliorum circa 2.0 cm longum; par secundum foliorum infra capitulum circa 1.8 cm longum; folia longissima plantae circa 2.4 cm longa; chromosomatum numerus **n** $= 16$.

TABLE 1. MORPHOLOGICAL FEATURES DISTINGUISHING L. MACRANTHA SSP. MACRANTHA AND SSP. PRISCA. RANGE AND SAMPLE SIZE ARE GIVEN IN PARENTHESES

Mean Measurement	ssp. *prisca*	ssp. *macrantha*
Number of phyllaries	10.7 (8-14; 10)	11.8 (9-16; 25)
Length of ray floret ligule	7.5 mm (5-9; 14)	10.3 mm (6-18; 28)
Number of ray florets	10.9 (8-15; 13)	11.8 (9-15; 28)
Length of peduncle above first pair of leaves	5.2 cm (2.0-8.0; 12)	8.5 cm (2.6-14.5; 23)
Length of leaf in first pair of leaves below head	1.3 cm (0.9-1.9; 12)	2.6 cm (1.4-2.7; 25)
Width of first pair of leaves below head	2.3 mm (1.8-3.0; 13)	2.8 mm (1.5-5.5; 23)
Internode length between first and second pair of leaves below head	2.0 cm (0.2-3.5; 13)	2.6 cm (1.0-6.5; 22)
Length of leaf of second pair of leaves below head	1.8 cm (0.8-3.3; 13)	3.2 cm (1.3-6.4; 18)
Length of longest foliage leaf	2.4 cm (2.0-4.0; 12)	5.6 cm (2.8-8.8; 25)

Phyllaries and ray florets usually 11 or fewer; ligules of ray florets averaging 7.5 mm long; peduncles averaging 5–6 cm long; first pair of leaves below capitulum each averaging 1.3 cm long and mostly less than 3 mm wide; first internode below first pair of leaves averaging 2.0 cm long; second pair of leaves below capitulum averaging 1.8 cm long; longest leaves averaging 2.4 cm long; $n = 16$.

Representative specimens (all Curry Co., Oregon): Cape Blanco, *J. W. Thompson 12546* (CAS, NY, UC, US), *N. P. Gale 355* (GH), *Ornduff 4985* (UC); Cape San Sebastian, *Ornduff 4986* (JEPS, UC); Bluffs north of mouth of Rogue river, *Ornduff 6981* (JEPS, UC); about 7 miles south of Ophir, *Bacigalupi & Heckard 8975* (JEPS); near mouth of Sixes River, *Peck 8542* (DS, F, GH, NY); bluffs along beach at Arch Rocks, *J. W. Thompson 12834* (CAS, NY, PH, WSU).

Measurements were made of 26 vegetative and floral characteristics of the specimens in eight field collections of hexaploid *L. macrantha* ssp. *macrantha* from throughout its range and including small specimens that superficially resembled the tetraploids. Four field collections of *L. macrantha* ssp. *prisca* from Oregon were examined. The nine characters that were most useful for distinguishing these two subspecies are given in Table 1. There was overlap in all of these measurements, but the averages of these 9 characteristics are different and most of the measurements for each subspecies are exclusive. Thus, without knowing the geographical origin of specimens, it is possible to separate the two subspecies with a high degree of accuracy.

Intersubspecific hybrids have been made in addition to those reported upon previously (Ornduff, 1966, pp. 25–27; new data in table 2) and

TABLE 2. POLLEN VIABILITY OF INTER- AND INTRASUBSPECIFIC HYBRID PROGENIES OF LASTHENIA MACRANTHA SSP. PRISCA (SEE ALSO ORNDUFF, 1966, 6. 27)

Cross	Number of hybrids grown	Average pollen viability (range)
(hexaploid × tetraploid)		
5059[1] × 4986[2]	4	78 (44-93)
Reciprocal	2	80 (77,82)
5059 × 6981	1	91
4709[3] × 4986	7	50 (15-93)
Reciprocal	6	77 (50-98)
4709 × 6981	7	50 (0-87)
Reciprocal	2	93 (-)
(tetraploid × tetraploid)		
4985 × 6981	7	93 (75-98)
Reciprocal	6	93 (89-97)
4985 × 4986	6	88 (72-96)
Reciprocal	6	94 (89-99)
6981 × 4986	6	93 (83-98)
Reciprocal	5	88 (84-92)

[1] Field number of author; ssp. *macrantha*, Noyo River, Mendocino Co., Calif.
[2] Field localities for ssp. *prisca* are listed in text.
[3] ssp. *bakeri*, Garcia River, Mendocino Co., Calif.

intrasubspecific hybrids have been made in *L. macrantha* ssp. *prisca* as well (table 2). Despite the low crossability between the tetraploids and hexaploids, their hybrids tend to produce pollen with a moderate to high viability (based on the staining reaction of 100 pollen grains mounted in aniline blue-lactophenol). It should also be pointed out that hybrids between *L. macrantha* ssp. *prisca* and tetraploid plants of the allopatric closely related annual *L. chrysostoma* also are generally fertile (Ornduff, 1966, p. 28). In many respects, *L. chrysostoma* may be viewed on an annual "version" of *L. macrantha*.

Lasthenia macrantha ssp. *prisca* is known from a very few populations that occur along the southern Oregon coast. Some of these populations, such as those at Cape Sebastian, are very small and in other areas real estate developments or grazing activities risk exterminating the subspecies locally.

The tetraploid chromosome number of *Lasthenia macrantha* ssp. *prisca* suggests that it is ancestral to the hexaploid subspecies of *L. macrantha*. The epithet *prisca*, which means "belonging to former times, ancient, primitive," is intended to reflect this relationship as well as the relic nature of this tenuously surviving subspecies.

LITERATURE CITED

ORNDUFF, R. 1966. A biosystematic survey of the goldfield genus Lasthenia (Compositae: Helenieae). Univ. Calif. Publ. Bot. 40:1-92.

NEW MOSS RECORDS FROM MEXICO

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The bryoflora of Mexico has been studied for many years by several workers (Hampe, 1869; Bescherelle, 1872; Müller, 1874) but the bryogeographical relationships have been examined critically only in the last twenty five years. Sharp (1939) observed a number of mosses distributed both in Mexico and eastern United States and discussed them in a subsequent series of papers (1944, 1945, 1946). Sharp and Iwatsuki (1965) have listed those species common to Japan and Mexico, and Crum (1956) has pointed out the existence of a bicentric (Afro-American) pattern of distribution of genera known from Mexico, sometimes with a third center of distribution in southeastern Asia.

In the summer of 1968 the senior author visited several high mountains of Mexico as a part of a study on the relationships of the alpine bryoflora of the country. One of these mountains was Cerro Potosí, the northernmost peak having an alpine vegetation, which is situated at 24°53′30″ N. Lat. and 100°10′30″ W. Long. near Galeana and the village of 18 de Marzo, Nuevo León. Among the species identified, we have recognized the following as not previously reported from Mexico:

Encalypta vulgaris Hedw. According to Nyholm (1954), the species is common in Fennoscandia. It is also found in Europe, the Canary Islands, Madeira, northern Africa, Asia, New Guinea, and New Zealand. In North America it occurs throughout the Rocky Mountains and westward (Flowers, 1938). Bartram (1949) noted it from the mountains of New Mexico and Arizona, and in Guatemala. This leaves a gap in the distribution of the species which is partially filled by the collections from Cerro Potosí.

Four collections were made on the mountain summit, *Delgadillo 2376* MEXU, TENN, and *2378a* MEXU, TENN, in the *Pinus culminicola* scrub near the alpine meadow. These were on boulders in open and moist places and were subalpine. Nos. *2345a* MEXU, TENN, and *2448a* MEXU, were from the alpine area, on soil and soil-covered rocks, in open and moist places. The rocks of the area are calcareous.

Grimmia anodon B.S.G. This species has been reported from Fennoscandia, northern, western, and central Europe, the Pyrenees, northern Italy, Algeria, Morocco, the Caucasus, western and central Asia and eastern India. From North America it has been reported from Greenland and New Brunswick (although, according to Howard Crum (personal communication), there are no specimens from New Brunswick at CAN, DUKE, or NY); also from British Columbia, Yukon southeast to South

Dakota and Saskatchewan and south to Arizona. All Mexican collections came from the summit of Cerro Potosí where they grew on exposed boulders in alpine and subalpine communities. *Sharp 3912,* collected in 1945 from the same mountain, is this taxon, although originally identified as another species of *Grimmia.*

The Mexican plants agree with the characteristics of the species except that the upper part of the leaf margin is bistratose. Jones (1933) indicated that in *G. anodon* the leaves are mostly bistratose.

Specimens examined: *Sharp 3912* TENN, *Delgadillo 2361* MEXU, TENN, *2412* MEXU, TENN, *2429* MEXU, TENN, also *2359a,* and *2445a* MEXU.

Orthotrichum anomalum Hedw. Crum (1951) indicated in his discussion on the Appalachian-Ozarkian-Mexican flora relationships: "It is probable that many other North American species, already reported from other parts of Latin America, will be discovered in Mexico." Among other species, he pointed out *Encalypta vulgaris* (reported here), and *O. anomalum.* Although Crum identified a Mexican specimen of the latter species (*Sharp 3005* MICH, TENN), he made no report on it.

Orthotrichum anomalum is circumpolar in distribution: throughout northern and central Asia and Europe, south to northern Africa. In North America it occurs on calcareous rocks from Nova Scotia, Alaska, south to Arizona and New Mexico; Iowa and Virginia; Mexico and Haiti. Bartram (1949) reported it from Guatemala; however, upon examining the specimen cited by him, we have concluded that the material is not *O. anomalum.* Sharp's specimen was collected from crevices of calcareous rocks on Cerro Potosí at about 9500 feet.

Orthotrichum cupulatum Hoffm. ex Brid. The species occurs throughout Europe, south to northern Africa and in central Asia. In North America it is restricted to the drier parts of the Rocky Mountains with outlying populations in the Black Hills, South Dakota, southwestern Wyoming, and central Texas. Infrequent in Washington, Oregon, and California. All the Mexican specimens have been collected on exposed boulders in alpine or subalpine communities on Cerro Potosí.

Morphologically *O. cupulatum,* in its typical form, has immersed, ovate capsules which are 16-ribbed. The exostome is finely striate (as opposed to papillose in *O. strangulatum*) and the endostome is rudimentary or lacking. The Mexican material compares well with typical *O. cupulatum,* except that the exostome teeth are coarsely papillose-striate and 8 short endostome segments are present.

Specimens examined: *Sharp 3911* TENN, *Delgadillo 2412* MEXU, MICH, TENN, *2403* MEXU, MICH, TENN, *2431* MEXU.

Orthotrichum pallens Bruch. This species is distributed with a sporadic pattern in boreal and montane regions over much of the Northern Hemisphere. In the Old World it has been recorded from Finland, Sweden, Norway, Austria, Germany, Switzerland, France, Italy, and Russia. In North America, *O. pallens* var. *parvum* was reported by

Venturi from Yellowstone National Park. However, material collected and named as such by Flowers from Utah does not compare well with Venturi's description and should be excluded from the species concept of *O. pallens*. A discussion of the taxonomy of this species is given by Miller and Vitt (1970).

Orthotrichum pallens is distributed discontinuously in North America throughout the western Cordillera; the Black Hills, South Dakota; eastward through Manitoba, Ontario, northern Michigan, the Gaspe Peninsula, Quebec, and Newfoundland. It is reported here from Cerro Potosí which appears to be the southernmost station in North America. The species was found as an alpine or subalpine epiphyte living on *Ribes* sp. and *Pinus culminicola*, often mixed with *O. pycnophyllum*.

Specimens examined: *Delgadillo 2364* MEXU, MICH, TENN, *2439a* MEXU, TENN, *2365b* MEXU, *2440* MEXU, and *2375b* TENN.

From the discussion it can be seen that the species reported here show northern affinities. For some species, Cerro Potosí seems to be situated at the end of the geographical range while for others, it represents a "stepping stone" for a wider distribution toward Central America.

All of these species have their closest stations to the west and north. Beaman and Andresen (1966) noted that 25% of the vascular plants of the summit of Cerro Potosí have an affinity with the flora of the southern Rocky Mountains. The affinities of this flora (as shown also by these moss records) are thus, with western North America, not with the flora of the southeastern United States as is the case for many mosses of eastern Mexico (Pursell and Reese, 1970). These species of mosses were probably associated with the Arcto-Tertiary flora and their present distribution is doubtless related to the history of glaciation and climatic changes during the Pleistocene. Apparently, the Sierra Madre Oriental, of which Cerro Potosí is a part, was uplifted in the Pliocene (Beaman and Andresen, 1966).

Noteworthy is the distribution of these species, all of which reach Mexico through the mountains of southwestern United States from western North America. If they have a wider distribution in Mexico along the Sierra Madre Occidental, no evidence yet has been provided. However, in view of the distribution of many other mosses, at least the *Encalypta* may be expected to have a wider distribution in Mexico, although only *E. ciliata* has been reported from the central part of the country.

Greatly appreciated is the help of Francisco González M. from the Instituto de Biología, U.N.A.M., while we were on Cerro Potosí. This paper is a contribution from the University of Tennessee Botanical Laboratory, N. Ser. 349 and the Department of Botany, University of Michigan.

LITERATURE CITED

BARTRAM, E. B. 1949. Mosses of Guatemala. Fieldiana, Bot. 25:1-442.

BEAMAN, J. H., and J. W. ANDRESEN. 1966. The vegetation, floristics and phytogeography of the summit of Cerro Potosí, Mexico. Amer. Midl. Naturalist 75:1-33.

BESCHERELLE, E. 1872. Prodromus bryologiae Mexicanae ou enumération des mousses du Mexique avec description des especes nouvelles. Mém. Soc. Sci. Nat. Cherbourg 16:144-256.

CRUM, H. A. 1951. The Appalachian-Ozarkian element in the moss flora of Mexico with a check-list of all known Mexican mosses. Unpublished Ph.D. dissertation, University of Michigan, Ann Arbor.

————. 1956. Notes on Hypnodon, a genus of Orthotrichaceae new to North America. Bryologist 59:26-34.

FLOWERS, S. 1938. Encalyptaceae. In A. J. Grout, Moss Flora of North America North of Mexico 1:137-145.

HAMPE, E. 1869. Species muscorum novae Mexicanae. Verh. K. K. Zool.-Bot. Ges. Wien 19:507-510.

JONES, G. N. 1933. Grimmiaceae. In A. J. Grout, Moss Flora of North America North of Mexico 2:1-60.

MILLER, N. G., and D. H. VITT. 1970. Additional bryophytes from sinkholes in Alpena County, Michigan, including Orthotrichum pallens new to eastern North America. Michigan Bot. 9:87-94.

MÜLLER, C. 1874. Novitates bryothecae Müllerianae. 3. Musci Mexicani. Linnaea 38:620-660.

NYHOLM, E. 1954–1960. Illustrated Moss flora of Fennoscandia. II. Musci. Fasc. 1–4.

PURSELL, R. A., and W. D. REESE. 1970. Phytogeographic affinities of the Gulf coastal plain of the United States and Mexico. J. Hattori Bot. Lab. 33:115-152.

SHARP, A. J. 1939. Taxonomic and ecological studies of eastern Tennessee bryophytes. Amer. Midland Nat. 21:i–vii, 268–354.

————. 1944. Some problems in American Bryology. Lilloa 10:265-283.

————. 1945. Notas sobre la flora de la región escarpada de la parte noroeste del estado de Puebla. Bol. Biol. Univ. Puebla 11-12:29-32.

————. 1946. Informe preliminar sobre algunos estudios fitogeográficos efectuados en México y Guatemala. Revista Soc. Mex. Hist. Nat. 7:35-44.

————, and Z. IWATSUKI. 1965. A preliminary statement concerning mosses common to Japan and Mexico. Ann. Missouri Bot. Gard. 52:452-456.

NOTES AND NEWS

TWO SPECIES OF PANICUM (POACEAE) NEW TO OREGON.—*Panicum villosissimum* Nash is native to the eastern one half of the United States and has not previously been reported from the West. A specimen of *Panicum* collected on July 29, 1931, by E. C. Johnston *(s. n.)* at Troutdale, Oregon (CAS), long left undetermined, was identified some years later as *P. pacificum* Hitchc. & Chase. This is the western species this specimen most closely resembles. The collection was made late in the growing season, after the spikelets had fallen from the terminal panicles, where the largest spikelets on the plants of this and allied species occur. Those spikelets on the branch panicles produced later in the season are about 2.1 mm long, at least 0.3 mm longer than the spikelets found on the branch panicles of *P. pacificum*. The

largest spikelets in that species, found on plants several hundred miles to the south, are on the terminal panicles also and only occasionally reach 2.1 mm in length. Johnston's specimen has long branches with the leaves crowded toward the end and appears not to have had the same habit as the tightly tufted plants with stiffly erect or ascending culms of most of the plants of *P. pacificum* found in northwest Oregon and southwest Washington. The hairs on the adaxial surfaces of the blades are short and dense, unlike the long sparse hairs found on rare hybrids between *P. pacificum* and *P. scribnerianum,* which this plant in a few respects resembles. The specimen in question is sparingly branched and has spreading to ascending hairs on the sheaths and culms, and is referable to *P. villosissimum* Nash var. *pseudopubescens* (Nash) Fernald. Many species are adventive along the lower Columbia River, near Portland, most having been introduced in ballast. Whether this species persists there has not been determined, but it was not found during a brief search of the sandy flats along the Columbia River near Troutdale in August, 1969.

Panicum agrostoides Spreng., also native to the eastern half of the United States, has been reported from California and British Columbia but not the intervening states. On September 8, 1966, it was found growing in moist sand well below the high water level of the Umpqua River at the Scott Creek Low Water Public Boat Access, 8 miles east of Scottsburg, Douglas Co. (*R. & M. Spellenberg 1632,* WTU, NY). Several plants were found at some distance from one another and the species is probably established along this section of the river.—RICHARD SPELLENBERG, Department of Biology, New Mexico State University, Las Cruces 88001.

SYSTEMATIC STUDIES OF LIMNANTHACEAE

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Continuing studies of the Limnanthaceae (Ornduff and Crovello, 1968; Ornduff, 1969) have provided data relevant to an understanding of the systematic and evolutionary patterns within this small, primarily western American family of annual herbs. The primary purpose of this paper is to present the results of an extensive inter- and intraspecific crossing program within *Limnanthes,* but also included are observations on the ecology of *L. macounii,* new distributional data for some species, and first chromosome counts for *Floerkea prosperpinacoides* and *L. macounii.*

ARTIFICIAL HYBRIDIZATIONS

Because of the strong barriers to crossing among the species of *Limnanthes,* obtaining hybrids for studies of pollen viability and meiotic behavior have been difficult. Mason (1952) obtained one artificial interspecific hybrid in the genus and by making interspecific pollinations in very large numbers I have been able to obtain additional interspecific hybrids. In the following discussion, the term "pollen viability' refers to the proportion of pollen grains (based on a sample of 100) that stain with aniline blue in lactophenol. A recent study (Hauser and Morrison, 1964) suggests that this staining method sometimes results in an over-estimate of the actual viability by perhaps as much as 15%, but in general stainability of fresh pollen by this technique seems to be a

TABLE 1. POLLEN VIABILITY OF LIMNANTHES HYBRIDS. ORIGIN OF THE PARENTAL PLANTS IS LISTED BELOW

Numbers given without collector are those of the author. All localities are in California except where noted. Vouchers for these collections are in UC or JEP: *T. Niehaus 367,* Hwy 99E, jcn. Oroville-Shippe rd., Butte Co.; *T. Niehaus 371,* Table Mt., Butte Co.; *522, D. E. Anderson s. n.,* Iaqua ranch, Humboldt Co.; *C. N. Smith 550,* Greenhorn Mts., Kern Co.; *R. Cruden 943,* N. of Jolon, Monterey Co.; *C. N. Smith 1106,* Greenhorn Mts., Kern Co.; *1963, Melburn s. n.,* Victoria, British Columbia, Canada; *1964, M. Botts s. n.,* Cuyamaca Lake, San Diego Co.; *R. M. Lloyd 3358,* nr. jcn. hwy. 88 and 49, Amador Co.; *R. M. Lloyd 3359,* W of jcn. of hwy. 88 and 49, Amador Co.; *4767,* Sonoma, Sonoma Co.; *6148,* Point Reyes, Marin Co.; *6778,* Lytton Springs rd., Sonoma Co.; *6780,* N of Willits, Mendocino Co.; *6781,* N of Willits, Mendocino Co.; *6795,* Merlin, Douglas Co., Oregon; *6828,* nr. jcn. hwy. 49 and 120, Tuolumne Co.; *6832,* S of Napa, Napa Co.; *6833,* N of Sonoma, Sonoma Co.; *6844,* Upper Lake, Lake Co.; *6845,* Between Ben Hur and Raymond, Madera So.; *6847,* Coarsegold, Madera Co.; *6849,* Coarsegold, Madera Co.; *6851,* Indian Mission valley, Fresno Co.; *6853,* Sobre Vista road, Sonoma Co.; *6854,* nr. Glen Ellen, Sonoma Co.; *6860,* Laguna de Santa Rosa, Sonoma Co.; *6863,* Manzana, Sonoma Co.; *6864,* Hessel road, Sonoma Co.; *6880,* 4.4 mi. SE Calistoga, Napa Co.; *6885,* N of Oroville, Butte Co.; *6915,* Junction City, Trinity Co.; *6927,* Pinehurst, Jackson Co., Oregon; *6980,* Ukiah, Mendocino Co.

Explanation of superscripts:

a, diakinesis normal; b, metaphase I normal; c, anaphase I normal; d, metaphase II normal; e, anaphase II normal; f, telophase II and pollen formation normal; and g, meiosis abnormal—see text.

Cross, ♀ × ♂	Collection Number	Number of hybrids	Average pollen viability	Range
Intraspecific				
douglasii nivea × douglasii nivea	522 × 6880	1	91	—
	943 × 6844	1	95	—
douglasii douglasii × douglasii douglasii	6832 × 4767	4	99	(97-100)
	6833 × 4767	2	100	—
	6854 × 6833	1	86	—
douglasii rosea × douglasii nivea	371 × 943	3	84	(73-98)
	371 × 6844	2	94	—
	371 × 6980	1	90	—
douglasii nivea × douglasii douglasii	943 × 4767	1	97	—
douglasii nivea × douglasii sulphurea	6148 × 6844	2	96	(92,99)
	6863 × 6148	2	99	(98,100)
	522 × 6148	1	98	—
floccosa floccosa × floccosa bellingeriana	6927 × 6885	1	87	—
	Reciprocal	2	95	—
striata	6915 × 3358[b,d,e]	2	76	—
	Reciprocal[b]	5	79	(72-89)
montana	550 × 1106	1	57	—
	550 × 6849	1	100	—
	550 × 6851	1	98	—
	1106 × 6845	1	100	—
	1106 × 6849	1	56	—
	6845 × 6847	1	100	—
	6845 × 6851	4	87	(82-90)
	6847 × 6845	1	99	—
	6849 × 6845	1	100	—
	6851 × 1106	3	98	(93-100)
	6851 × 6847	1	100	—

Interspecific, *Inflexae*				
montana × *alba alba*	550 × 367[g]	7	27	(2-55)
	550 × 6853[g]	2	32	(17,47)
	1106 × 367[g]	3	29	(24-35)
	1106 × 6853[a]	5	48	(30-61)
	6847 × 6853	3	53	(34-66)
	6849 × 367	2	43	(41,45)
	6849 × 6853	2	43	(36,50)
montana × *gracilis gracilis*	550 × 6795	1	19	—
	1106 × 6795[b, c]	7	35	(1-68)
	6795 × 6851	4	3	(0-7)
	6847 × 6795	2	16	(1,30)
	6849 × 6795	3	46	(20-60)
montana × *gracilis parishii*	550 × 1964[b, d]	6	37	(8-47)
	1106 × 1964[b, e]	5	37	(24-55)
	1964 × 6851	1	14	—
gracilis parishii × *alba alba*	1964 × 367[b, c]	1	74	—
	1964 × 6853	3	58	(56-61)
gracilis gracilis × *alba alba*	6795 × 6853	1	100	—
	F_2	26	85	(24-100)
Interspecific, *Reflexae*				
striata × *douglasii nivea*	3358 × 6980	1	35	—
	3359 × 6844	1	66	—
striata × *douglasii rosea*	6828 × 371	5	90	(78-95)
striata × *douglasii douglasii*	6915 × 4767	2	100	(99,100)
bakeri × *striata*	6781 × 3358[b, c]	2	10	(4,16)
	6781 × 6915[b]	4	56	(35-70)
macounii × *striata*	1963 × 3358[g]	3	48	(45-50)
	F_2	4	77	(7-82)
	1963 × 6915[g]	6	55	(41-72)
douglasii nivea × *vinculans*	6780 × 6861	2	94	(91,97)
macounii × *douglasii nivea*	1963 × 6778	1	58	—
	F_2	38	65	(39-89)
	F_3	46	55	(1-100)
	1963 × 6880	2	42	(40,43)
macounii × *vinculans*	1963 × 6864[g]	3	52	(35,75)
macounii × *bakeri*	1963 × 6781	2	32	(19,44)
bakeri × *vinculans*	6781 × 6864[b]	3	44	(35-55)
striata × *vinculans*	6915 × 6860[b]	1	64	—
Intersectional				
macounii × *montana*	1963 × 6847	1	0	—

reliable and simple indicator of viability. The pollen viability figures for the hybrid progenies are given in Table 1. The origins of the plants used in the hybridization program are given in the appendix.

Interspecific hybridizations: In section *Reflexae,* hybrids between *L. striata* Jeps. and *L. douglasii* R. Br. var. *nivea* C. T. Mason showed a markedly reduced pollen viability, but those between *L. striata* and *L. douglasii* var. *rosea* (Benth.) C. T. Mason or *L. douglasii douglasii* had a high pollen viability. Since the *striata* parent of each of the above crosses originated from different populations, these variable results may be attributable to genetic differences among populations of this species rather than to a consistent trait of this species or to genetic

differences among the varieties of *L. douglasii*. This suggestion receives support from the lowered pollen viability of interpopulation crosses within this species (see below) as well as in the crosses with *L. bakeri* J. T. Howell.

Hybrids between *L. vinculans* Ornduff and the morphologically similar and near sympatric *L. douglasii nivea* (Ornduff, 1969) had a high pollen viability; hybrids between *L. vinculans* and the somewhat similar *L. bakeri* showed a sharply reduced pollen viability. Hybrids between *L. striata* and *L. vinculans* showed a moderately reduced pollen viability. One of the hybrid progenies of *L. bakeri* and *L. striata* showed a very low pollen viability; the other progeny of this hybrid combination had a higher pollen viability of 56%.

Hybrids between *L. macounii* Trel. and *L. striata*, *L. douglasii nivea*, *L. bakeri*, or *L. vinculans* all showed a low pollen viability. The F_2 progeny of *L. macounii* $\times$ *L. striata* showed an increase in average pollen viability as well as an increase in the range of pollen viabilities in the progeny. The F_2 of the cross between *L. macounii* and *L. douglasii nivea* showed a similar response; however, the average pollen viability of the F_3 was lower than that of the F_2 and approximately equal to that of the F_1. Nevertheless, individuals were present in the F_3 which had higher pollen viabilities than any individuals in either the F_1 or the F_2.

In Section *Inflexae*, a number of hybrids were obtained between *L. montana* Jeps. and *L. alba* Benth. var. *alba*. The pollen viabilities of these progenies were rather low. Likewise, hybrids between *L. montana* and the morphologically similar *L. gracilis* Howell var. *gracilis* also had pollen with a low viability. Hybrids between *L. alba* and *L. gracilis* var. *parishii* (Jeps.) C. T. Mason had relative sterile pollen, but those of *L. alba alba* and *L. gracilis gracilis* had highly viable pollen. The F_2 of one progeny of the latter cross showed a reduction in average pollen viability.

The sole intersectional hybrid obtained was from a cross between *L. macounii* and *L. montana;* this plant produced no viable pollen.

Intraspecific hybridizations: A number of intra- and intervarietal hybridizations were carried out in *L. douglasii* with particular emphasis on using parents from populations that are widely separated geographically. Although a slight reduction in pollen viability occurred in two progenies, in general these hybrids were fertile. These observations confirm those reported by Mason (1952), although he had no hybrids between *L. douglasii rosea* and *L. douglasii nivea*. Similarly, intervarietal hybrids between *L. floccosa* Howell var. *floccosa* and *L. floccosa* var. *bellingeriana* (Peck) C. T. Mason were fertile. The interpopulation hybrids in *L. striata* were between parents originating from the two disjunct areas of the range of this species on the western and eastern side of the Sacramento Valley (see below). These intraspecific hybrids showed a reduced pollen viability.

A large series of interpopulation hybridizations was carried out in *L. montana* because of the substantial population-to-population morpho-

logical variation this species shows and because some of its populations morphologically approach one or the other varieties of *L. gracilis* (Ornduff and Crovello, 1968). The number of hybrids obtained from each cross was very low, attesting to the low intraspecific, interpopulation crossability in this species that is reminiscent of similar barriers in *Blennosperma nanum* (Hook). Blake and *Lasthenia chysostoma* (F. & M.) Greene (both Compositae, see Ornduff 1963; 1966). In general, however, the pollen viability of the interpopulation hybrids in *L. montana* was high, with the exception of some of those utilizing plants from population 1106 at the southern edge of its range. However, plants from this population may also form fertile hybrids in other intraspecific combinations.

CYTOLOGICAL OBSERVATIONS

In 11 of the 17 hybrid progenies examined in which pollen viability ranged from 1 to 79%, meiosis associated with microsporogenesis appeared to proceed normally (see footnotes, Table 1). In the remaining 6 hybrid progenies (representing two interspecific combinations) various meiotic abnormalities were noted. The unusual meiotic behavior of hybrids between *L. montana* and *L. alba alba* consisted of the formation of three bivalents and one loosely associated quadrivalent in all cells examined (550 $\times$ 367) or in 25% of the cells (550 $\times$ 6853) with the remaining cells having 5 bivalents, or of bivalents only with a slight association between two of the bivalents (1106 $\times$ 367)). Anaphase 1 of all hybrids was characterized by the appearance of one or two tenuous bridge-like figures between homologous chromosomes migrating toward opposite poles. These observations suggest that the chromosomes of *L. montana* and *L. alba alba* may differ by one or more very small translocations. Of the 11 metaphase 1 figures examined in one hybrid progeny between *L. macounii* and *L. striata* (1963 $\times$ 3358) four showed normal bivalent formation and 7 showed three bivalents and one chain or ring quadrivalent. In another hybrid progeny of these two species five bivalents were present, but three of these bivalents were loosely associated with each other at metaphase 1 although it is not clear whether the latter constituted a true multivalent. In hybrids between *L. macounii* and *L. vinculans* three bivalents were present along with variable asymmetrical multivalent configurations of four chromosomes whose exact cytological nature was not determined. These superficial chromosomal studies of hybrids between *L. macounii* and *L. vinculans* suggest that these two species may also differ by at least one very small translocation or, alternatively, that the chromosomal set of one species contains some duplicate chromosomal segments of the other species.

The absence of meiotic chromosomal irregulatrities in the majority of interspecific hybrids of *Limnanthes* indicates that a number of species in the genus have similar gross chromosomal structure. The nature of the cytological irregularities observed in a few of the interspecific hybrid progenies suggests that those interspecific chromosomal differences which

do exist are of a relative minor nature. It is probable, therefore, that the sterility obesrved in these hybrids primarily has a genetic basis rather than a cytological one since sterility may also occur in the absence of meiotic irregularities. Progeny-to-progeny variation in average pollen stainability of intraspecific, interpopulation hybrids (notably within *L. montana*) as well as in interspecific hybrids (e.g. *L. montana* $\times$ *L. gracilis*) suggests that the substantial morphological variation within some *Limnanthes* species may be associated with genetic differences which affect the pollen viabilities of their hybrid progenies, although the well-marked geographical differences characteristic of the varieties of *L. douglasii* are not associated with such "sterility" genes.

In section *Inflexae,* it is interesting to note that *L. montana* and *L. gracilis* are morphologically so similar that some populations of the two species are barely separable (Ornduff and Crovello, 1968) yet these two species are consistently separated by a sterility barrier which reinforces their mutual geographical isolation. In contrast, the relatively dissimilar *L. gracilis* and *L. alba alba* may form relatively fertile hybrids. In section *Reflexae,* there is likewise no consistent relationship between morphological similarity of the parents and fertility of their hybrids. For example, the relatively similar *L. bakeri* and *L. vinculans* produce rather infertile hybrid progeny, whereas the rather more dissimilar *L. striata* and *L. douglasii rosea* form relatively fertile hybrids.

The lack of relationship between geographical distribution, ease of crossability, and hybrid fertility deserves further comment. The range of the morphologically distinctive *L. macounii* is geographically well removed from that of other members of the genus. The large number of interspecific hybrid combinations in which this species was a parent (including the only intersectional hybrid obtained) attests to its comparatively high crossability with other members of the genus. Despite this, however, all hybrid progenies of *L. macounii* showed a substantially reduced pollen viability. In contrast, hybrids between sympatric or marginally sympatric species of *Limnanthes* are difficult to obtain. In the field, I have observed the following sympatric combinations of species: *L. bakeri* with *L. douglasii nivea; L. alba versicolor* and *L. alba alba* with *L. floccosa floccosa;* and *L. vinculans* with *L. douglasii nivea.* Despite repeated attempts, no artificial hybrids have been obtained in the first three combinations. Two hybrid individuals were obtained between *L. douglasii nivea* and *L. vinculans,* but only when individuals from allopatric populations were used. When individuals were used that had originated from localities where interspecific population contact occurs all hybridization attempts failed.

Chromosome Counts

Despite its abundance in much of North America, there are no reported chromosome counts for *Floerkea proserpinacoides* Willd. Cytological examination of greenhouse-grown plants from seed collected near

Bloomington, Monroe Co., Indiana (*Heiser 6305*, UC) and from Tre-
lease Woods, Champaign Co., Illinois (*D. M. Smith* in 1964, UC) indi-
cate that this species has $n = 5$. Mason (1952) reported $n = 5$ for all
species of *Limnanthes* that he recognized with the exception of *L.
macounii*, which he believed to be extinct. My investigations of this
species based on plants grown from seed collected in Uplands Park,
Victoria, British Columbia, by Miss M. Melburn, indicate that this
species has $n = 5$.

Ecology of L. macounii

Mason (1952) and Hitchcock (1961) believed that *L. macounii* pos-
sibly was extinct since it had not been collected since 1926 and the few
localities known for it on Vancouver Island had been subjected to eco-
logical disturbance by man. However, in 1958 Miss M. C. Melburn of
Victoria located a population of this species in Uplands Park, Victoria,
just above the Straits of Georgia. A second recent collection of *L.
macounii* was made from a single population on Trial Island (*Calder &
Mackay 28917*, DAO). This island is less than a half mile from the
coastline of Victoria. However, in a recent visit to this locality, Miss
Melburn was unable to find any plants on this island. The total known
range of this species (including five other sites where it is now extinct)
is included in a radius of three miles. In view of the unusual disjunct
distribution of this species relatives to the rest of the genus in southern
Oregon and California and in view of its present rarity, the following
information is presented concerning the habitat and associates of *L.
macounii* based on Miss Melburn's notes: *Limnanthes macounii* occurs
in one or two populations where the prostrate plants are densely crowded
and associated with other herbaceous annuals such as *Alchemilla occi-
dentalis* Nutt., *Microseris bigelovii* (Gray) Sch.-Bip., *Montia dichotoma*
(Nutt.) Howell, *Montia howellii* Wats., *Myosurus minimus* L., *Ortho-
carpus faucibarbatus* Gray subsp. *albidus* Keck, *O. pusillus* Benth.,
Plagiobothrys scouleri Johnst., *Plantago bigelovii* Gray, and various
annual grasses. The site is a vernal pool which has a very thin mantle of
soil on a rock bed. Based on observations extending over 8 years, first
flowering dates of *L. macounii* extend from March 27 to April 22. Insects
have not been observed visiting the flowers. In cultivation, the species
is wholly autogamous.

New Distributional Data

Mason (1952) cites a collection of *L. alba alba* from Sonoma Co.,
(Glen Ellen, *M. S. Baker* in 1923, JEP) but does not include this col-
lection in his description of the range of the species nor is it indicated
on his map of its range. Other collections of *L. alba alba* from Sonoma
Co. are: Near Santa Rosa, *Mrs. (A. E.?) Alexander* in April, 1944
(CAS); Warfield, *M. S. Baker 4996* (CAS); Agua Caliente, *L. Rose
51007* (CAS); Jack London Ranch, *P. Raven 347* (CAS); Sobre Vista
road, *R. Ornduff 6846* (UC). This variety is also known from a single

locality in Lake Co.: Junction of highways 175 and 29, *Cruden 1001* (UC). *Limnanthes floccosa*, likewise considered to be a species unrepresented in California west of the Sacramento Valley, occurs in a single population very near the Lake County population of *L. alba alba*. This population is referable to *L. floccosa floccosa;* it occurs in an extensive area of a vernal lake bed north of the junction of highways 29 and 175 (*Ornduff 6811,* UC). Another collection which is probably from the same population is: 5 or 6 miles south of Kelseyville, *M. S. Baker 5989,* Santa Rosa Junior College Herbarium. *Limnanthes douglasii sulphurea,* known previously only from Point Reyes, Marin Co., recently has been collected in coastal San Mateo Co., Canyon Road, *W. Anderson* in 1966 (CAS); Butano Creek Canyon, *J.* and *B. McClellan* (CAS).

The taxon designated as L. "trinity" in an earlier paper (Orduff and Crovello, 1968) is now referred *L. striata.* The populations given this provisional name are disjunct from the chief range of *L. striata,* which extends along the eastern side of the Central Valley from Eldorado Co. south to Mariposa Co. Plants initially called L. "trinity" were collected from a population well to the northwest of this area, west of the Sacramento valley in the northern Coast Range of Trinity Co. Plants in this population were small and had very small flowers. These characteristics were retained in garden progeny. Subsequent field studies in this region turned up additional populations consisting of larger plants with larger flowers that are indistinguishable from those of *L. striata* in the southeastern main portion of its range.

These collections of *L. striata* from this disjunct northwestern area of distribution are: Trinity Co., 3.2 miles northwest of Junction City, *Ornduff 6915* (UC), *Heckard & Ornduff 1488* (JEP), *Cruden* in 1965 (UC); Shasta Co., west edge of Platina, *Ornduff 6918* (UC), *Heckard & Ornduff 1505* (JEP); Tehama Co., near Beegum, *Ornduff 6919* (UC), *Heckard & Ornduff 1507* (JEP); six miles SE of Platina, *Heckard & Ornduff 1508* (JEP). Despite the unusually small size of the Junction City collections, I am inclined to refer all of these northwestern plants to *L. striata.*

Summary

An extensive crossing program among species of *Limnanthes* confirms earlier observations that interspecific crossability in this genus is low. However, once artificial interspecific hybrids are obtained they show various levels of pollen sterility which seem unrelated to the degree of morphological difference between the parents. Observations of meiosis in

interspecific hybrids suggest a large degree of chromosomal homology among the species, although small translocations or duplications may exist. Intraspecific, interpopulation hybrids in *Limnanthes* are generally fertile, with a few exceptions in *L. montana* and *L. striata*. Chromosome counts of $n = 5$ are reported for *Floerkea prosperpinacoides* and *L. macounii*, thus completing a cytological survey of the family. Habitat data are recorded for *L. macounii*, now known from only a single population on Vancouver Island. Range extensions of *L. alba alba*, *L. floccosa floccosa*, and *L. striata* are given in the North Coast Ranges, and *L. douglasii sulphurea* is reported from San Mateo Co. Further field work on *Limnanthes* "trinity," considered to be an underscribed species in an earlier paper, indicates that these disjunct populations of this entity are best referred to *L. striata*.

LITERATURE CITED

HAUSER, E. J. P., and J. H. MORRISON. 1964. The cytochemical reduction of nitro blue tetrazolium as an index of pollen viability. Amer. J. Bot. 51:748-752.

HITCHCOCK, C. L. 1961. Limnanthes. *In* C. L. Hitchcock, A. Cronquist, M. Ownbey, and J. W. Thompson, Vascular Plants of the Pacific Northwest. Part 3. Univ. Washington Press, Seattle.

MASON, C. T. 1952. A systematic study of the genus Limnanthes R. Br. Univ. Calif. Publ. Bot. 25:455-512.

ORNDUFF, R. 1963. Experimental studies in two genera of Helenieae: Blennosperma and Lasthenia. Quart. Rev. Biol. 38:141-150.

————. 1966. A biosystematic survey of the goldfield genus Lasthenia. Univ. Calif. Pub. Bot. 40:1-92.

————. 1969. Limnanthes vinculans, a new California endemic. Brittonia 21:11-14.

————, and T. J. CROVELLO. 1968. Numerical taxonomy of Limnanthaceae. Amer. J. Bot. 55:173-182.

REVIEWS

Flora of the Galápagos Islands. By IRA L. WIGGINS and DUNCAN M. PORTER. xx +998 pp., 96 color photos, 268 line figures, 170 range maps. Stanford University Press. 27 May 1971. $37.50.

The Galápagos continue to be fascinating as much in fact as in fancy since they became famous to biologists following the visit of Charles Darwin. He had been preceded by only a few other plant collecting enthusiasts, among them David Douglas and John Scouler. The book by Wiggins and Porter, which includes the contributions from 28 other botanists, goes a long way towards confirming that in addition to the fabled animals, these islands do indeed have plants, many of them also interesting. According to G. L. Stebbins (1966, p. 46. In: *The Galápagos*, Ed. R. I. Bowman, Univ. Calif. Press), some aspects of the specimens of higher plants of this archipelago collected by Darwin helped to lead the latter "along the road toward the Origin of Species . . ."

The taxonomic portion includes 107 families, 348 genera, and 642 species. Better than a third (228 species and subspecies) are endemic. "Some" 395 taxa are illustrated, "at least one species in every genus considered." There are identification keys to all taxa, generous descriptions usually with valuable supporting commentaries,

distribution maps for each species within the Galápagos, and some 50 new chromosome number reports. Since this taxonomic portion is so competently presented, the cost of approximately 6 cents per species ought to seem less painful.

The taxa are organized into non-seed bearing vascular plants; Dicots divided into Apetalae, Gamopetalae, and Polypetalae; and finally, Monocots. All taxa within each of the above categories are in alphabetical sequences. The line drawings, contributed by several artists, generally are excellent. The two most frequent initials appear to be those of the senior author, who is thus shown to be an accomplished artist, and of Jeanne R. Jannish whose careful work has embellished many publications. In some instances, the expertly drawn dissections lack explanations in the legends. These will pose no problem for the trained botanist but will be a little mysterious to the inexperienced. The inclusion of synonyms in the text and in the Index will prove most useful to the serious taxonomist, geographer, and ecologist since many of the taxa are widely distributed in Mexico, Central America, Caribbean, and South America where sometimes they have been known by other Latin names. There also is a glossary and nine pages of bibliography.

The preliminaries and the 52 pages of Introduction are a welcome dividend which will prove valuable to all planning research in the Galápagos. Included is a table of English and Ecuadorian names for the approximately 45 land masses in this archipelago. These range in size from almost negliglible to approximately 1800 square miles in area and attaining an altitude of 5600 feet. Among the primary characteristics appear to be vulcanism, isolation, aridity, and the introduction of feral animals. The authors have cautiously dealt with dubious records of plants and point out the incomplete nature of the botanical information as hundreds of square miles probably have not been visited and difficult landings as well as the lack of water make many areas essentially inaccessible.

For the botanist the discussion of Vegetation Zones with lists of principal species, the History of Botanical Collecting, Scope of the Book and Methods of Treatment are of particular interest. The discussion of Materials Utilized, which identifies the major collections of plant specimens from the Galápagos and the institutions where housed and studied, reduces the need for citations of individual specimens. Table 2 neatly summarizes the numbers of taxa in each of the hierarchal groups of plants covered in the book. The 96 annotated and spectacular color photos show typical plants, vistas, and animals. Other topics dealt with are Settlement Pattern, Physiography, Geology, Climate, Soil Zones, Fauna, Discovery and Early History.

This reviewer would be the first to agree with Wiggins (1966, p. 175. In: *The Galápagos,* Ed. R. I. Bowman, Univ. Calif. Press) that often . . . "more emphasis has been placed on differences between the flora of tlhe Galápagos Islands and that of the northern part of South America than on similarities that might have been observed had the latter features been sought with equal diligence. Botanists . . . have been prone to stress the number of "new species" or "new varieties" rather than seek similarities that would relate insular plants to those growing on the mainland of South America or in Mexico . . . [and] lack of information about . . . full distribution scope . . . [continues to] make it difficult to determine relationships of many Galápagos plants."

Perhaps in view of this there was conscious effort to leave endemism a little underdone. Wiggins and Porter note endemics following the species descriptions, but for the most part, the endemics are thereby lost by being distributed through some 900 pages. I would have wished for a discussion of endemism in the present book and an itemizaiton of the 228 taxa—or some earmark in the Index to indicate presumed endemics so that one might begin to understand a little better their systematic distribution or single them out for more intensive study. Any criticisms, however, must remain picayune as the botanical contributors, artists, and the Stanford University Press clearly deserve congratulations on this significant and handsome first comprehensive taxonomic coverage of the vegetation of the Galápagos.—WALLACE R. ERNST, Department of Botany, Smithsonian Institution, Washington, D. C. 20560.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication should not exceed an estimated 15 pages when printed unless the author agrees to bear the cost of the additional pages at the rate of $20 per page. Illustrative materials (including "typographically difficult" matter) in excess of 30 per cent for papers up to 10 pages and 20 per cent for longer papers are chargeable to the author. Subject to the approval of the Editorial Board, manuscripts may be published ahead of schedule, as additional pages to an issue, provided the author assume the complete cost of publication.

Shorter items, such as range extensions and other biological notes, will be published in condensed form with a suitable title under the general heading, "Notes and News."

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Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum, Part 1. The Herbaria of the World*. Utrecht, Fifth Edition, 1964). Cited specimens should be in established herbaria.

Abbreviations of botanical journals should follow those in *Botanico-Periodicum-Huntianum* (Hunt Botanical Library, Carnegie-Mellon University, Pittsburgh, Pennsylvania, 1968). In cases where the author is unable to determine the correct abbreviation for a journal title, he should write it in full. Titles of books should be given in full, together with the place and publication, name of publisher, and an indication of the edition if other than the first. Do not underline any words in the literature cited, including binomials.

Membership in the California Botanical Society is normally considered a requisite for publication in MADROÑO.

MADROÑO

Contents

SEASONAL DIMORPHISM
IN BACCHARIS GLUTINOSA (COMPOSITAE)

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Baccharis glutinosa Pers. and *B. viminea* DC. are shrubs of ephemerally moist washes and the margins of permanent water courses at elevations rarely exceeding 5000 ft. They have been recognized as distinct species in several regional floristic treatments (Munz, 1959; Kearney and Peebles, 1951; Shreve and Wiggins, 1964). Mason (1957) notes, however, that the two species "are closely related and are not always easy to distinguish from each other." Recently Thorne (1967) has suggested that *B. glutinosa* is "doubtfully distinct from *B. viminea.*"

Baccharis glutinosa has virgate stems with glutinous, lance-linear, usually serrate leaves and a terminal corymbose inflorescence. *B. viminea* has woodier stems and smaller, obscurely glutinous, entire leaves. The capitula are disposed in dense, cymose clusters at the ends of numerous, short, lateral branches. The former species blooms during late summer and fall, the latter usually between spring and early summer. This array of contrasting morphological features distinguishes the two taxa, but investigation of herbarium specimens and natural populations has revealed overlapping variation and evident seasonal differences, suggesting that *B. glutinosa* and *B. viminea* are conspecific.

METHODS AND MATERIALS

Twenty plants in each of 21 large populations were randomly tagged during Feb. and Mar. 1967 (fig. 1). Sixteen of the tagged populations were situated in or near stream channels, one was located along the margin of a brackish slough and the remaining four occurred on relatively xeric sites. Two of the latter (Mill Creek and Oak Grove) were planted by the U. S. Forest Service for erosion control (N. Popovich, Arroyo Seco District, Angeles National Forest, pers. comm.).

Six characters were chosen for study: 1, number and 2, length of flowering branches disposed along the terminal two-meter segment of an erect woody stem; 3, the number of capitula per inflorescence; and
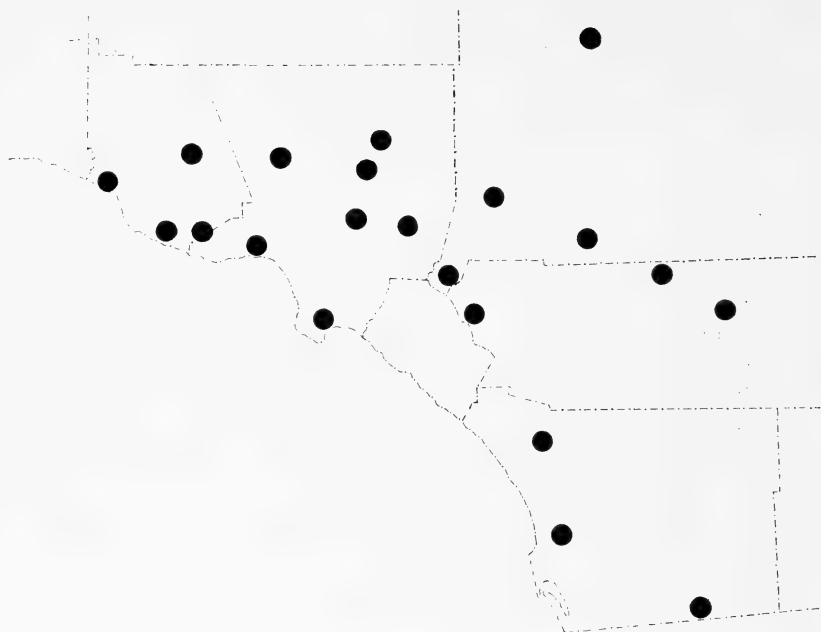
Fig. 1. Map of southern California showing locations of populations referred to in this paper.

4, the length, 5, width and 6, margin of 10 mature leaves from each plant. Each character was measured in all 21 populations during Mar. and Sept., 1967 with additional observations during 1968 and 1969. The data were analyzed by applying the "student's" t-distribution (Snedecor 1956). All comparisons between Mar. and Sept. samples for each population were significant at 5% unless otherwise noted.

Leaf margin was scored subjectively and consequently was not amenable to statistical analysis. Application of the terms *entire, denticulate* and *serrate* is exemplified in Fig. 2. Although *Baccharis* species are dioecious no significant differences were observed between staminate and pistillate plants for any of the characters studied.

RESULTS

Data derived from this study are summarized in Table I and the seasonal differences of five characters are demonstrated in Fig. 3.

The number and length of flowering branches are apparently inversely related as shorter, more numerous branches were produced in Mar. than in Sept. Not all twenty plants in each of five populations were in bloom during Sept.; consequently the range of population means was less than 1.0. The Ventura population exhibited no significant difference between Mar. (0.5) and Sept. (1.4) samples of flowering branch number although the difference in branch length was significant.

Entire

10 CM.

Denticulate   Serrate
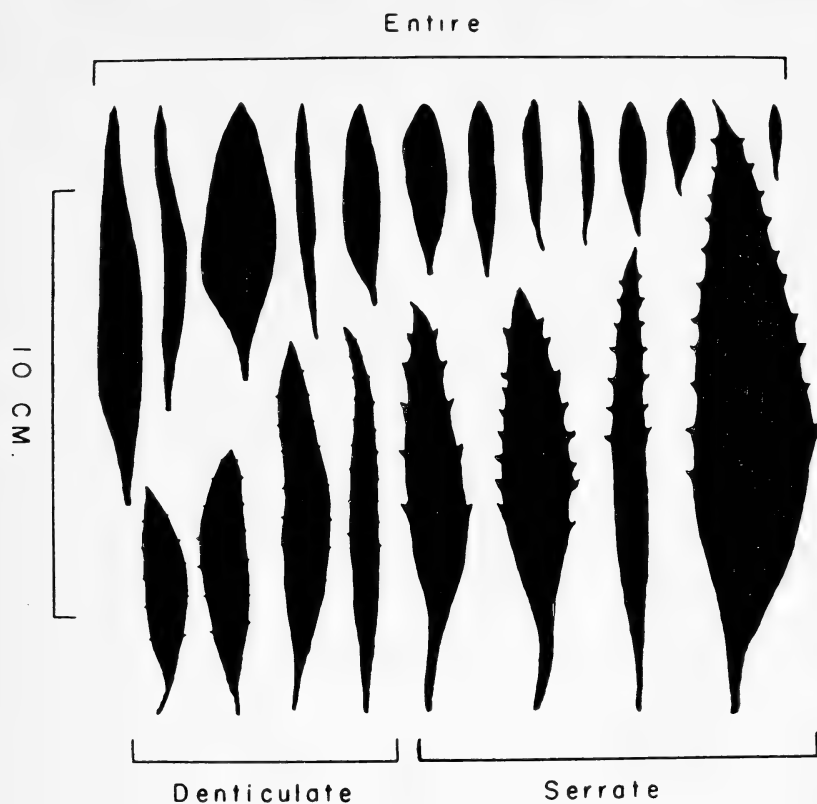
FIG. 2. Range of leaf variation observed during the course of the study with exemplification of the terms entire, denticulate and serrate.

Leaf length and width were generally greater during Sept. than in Mar. Seasonal comparisons of both characters in the Ventura, Pt. Mugu, Miramar and Harbor Park populations proved insignificant. Short, entire to denticulate leaves were observed most frequently during Mar., and the Sept. samples were usually distinctly serrate. Although a relationship between leaf size and margin might be expected the variation indicated in Fig. 2 suggests considerable plasticity of leaf morphology.

An attempt was made initially to score leaf glutinosity but no consistent method could be applied. Glutinosity does vary considerably, however, without any consistent correlation to population location or season. The most glutinous leaves were found in March samples of desert populations such as Little Rock and Whitewater.

The seasonal difference in the number of capitula reflects the difference in size of the Mar. and Sept. inflorescences. The dense lateral clusters of Mar. possessed fewer capitula and were smaller than the more open terminal inflorescences of Sept. Random measurements of both staminate and pistillate capitula height revealed a slightly larger
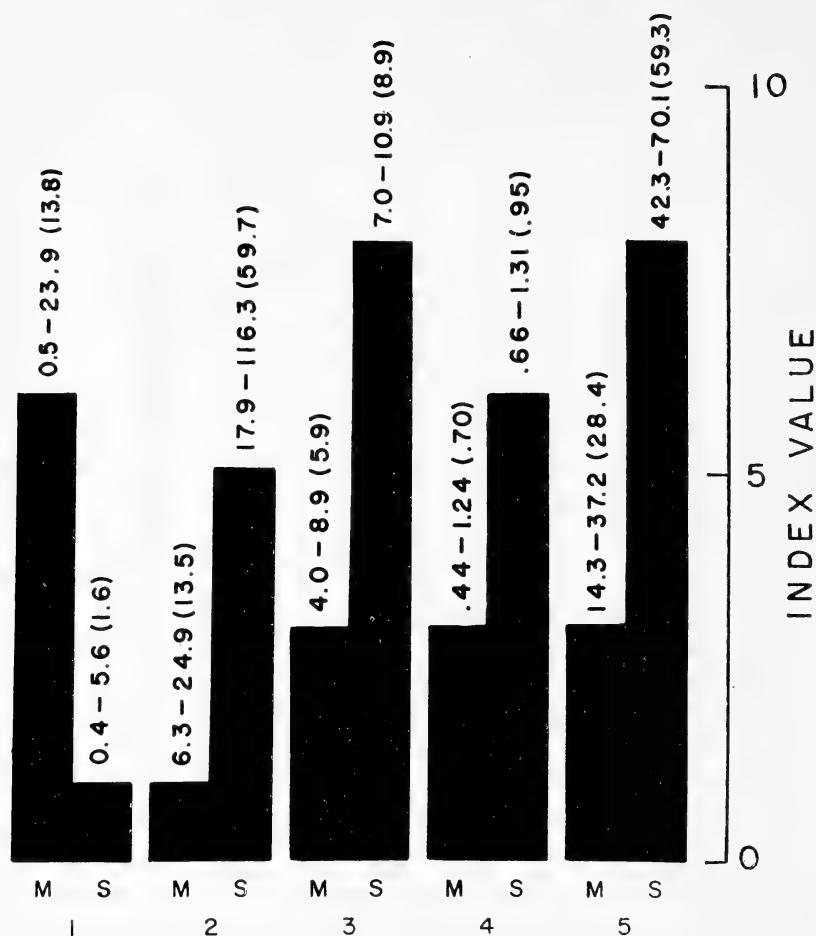
Fig. 3. Bar graph demonstrating seasonal differences of five characters in 21 populations: M = Mar.; S = Sept.; 1, number of flowering branches; 2, length of flowering branches; 3, leaf length; 4, leaf width; 5, number of capitula per inflorescence. Ranges of population means are shown for each character in Mar. and Sept. with the total mean given in parenthesis.

size in Mar. While examining herbarium specimens and living plants, attention was given to the bract margins. Those of *B. viminea* have been described as ciliolate in contrast to the scarous fimbrillate bract of *B. glutinosa*. No distinctive seasonal pattern was observed although the margins of mature outer involucral bracts are from one—three cells thick and bear short, biseriate, eglandular trichomes. Following anthesis the bracts reflex and fray along their margins resulting in a fimbrillate or erose condition.

TABLE 1. MEAN POPULATION VALUES FOR A SERIES OF CHARACTERS IN
BACCHARIS IN MAR. AND SEPT.

Collection numbers are those of the author and the specimens are at UCSB.
Serration: D = denticulate, E = entire, S = serrate.

	Number of Flowering Branches, cm		Length of Flowering Branches, cm		Leaf Length, cm		Leaf Width, cm		Number of Capitula per Inflorescence		Serra-tion	
	M	S	M	S	M	S	M	S	M	S	M	S
Azusa 1382	12.0	2.9	11.0	40.6	4.8	8.1	.66	1.05	17.6	60.1	D	S
Barstow 1405	17.2	.8	12.1	109.2	4.2	10.4	.47	1.10	14.3	47.0	E	S
Bonsall 1319	15.6	.9	14.6	39.6	4.8	8.7	.59	.82	31.3	57.5	D	D-S
Cajon 1407	19.4	5.6	14.3	51.2	6.2	9.9	.80	1.07	35.4	60.2	D	S
Campo 1277	8.3	.4	16.1	95.7	7.1	8.9	.63	.87	21.6	63.4	D-S	S
Harbor Park 1411	6.4	2.4	23.8	31.6	8.0	8.3	1.03	1.09	33.7	70.1	S	S
Little Rock 1193	23.9	.8	10.0	101.0	4.0	10.3	.68	.91	15.1	56.7	E	S
Mentone 1406	19.1	1.9	9.7	36.2	4.1	8.5	.44	.67	30.1	48.4	E	D-S
Mill Creek 1412	21.6	1.4	6.3	94.6	4.0	8.4	.56	1.00	23.3	59.1	E	D-S
Miramar 1298	12.6	1.3	11.3	39.8	6.6	7.0	.69	.77	31.0	68.2	D-S	S
Oak Grove 1172	13.7	1.2	12.5	48.5	5.8	8.0	.77	1.08	36.0	58.3	D-S	D-S
Pt. Mugu 1408	9.1	2.5	23.4	27.9	7.6	8.7	.69	.79	29.6	67.9	D-S	S
Prado 1361	11.9	1.7	12.9	42.5	7.5	10.7	.73	1.02	35.4	59.1	D-S	S
Saugus 1214	19.8	1.7	11.6	49.7	6.5	8.9	.82	.96	22.5	67.6	D	S
Sespe 1235	12.4	1.3	10.7	50.8	6.8	9.4	.77	.88	28.9	63.4	D	D-S
Sherwood 1409	12.3	2.0	13.3	48.3	6.3	7.5	.63	.91	33.4	68.3	E-D	D-S
Temescal 1340	9.4	1.1	11.1	54.3	5.0	7.6	.71	.82	36.7	55.3	E-D	S
1000 Palms 1404	16.3	.7	14.2	116.3	7.4	10.9	.54	1.00	37.1	59.8	S	S
Topanga 1410	13.3	1.6	11.9	32.6	5.8	7.9	.66	.82	29.6	60.1	E-D	S
Ventura 1256	.5	1.4	24.9	33.9	8.9	9.7	1.24	1.31	37.2	54.3	D-S	D-S
Whitewater 1403	16.1	1.2	8.5	111.4	4.5	10.5	.69	1.17	18.6	42.3	E	S
X =	13.8	1.6	13.5	59.7	5.9	8.9	.70	.95	28.4	59.3		

DISCUSSION AND CONCLUSIONS

The recognition of *B. glutinosa* and *B. viminea* as distinct taxa has depended on the variation of essentially two characters: the disposition of the flowering branches and the morphology of the leaf. The results of this study indicate, however, that the critical differences between these characters, hence the critical differences between the two species, are of a phenological nature rather than inherently genetic. This seasonal "dimorphism" is analogous to that occurring in *Pinguicula* section *Orcheosanthus* DC. (Casper, 1966). Species in this group showed marked morphological changes between summer and winter rosettes of leaves.

The range of variation observed during Mar. is comparable to that found on many herbarium specimens cited as *B. viminea*. The short, lateral, flowering branches bearing small entire leaves are initiated from axillary buds usually within one meter of the summit of the mature woody stems. The shortest of these are essentially compact cymose inflorescences and occur near the summit. The branches are progressively longer and are more widely spaced on the axis below. Herbarium specimens of the latter are often labeled *B. glutinosa* since in all respects they appear as terminal inflorescences on herbaceous shoots. Usually

such specimens are intermediate in regard to leaf morphology. After anthesis most of the lateral branches die back to the stem. This is followed by growth of a few herbaceous shoots derived either from nodes near the base of the plants or along the erect stems. The leaves of these shoots differ markedly. They are longer, wider and usually distinctly serrate; rather than being clustered they are well spaced along the stem. These herbaceous shoots complete growth late in the year and produce terminal corymbose inflorescences characteristic of *B. glutinosa*.

In successive years, the erect herbaceous shoots undergo secondary growth and become distinctly woody. Continued addition of herbaceous shoots results in the characteristic broom-like appearance of older shrubs. Many of the populations examined during this study continued to bloom at a reduced level throughout the year. Although the short inflorescences near the summit of the main axis develop and mature centripetally, branches ranging from 10–50 cm in length and ranging to two meters below the apex may produce inflorescences sporadically throughout the year. In addition, not all the plants in a population may be in bloom at any given time.

The variation observed in this study may be in part attributable to environmental modification. Desert and montane populations (i.e., Barstow, Whitewater, Mill Creek), subject to seasonal extremes in temperature, typically had a greater number of flowering branches in Mar., longer flowering branches in Sept. and the largest serrate leaves. Coastal stations (i.e., Ventura, Pt. Mugu, Harbor Park) under the influence of a more equable climate, in contrast, exhibited the least seasonal variation of any of the populations examined.

Their occurrence near a source of abundant water might preclude an environmental effect by this factor. A number of the populations observed, however, are annually subjected to spring and summer flash-floods, a common phenomenon in the area studied. Plants damaged by such events rarely attain the broom-like appearance of undisturbed shrubs. Occasionally observed during the investigation was the initiation of erect herbaceous shoots from the fallen branches. These were often seen bearing large serrate leaves and occasionally had terminal inflorescences while neighboring undamaged plants possessed inflorescences and leaves characteristic of *B. viminea*. Such a situation in fact first suggested the problem and the approach used in this investigation.

The genus *Baccharis* is best represented in Central and South America. Species occurring in the United States are distributed primarily in the south and southwest (i.e., *B. halimifolia, B. emoryi, B. sergiloides*) and are probably of Neotropical-Tertiary origin. This is reflected in part by the retention of the summer and fall blooming habit. The taxon considered in this paper is unusual in respect to the floral phenology of the genus as a whole since it has been demonstrated that, at least in the area studied, flowering begins between February and March and con-

tinues throughout the summer and well into fall. This habit may be of adaptive value in promoting seed production which, in combination with the exceptional dispersability afforded by light achenes and fine capillary pappus, could result in a greater potential for wide geographic distribution. Dioecism and a prolonged flowering period might, in addition, favor maximum genetic exchange and heterozygosity within a population. A broad and disjunct distribution of populations, particularly as occurs in the arid southwest, might on the other hand restrict gene flow and foster intrapopulation uniformity and interpopulation variation within the species. The differences between desert and coastal populations referred to earlier may well be the result of such genetic variability.

Baccharis glutinosa was first described from material apparently collected in Chile. The species in a broad sense ranges from Califorina to Texas and southward throughout much of Mexico to Guatemala and Honduras. It occurs disjunctly in Peru and Chile. Blake (1926; 1930) has reviewed a number of cases of synonymy for *B. glutinosa*, derived from his studies in European herbaria. DeCandolle applied the name *B. viminea* to a collection made by Douglas "in California." Careful examination of a photograph of the type revealed leaves ranging from two to four cm. in length and with entire to denticulate margins. From herbarium records, all specimens referrable to *B. viminea* indicate a completely "sympatric" occurence with *B. glutinosa*. From the data presented it is apparent that the differences between the two taxa represent a case of seasonal dimorphism and that specimens of *B. viminea* are merely phenological variations of the species *B. glutinosa*.

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LITERATURE CITED

BLAKE, S. F. 1926. In P. C. Standley, Trees and shrubs of Mexico. Contr. U. S. Natl. Herb. 23.
————. 1930. Notes on certain type specimens of American Asteraceae in European herbaria. Contr. U. S. Natl. Herb. 26:227–263.
CASPER, S. J. 1966. Once more: The orchid-flowered butterworts. Britonia 18:19–28.
KEARNEY, T. H., and R. H. PEEBLES. 1951. Arizona flora. Univ. California Press, Berkeley.
MASON, H. L. 1957. A flora of the marshes of California. Univ. California Press, Berkeley.
MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.
SHREVE, F., and I. L. WIGGINS. 1964. Vegetation and flora of the Sonoran Desert. Stanford Univ. Press.
SNEDECOR, G. W. 1956. Statistical methods. Iowa State Univ. Press, Ames.
THORNE, R. F. 1967. A flora of Santa Catalina Island, California. Aliso 6:1–77.

ITINERANT POLLINATORS IN A FOREST

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The familiar sight of flowers in a sunny meadow beset by a profusion of insect-visitors sharply contrasts with that of flowers inhabiting a quiet forest, apparently unvisited by flower-loving insects. Yet many plant species bear entomophilous flowers in deep shade beneath trees where there appears to be an extreme paucity of anthophilous insects. Several authors have commented upon the importance of sunlight to insect visits with the observation that shade inhibits many flower visitors (Perkins, 1919; Linsley, 1958; Free, 1960) while others will not penetrate the comparative gloom of the interior of a wood or forest (Kerner and Oliver, 1895). The presentation of entomophilous flowers by shade-loving species with such an apparently meagre chance of insect visits appeared anomalous, and worth investigation.

A shade-loving violet, *Viola glabella* Nutt., was selected for study. This species possesses delicate, deep yellow flowers 6–16 mm long. They are clearly entomophilous in common with the chasmogamous flowers of the majority of the other species in the genus. The population studied was located in the coastal redwood, *Sequoia sempervirens*, forests of the Santa Cruz mountains at an altitude of 450 ft in San Mateo Co., California.

To discover whether or not they were self-pollinating 20 flowers on the point of opening were enclosed in fine-mesh nylon bags to exclude insect-visitors. Eighteen flowers did not develop seed while 2 contained a small proportion of enlarged ovules. These results strongly suggest that selfing was uncommon and that insects were required for pollination.

Preliminary observations suggested that flower visitors were present in the forest but were confined to the pools of sunlight resulting from gaps in the canopy. Consequently, three study sites were chosen, each of approximately 1 sq m, which were known to be hit by sunshine for a short time during the day. Each site harboured at least 20 open flowers of *Viola glabella* and 1 to 5 flowers of *Oxalis oregana* and/or *Trillium chloropetalum*. Observations were continued for five days from 10:00 a.m. to 4:00 p.m. each day.

Light intensity readings were taken from a Weston Illumination Meter with the probe held level with the leaf subtending an open violet flower, see Fig. 1. A Yellow Springs Tele Thermometer with 8 probes was used to measure the temperature throughout each site. Each thermistor was secured immediately below a leaf subtending an open flower, see Fig. 1. A constant watch on insect activity was maintained (with the aid of an assistant) and all flower visits and insects counted.
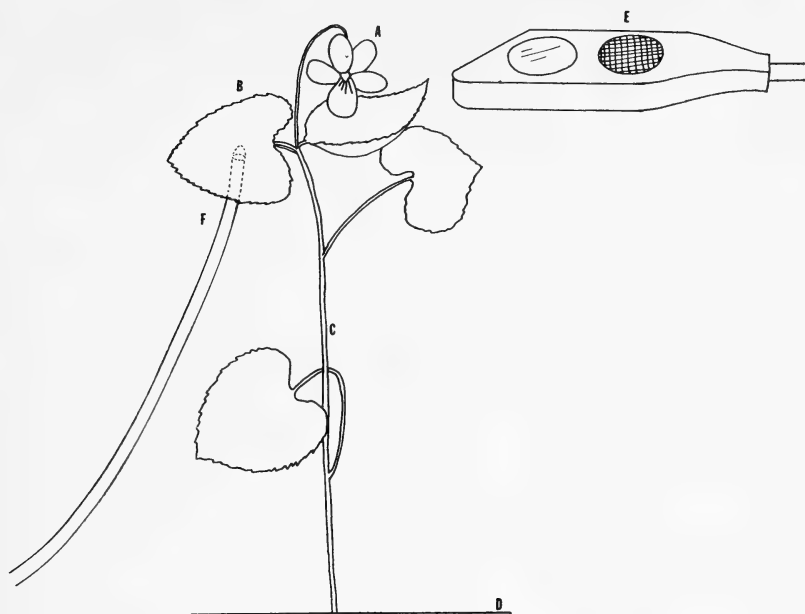
Fɪɢ. 1. Sketch to show a plant of *Viola glabella* with thermometer and lightmeter in position: A, flower; B, leaf subtending flower; C, main stem; D, ground level; E, lightmeter; F, thermometer probe.

Light intensity and temperature readings were taken at half-hour intervals throughout the day. However, these remained relatively constant except around the immediate period when direct sunlight fell on the site. Therefore, attention from now on will be focused upon the half-hour immediately before the arrival of direct sunlight at the site, the half-hour during which it was present and the half-hour immediately following its departure. During this 1½ hours of intensive observation readings were taken every minute. The period of direct sunlight was never longer than 15 minutes but sun specks were generally present for up to 30 minutes.

Figure 2 summarizes the findings. Temperature and light readings remained fairly constant throughout the day. With the advent of direct sunlight at the site, however, there was a dramatic increase in both over a period of 4–5 minutes. The temperature rose by approximately 5 degrees and the light intensity by up to 8000 foot candles. Whilst in shade each site received occasional visits from Muscid or Calliphorid flies, crane flies (Fam. Tipulidae) and winter crane flies (Fam. Trichoceridae). No insects present were conspicuously anthophilous and no flower visits took place. By contrast, as each site received direct sunlight, many insects would quite suddenly appear. It was astonishing how rapidly insect activity increased: Bibionid, Muscid, Calliphorid and Tachinid flies appeared, apparently to bask in the warmth. Sawflies
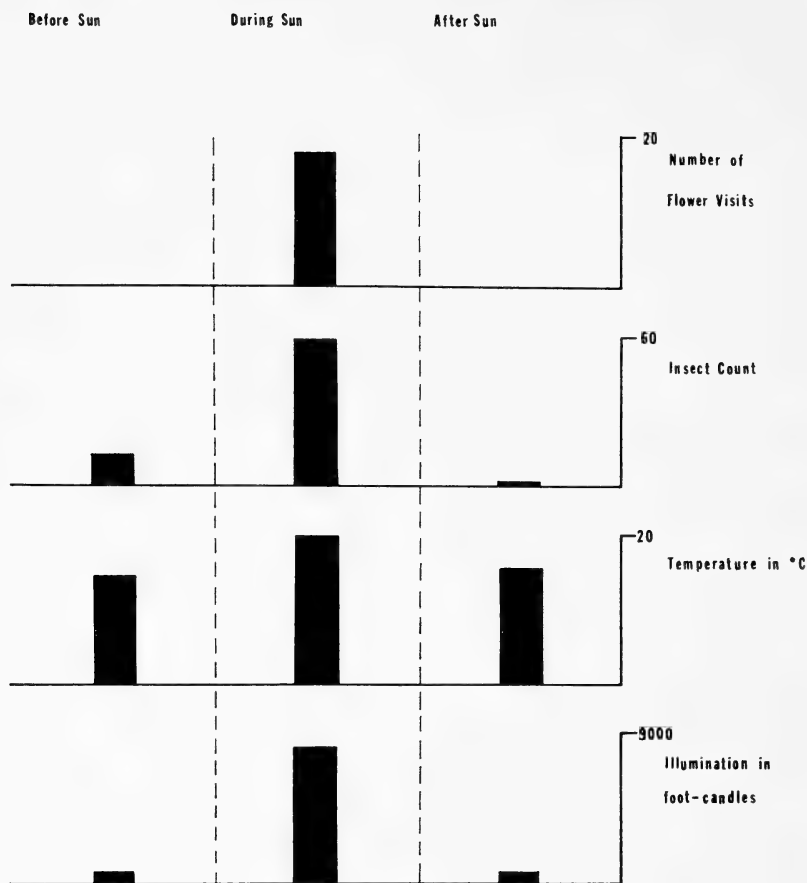
Fig. 2. Histograms to show the correlation between the number of flower visits, insect counts, the temperature and the light intensity. Each represents the average of the figures from 5 days of observation.

(Fam. Tenthredinidae), hoverflies (Fam. Syphidae), small bees (Fam. Andrenidae, Halictidae) and occasional butterflies would fly in and alight on leaves or visit flowers. It was interesting to find that shortly following the arrival of the van of insects there was often a quiet influx of a few parasitic species particularly Ichneumons, Conopids and solitary wasps. Figure 2 clearly shows that all flower visits observed took place during the 15 minutes or so when the sun shone on the site.

As the sunlight left each site the insects disappeared just as suddenly as they had appeared. A mere 5 minutes later the temperature had dropped by 4–5 degrees, the illumination by 7000–8000 ft candles and the insects had almost entirely deserted the spot. Those remaining were invariably species which moved with impunity through the forest ap-

parently indifferent to the quantity of light in their path (Tipulidae and Trichoceridae).

Viola glabella was visited by 3 species of hoverflies, kindly identified by Lloyd Knutson: *Sphegina infuscata* Loew, *Sphegina armatipes* Malloch and *Xylota rainerei* Shannon, and by species of solitary bees, kindly identified by G. I. Stage: *Andrena* sp. and *Lasioglossum* subgenus Evylaeus. I have no information on the distribution or ecology of these species but investigation of the stigmas of the flowers they visited confirmed that they were capable of pollination. *Oxalis* flowers received occasional visits from these species but *Trillium* was entirely ignored by them. The violets appeared to monopolize the attentions of flower-visitors.

The work described here was a pilot project for a much larger study of pollen exchange in a forest environment to be carried out over a period of 2 years. However, the rapid emergence of 2 important points of pollination ecology prompt this early discussion: firstly, the study has emphasized the need for caution concerning generalizations in pollination ecology. The present case, in common with a number of others, shows that a detailed investigation may reveal the situation to be more complex than was originally supposed. In the study sites the flowers of plants which inhabited deep shade were visited by efficient pollinators— including those belonging to groups more frequently thought of as sun-loving, such as hoverflies and solitary bees. A continuous watch on the habitat confirmed that pollinators were available but that they were itinerant, moving on with the progress of patches of sun. Outside of these paths of illumination flower visits may have indeed been very rare. Pollination by nocturnal or crepuscular visitors was always a possibility but the main point is that diurnal visitors were there, albeit confined to small and ephemeral patches of sunlight, and that a thorough study was required to discover this.

The pool of sun had to be sufficiently prolonged to draw anthophilous insects to the spot. This observation leads directly to a second point, previously noted by several authors but still requiring reiteration, that the immediate locality of a plant may be of prime importance in its pollination. For violets in the study sites the precise location of the plant relative to gaps in the canopy directly affected the frequency of insect visits and, therefore, the frequency of cross-pollination. The species in question produces seed by means of self-pollinated cleisto-gamous flowers later in the season but insect visits provide the sole opportunity for out-breeding and they are, therefore, the only agents for genetic exchange within the population. That within a small area insect visits may be confined to narrow tracts of sunlight resulting from gaps in the canopy means that only a fraction of the population may be out-breeding. In the event of change or disturbance of the environment this fraction, in providing new genetic recombitants, may be vital to the further evolution of the species.

I wish to thank Professor Richard Holm for reading and commenting upon the manuscript. The work was supported by the Ford Foundation grant 68–256.

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LITERATURE CITED

FREE, J. B. 1960. The behaviour of honeybees visiting flowers of fruit trees. J. Anim. Ecol. 29:385–395.
KERNER, A., and F. W. OLIVER. 1895. The natural history of plants. Henry Holt, New York.
LINSLEY, E. G. 1958. The ecology of solitary bees. Hilgardia 27:543–599.
PERKINS, R. C. L. 1919. The British species of Andrena and Nomada. Trans. Entomol. Soc. London. 11:218–319.

NOTES AND NEWS

THE INTRAGENERIC POSITION OF SALIX ORESTERA.—*Salix orestera* was described by Schneider (J. Arnold Arbor. 1:164. 1920) and placed in the section *Adenophyllae*. Prior to the naming of this species, specimens had been identified as *S. glauca* L. var. *villosa* (Hook.) Anderss. by such botanists as Bebb (*in* S. Watson, Bot. Calif., Vol. 2, Cambridge, 1880) and Jepson (Fl. Calif., Part 2, Berkeley, 1909). Later Jepson (Manual Fl. Pl. Calif., Berkeley, 1923) changed *S. orestera* to a variety of *S. glauca*.

Taxonomists have not agreed on the position of *S. glauca* within the genus. Schneider (op. cit.) stated that *"Salix orestera* seems to be most closely related to *Salix eastwoodiae."* Archer (Contrib. Fl. Nevada. 50. 1965) combined *S. orestera* and *S. eastwoodiae* under the latter name. Argus (Contr. Gray Herb. 196:1–242. 1965) stated that "other species including *Salix eastwoodiae* (incl. *orestera*) seem to be closely related to this group and further study may include them."

The three taxonomists, mentioned in the paragraph above, all have mentioned a relationship of some kind between *S. eastwoodiae* and *S. orestera*. However, these two taxa are distinct. The leaves of *S. eastwoodiae* are green on both sides, with cream-colored glands on the surfaces and margins of the blade. The leaves of *S. orestera* are green above and glaucous beneath, and glands are not present on the surfaces and margins of the blade. The relationship that exists is one of intensive hybridization and introgression between *S. orestera* and *S. eastwoodiae*. Many herbarium specimens are intermediate between these two species, and it is easy to understand why Schneider and Archer treated these two taxa as they did.

Salix orestera is closely related to *S. glauca* and should not be included in section *Adenophyllae*. *Salix orestera* occurs in the Sierra Nevada and San Bernardino Mountains of California, northeastern Nevada, and the Cascade Mountains of Oregon. Argus (op. cit.) listed the *S. glauca* complex as occurring in every western state including Canada except for California, Nevada, Oregon, and Washington. Thus, the distribution of *S. orestera* indicates that it should be considered a major geographical segment of *S. glauca*. After studying many specimens including the types of the taxa involved, I propose a new combination.

SALIX GLAUCA L. ssp. **orestera** (Schneider) Youngberg, comb. nov. *S. orestera* Schneider, J. Arnold Arbor. 1:164. 1920.—ALV DAN YOUNGBERG, 5659 Rudy Drive, San Jose, California 95124.

A PUTATIVE DISTICHLIS × MONANTHOCHLOE (POACEAE) HYBRID FROM BAJA CALIFORNIA, MEXICO

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This report describes a population of putative intergeneric hybrid salt grasses involving the two eragrostoid genera *Distichlis* and *Monanthochloe*. Intergeneric hybrids in the Gramineae are known from most tribes of the Festucoideae and from the panicoid tribe Andropogonae (cf. Knobloch 1968), however, they apparently have not been reported from the Eragrostoideae.

I collected the plants in October 1968, at the margin of a large salt marsh 1 km south of the village of Rosarito, Baja California Norte, México (28°35' N. Lat., 114°05' W. Long.). The salt marsh is located in the bed of an arroyo which drains into the Pacific Ocean 25 km to the west of the collection site. The marsh condition, which covers several km², is apparently maintained by a series of mineral springs and seeps.

The moist central portion of the marsh is dominated by *Juncus acutus* L. which forms large, compact clumps. A drier marginal zone, of variable width, is dotted with scattered clumps and mats of *Salicornia* and *Allenrolfea*. The salt grasses form a nearly continuous ground cover over much of the marginal zone, but in the interior are restricted to the larger openings between *Juncus* clumps. Burros and goats had severely grazed both the marsh and the adjacent desert vegetation, and as a consequence, only fragmentary grass specimens could be obtained.

The grass mixture consisted of nearly equal proportions of typical *Distichlis spicata* (L). Greene and plants of the putative hybrid, which most closely resembles *Monanthochloe littoralis* Engelm. I found one reproductive specimen, a pistillate plant, of *D. spicata;* an extensive search, however, failed to produce any reproductive plants which could be assigned to *M. littoralis*. Both species were collected elsewhere in Baja California but no further indications of hybridization were noted.

The outstanding features of the putative hybrids, the numerous spikelets in a long-pedicelled inflorescence, demonstrate the plants' affinities to *Distichlis* (fig. 1). None of the specimens collected have the solitary sessile spikelets typical of *Monanthochloe,* although several specimens possess one or more sessile spikelets located at the base of an inflorescence pedicel (fig. 1e). The pistillate and staminate spikelets of the putative hybrid are similar in size and shape, and most closely resemble those of *Distichlis* (fig. 1f). In vegetative appearance the plants most closely resemble *Monanthochloe*. The leaves are clustered and short, especially on reproductive and lateral branches, but tend to be somewhat broader and distinctly longer on the stolons than in typical *Monanthochloe* (table 1). Pistillate plants (fig. 1e, g) tend to have longer stolon inter-
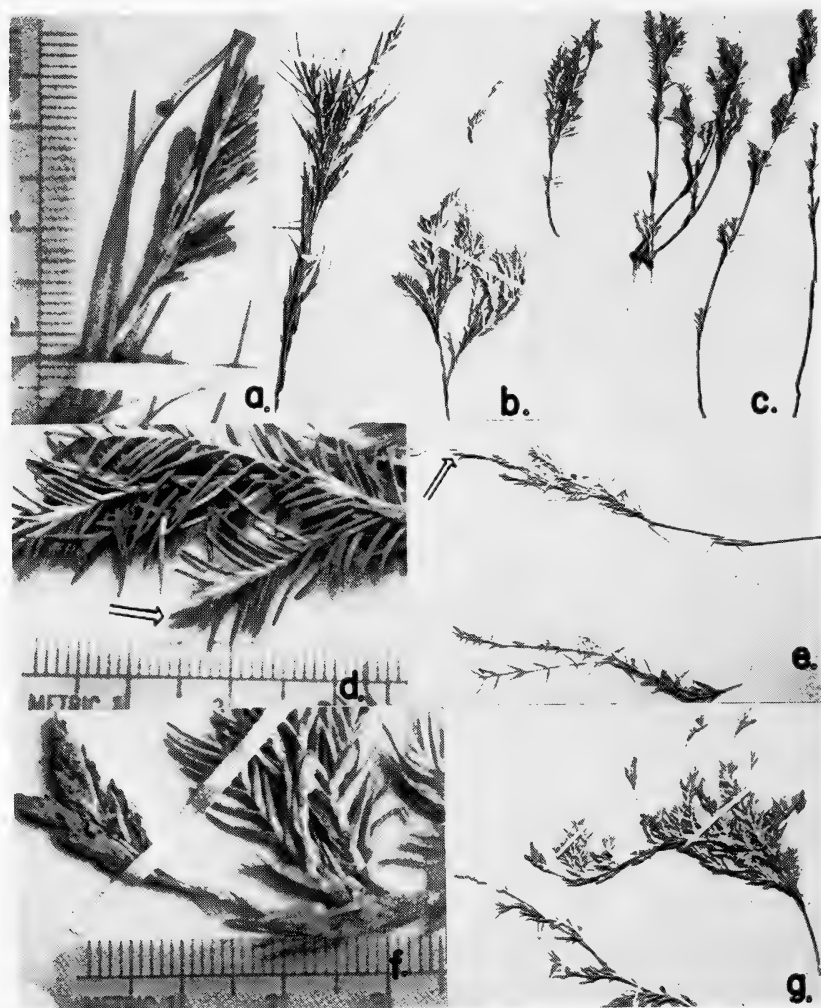
FIG. 1. a, Pistillate inflorescence of *Distichlis*, Rosarito; b, pistillate plant of *Distichlis*, Rosarito (left), staminate putative hybrid plant, Rosarito (right); c, typical *Monanthochloe*, Bahía de la Concepción; e, pistillate putative hybrid plants, Rosarito; f, staminate putative hybrid showing inflorescence; g, putative hybrid plants, staminate (above), pistillate (below), Rosarito.

nodes, larger, less crowded leaves, and sessile spikelets at the pedicel bases, in comparison to staminate plants (fig. 1f, g). This apparent sexual dimorphism is especially interesting since neither of the putative parent species display conspicuous vegetative dimorphism, a feature considered important in the systematics of the Aeluropodeae (Soderstrom and Decker, 1964).

Although caryopses had not developed in any of the material collected, pistillate spikelets contained poorly developed ovaries and unbranched

TABLE 1. COMPARISON OF SELECTED CHARACTERISTICS OF DISTICHLIS,
MONANTHOCHLOE, AND THE PUTATIVE HYBRID.

Distichlis spicata, Rosarito, Baja California, *Stephenson 68-304b, MSU;*
Monanthochloe littoralis, Bahia de la Concepcion, Baja California, Stephenson
67-316a, MSU; putative hybrid, Rosarito, Baja California, *Stephenson 68-304,* MSU·

Character	*Distichlis*	Putative Hybrid	*Monanthochloe*
Leaf blade length, cm	2.5 - 5.0	0.6 - 2.5	0.5 - 1.2
Spikelet length, cm	0.7 - 1.5	0.7 - 1.4	0.4 - 0.7
Pedicel length, cm	1.0 - 1.5	1.7 - 2.5	spikelets sessile
Inflorescence length, cm	1.5 - 3.5	1.0 - 2.2	spikelets solitary
Number of lemmas/spikelet	7 - 14	7 - 11	3 - 5

stigmas. Partially exerted anthers on staminate plants carried some pollen, although amounts were deemed insufficient for staining. In all cases the spikelets appeared to have ceased development shortly after anthesis.

The occurrence of hybridization between *Distichlis* and *Monantho-chloe* is not surprising in view of their ecologic and morphologic similarity. However, it is apparently an uncommon event. Observations elsewhere in Baja California indicate that the two species occupy somewhat differing micro-topographic sites, but not infrequently occur in thoroughly intermixed colonies. The major difference noted between the Rosarito and other sites was the extreme grazing disturbance. The constant disturbance may have negated any differences between normal flowering periods of the two species (if such exist) and thus made possible the crossing. The apparent absence of typical *Monanthochloe* at Rosarito suggests that either it was initially uncommon, has been swamped out genetically or is competitively inferior to the putative hybrid. The first alternative seems the most plausible since typical *Monanthochloe* was never observed far from maritime environments whereas *Distichlis* is widely distributed in both maritime and inland habitats in Baja California. The widespread occurrence of the putative hybrid in the collection locality may simply reflect its facility for vegetative reproduction and not past or present frequency of hybridization or any degree of sexual reproduction.

The large number of characteristics shared by *Distichlis, Reedero-chloa* and *Monanthochloe* (Soderstrom and Decker, 1964) and the observation that the characteristic of sex-related dimorphism of the putative hybrid is shared in the New World Aeluropodeae only by *Reedero-chloa* suggests a possible hybrid origin for that genus. Reciprocal *Distichlis-Monanthochloe* crosses may differ substantially and add to our understanding of evolution in the Aeluropodeae.

LITERATURE CITED

KNOBLOCH, I. W. 1968. A Check-List of Crosses in the Gramineae. (Privately published).

SODERSTROM, T. R., and H. F. DECKER. 1964. Reederochloa, a new genus of dioecious grasses from Mexico. Brittonia 16:334–339.

A NEWLY DETERMINED SPECIES OF ELAPHOMYCES FROM OREGON

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In type studies of *Scleroderma* species (Guzmán, 1967), the junior author determined *S. subviscidum* (Zeller, 1947) to be a species of *Elaphomyces*. Subsequent study of the type collection by the senior author confirmed this conclusion and established that the species is distinct from others in the genus *Elaphomyces*.

Freehand sections mounted in 5% KOH were used in the anatomical studies needed for redescribing the species. Sections mounted in Melzer's solution showed no distinctive reactions. The term "peridium" in the description denotes the entire structure surrounding the gleba in conformance to normal mycological usage; past workers with *Elaphomyces* have often used "peridium" to denote only the innermost layer of that structure.

Elaphomyces subviscidus (Zeller) Trappe and Guzmán, comb. nov. (fig. 1). *Scleroderma subviscidum* Zeller, Mycologia 39:296. 1947.

Ascocarp subglobose, 3 $\times$ 5 cm; surface smooth, white to grayish, drying yellowish, nonreactive with KOH, encrusted with soil held by inconspicuous but abundant pale hyphae emerging from the surface; peridium 1–2 mm thick when dry, reviving to a thickness of $2\frac{1}{2}$–3 mm, with a thin, yellowish outer layer and a thick, pallid inner layer; gleba dark brown, powdery. Peridium: Emergent superficial hyphae sinuous, hyaline, thin-walled, $2\frac{1}{2}$–4μ broad. Outer $\pm$ 150μ of peridium yellowish in cross section, densely interwoven of single to fascicled hyphae 3–5μ broad, with walls mostly hyaline and thin but in places thickened to 0.5μ and often yellowish, the entire stratum obscured by hyaline to yellowish, amorphous debris. Inner layer $\pm$2,500μ thick, abruptly differentiated from the outer layer as $\pm$ circumferentially aligned but interwoven fascicles of a few to nearly 100 hyaline, highly refractive hyphae 4–8μ broad with the walls mucilagenous-thickened to nearly filling the cells; yellowish, amorphous debris scattered throughout. Gleba hyphae dispersed among spores, thin-walled, hyaline to pale yellowish-brown, mostly 1$\frac{1}{2}$–3μ broad but a few 5–6μ; dark brown, amorphous deposits scattered throughout between hyphae. Spores globose, 12–21μ broad exclud-
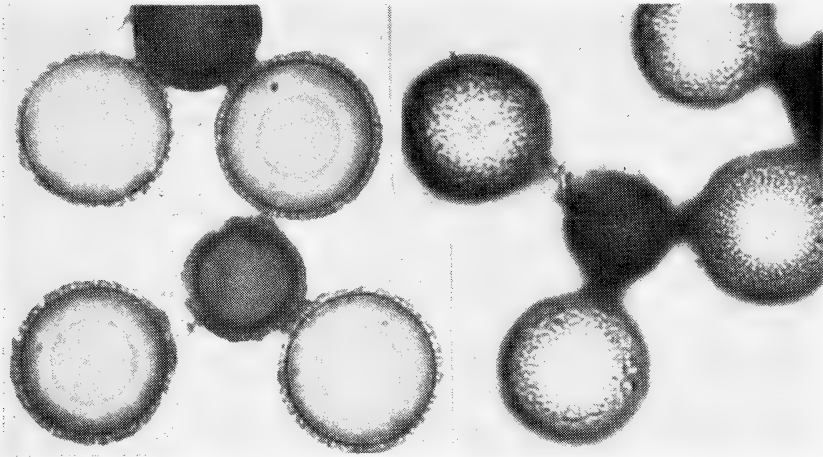
Fig. 1. Spores of *Elaphomyces subviscidus* (holotype) $\times$ 1,000: left, in optical cross section; right, focused on spore surfaces.

ing ornamention, 14–23 (–24)μ with ornamentation, the smaller spores very dark brown, the larger tending to be lighter brown, all containing a large, spherical oil droplet; larger spores thin-walled, smaller ones with walls up to 0.5μ thick; ornamentation of crowded spines 1–2μ long and $\pm$0.2μ thick, separated by 0.2–0.5μ or sometimes joined in two's and three's by ridges but never formed into a partial reticulum, embedded in an inconspicuous, mucilagenous matrix. No asci detected, but spores frequently clinging together in globose clusters of 8.

Holotype. Epigeous on decayed granite soil, Oregon, Jackson Co., Prospect, *R. A. Pendleton,* June 28, 1925 (Zeller 6842, NY). Known only from the type collection.

Although neither asci nor basidia were seen, the species is clearly an *Elaphomyces* by virtue of its large, closely echinulate spores often clustered in groups of 8 and the anatomical organization of peridium and gleba. The epigeous habit and "somewhat viscid" peridium noted by Zeller are atypical for *Elaphomyces* and need to be confirmed by additional collections. *Elaphomyces* are commonly dug out by rodents, which occasionally leave them lying on the surface of the ground. No suggestion of viscidity can be seen in KOH mounts; if the specimen was wet when collected, the adherent soil and hyphae might have given the ascocarp a slippery feel.

Elaphomyces subviscidum differs from the other smooth surfaced, noncarbonaceous species of the genus in its pale peridial coloration, brown spore mass, and relatively large spores. The outer peridial layer (the "cortex" of past terminology for the genus) completely lacks the *Cenococcum* type of structural organization that characterizes many species of *Elaphomyces* (Trappe, 1971).

LITERATURE CITED

GUZMÁN, G. 1967. Taxonomía del género Scleroderma Pers. emend. Fr. Ciencia (Mexico) 25:195–208.
TRAPPE, J. M. 1971. The mycorrhiza-forming Ascomycetes. *In* E. Hacskaylo, ed., Proc. 1st No. Amer. Conf. on Mycorrhizae, Urbana, Ill. U. S. Government Printing Office, pp. 19–37.
ZELLER, S. M. 1947. More notes on Gasteromycetes. Mycologia 39:282–312.

REVIEWS

Plant Speciation. By VERNE GRANT. × + 435 pp. Columbia University Press, New York, 1971. $15.00.

Plant Speciation was written to complement the author's earlier work, *The Origin of Adaptations.* In that work he dealt only with the processes and patterns of evolution found in diploid sexual organisms. The present book is intended to be a detailed treatment of those evolutionary phenomena that are unique to plant populations.

Although such an undertaking could have resulted in an important contribution, *Plant Speciation,* in fact, offers little that is new to the student of plant evolution. The book is divided into five sections: Nature of Plant Species, Divergence of Species, Refusion and Its Consequences, Derived Genetic Systems and Evolution of Hybrid Complexes. Much of the classical and current literature in these areas is discussed. In particular, the author's own research over the last twenty odd years is integrated into this body of information.

The fundamental framework of this book represents an approach to plant evolution that has passed its zenith. To be sure, the author is not the only biologist who views the species as a basic biological unit (indeed, he most likely holds the majority opinion). However, alternative considerations to the "species problem" have had a wide acceptance. There are, for instance, a great many biologists (both botanists and zoologists) who emphasize in their own work the population as the basic unit of evolution and regard species only as taxonomic units. This view is not only supported by the fundamental concepts of population genetics but also by the current data on gene flow. These data indicate that the role of gene flow in limiting the differentiation of populations (evolution) is at best minor. In other words, there appears to be no good evidence that gene flow is responsible for integrating populations into natural units called species. There is every reason to believe that it is similar selection pressures operating at different places, and not gene flow, that limits the divergence of populations of sexual organisms just as it is in the case of geographically disjunct groups of apomictic organisms.

In Grant's book, there is no mention of the contributions that the theory and practice of numerical taxonomy and taximetrics have made toward clarifying the "nature of species." Also, noticeably missing is any significant discussion of the role studies of protein analysis (amino acid sequences) and isozyme variation in natural populations have played and will play in our understanding of the processes of plant evolution.

Plant Speciation will be of limited use to the beginning graduate student. However, it falls far short of being the successful synthesis *Variation and Evolution in Plants,* by G. L. Stebbins, was two decades ago.—DENNIS R. PARNELL, Department of Biological Science, California State College, Hayward 94542.

A FLORA OF THE FARALLON ISLANDS, CALIFORNIA

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Introduction

The South Farallon Islands are a group of islands and rocks situated off the coast of California, 20 miles from Point Reyes, the nearest point on the mainland. They are part of the Farallon Ridge, which extends parallel to the coast (in a northwest-southeast direction) almost on the edge of the continental shelf, from the vicinity of Point Reyes to that of the Golden Gate. Other elevations along this ridge are the Mid Farallons, about 2½ miles northwest of the South Farallons; the North Farallons, a group of five rocks about 5 miles farther northwest; and farther northwest still, Noonday Rock, almost awash, and Cordell Bank, 20 fathoms below the ocean surface. Geologically similar to Point Reyes, they are of a granite formation like that found at the Point Reyes Lighthouse (Hanna, 1951).

For three months, from early April to mid July, 1968, while studying birds on the South Farallon Islands, I collected plants and took notes on the vegetation. I also worked on the islands in June, 1969, May through July, 1970, and mid-May to mid-June, 1971. I did not collect plants in the last 3 years, but noted any change in status. Only two papers (Blankenship, 1892; Ornduff, 1961) have previously been published on the plants of the islands. Blankenship, who was on the islands from July 3–6, 1892, collected 28 species, 11 native and 17 introduced plants. 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. I was there for a somewhat longer time and while I missed 3 of Ornduff's plants I found 14 previously unnoted species most of which probably arrived since Blankenship's visit. They are interesting in this respect. I found 36 species, 13 native and 23 introduced.

I did all my work on the south Farallon Islands, the other projections along the Farallon Ridge being inaccessible. However, the other projections are merely rocks. Their vegetation is probably scarce and similar to that on the cliffs of the South Islands.

The South Farallon Islands comprise about 92 acres (Henry Robert, pers. comm.) They have been uplifted and there are sea terraces around the islands: one at 27 and one at 50 feet above the sea (Blankenship, 1892). Th one at 50 feet is the more extensive, reaching a width of 300 yards on the south and 75 yards on the north and east while it is little noticeable on the west.

The temperature on the islands is even throughout the year. During a ten-year period the average maximum was 55° F (58° in the summer;
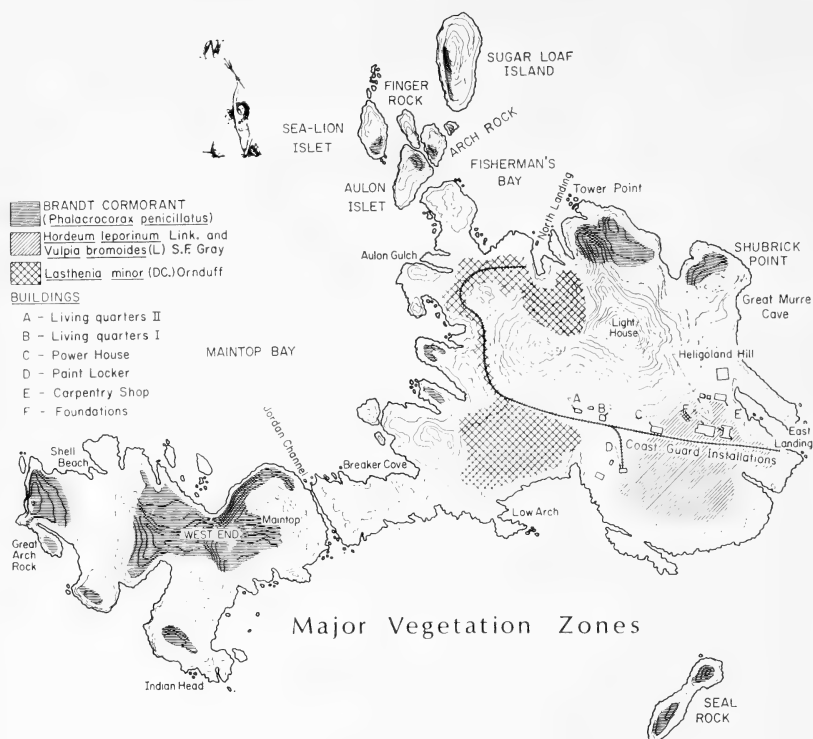
FIG. 1. Map of the Farallon Islands, showing the major vegetation zones.

54° in the winter) and the average minimum was 51° (53° in the summer; 48° in the winter). The rainfall over a ten-year period averaged 25.29 inches yearly. It is concentrated in the winter. The sky is generally clear during the spring and fall; fog prevails during the summer.

GENERAL VEGETATION

The major vegetation zones are shown on the map. During most of my stay West End was a restricted study area so that I have no data on the plants there. Seal Rock, Sugar Loaf Rock, Finger Rock and Sea-Lion Islet where inaccessible but their vegetation is sparse and probably similar to that of the rocky cliffs on the main island. Except for the 50-foot sea terrace, the main island is largely rocky cliffs which offer little foothold for plants. Among the rocks the main plants are *Erigeron glaucus, Lasthenia minor* subsp. *maritima, Spergularia macrotheca* and *S. marina.* The extensive 50-foot terrace, on the other hand, does offer a good site for thick vegetation. In the north (above North Landing) and in the south the vegetation is largely *Lasthenia minor* which grows in thick mats up to 4 dm tall. The soil here is soft and loose. These areas (as well as the hills and rocky cliffs) are used by nesting Western Gulls,

Larus occidentalis, who use the *Lasthenia* for nest material. Above North Landing the *Lasthenia* grows thick with *Stellaria media* which is lacking in the Lasthenia vegetation of the south. In the southeastern and eastern portions of the island *Lasthenia* is replaced by a grassy vegetation. *Hordeum leporinum* and *Vulpia bromoides* are the main plants in this area where the soil is not as loose and is matted with grass roots. In the northern and northeastern parts of the island, the 50-foot terrace is used by nesting colonies of Brandt Comorants, *Phalacrocoras penicillatus*. The birds' activities severely restrict if not completely inhibit plants from growing in this well fertilized area.

There are other distinct vegetation zones. Between the living quarters and the power house and also just south of the carpentry shop where the soil is thin, fine and gravelly, the vegetation is of small grasses: mainly *Vulpia bromoides* sparsely interspersed with *Poa annua*. Directly in front of the living quarters the soil is hard and gravelly. *Plagiobothrys reticulatus, Crassula erecta, Clatonia perfoliata,* and *Cornopus didymus* grow here. Also, east of the power house—along the walks and tram tracks and around the foundations—*Sonchus asper, S. oleraceus, Senecio vulgaria* and *Chenopodium murale* are found.

The major precipitation is during the winter. By April the rainy season is over; during my stay we experienced only one brief mizzle. Consequently, when I arrived the island was green and many of the plants were well advanced in their flowering and others like the grasses were far along in their seeding.

Following is a species by species list of the plants of both islands. Unless otherwise noted the plants were found by both Blankenship and Ornduff. Any change in status since 1968 is noted. The names are given according to Munz (1959) and where they have been changed Munz's names are in synonymy. The asterisked names are those of introduced species. The flowering dates pertain only to the time of my stay, April 3 to July 10, 1968. Specimens are in the Dudley Herbarium, except as noted.

Amsinckia spectabilis F. & M. Added to the island list by Ornduff, this species is found sparsely in the southern and southeastern sections of the island: along the tram tracks and among the foundations. Throughout my stay.

*Anagallis arvensis L. This species grows along the tram tracks. The population consists almost exclusively of the pin-orange variety, the blue variety not being found until 1971. In that year a small patch of only a few plants was found just south of the tram tracks near East Landing. Throughout my stay.

*Bromus diandrus Roth (*B. rigidus* Roth). This grass was recorded by neither Blankenship nor Ornduff. It is found scatteringly in small clumps in the southern and southeastern portions of the island. From my arrival to mid April.

Calandrinia ciliata (R. & P.) DC. var. *menziesii* (Hook.) Macbr. Not

previously reported, this species is sparsely found along the tram tracks. From my arrival to mid April.

Chenopodium murale L. Probably Blankenship's *C. album* L. and Ornduff's *C. sp.* This species is found commonly along the tram tracks and sidewalks in the southeast. Throughout my stay.

Cirsium vulgare (Savi) Ten. Not previously reported, this large thistle now grows around the carpentry shop. Found in 1968 and 1969, the plant was not found in 1970 and 1971 and seems to have disappeared. Mid May to my departure.

Claytonia perfoliata Donn (*Montia perfoliata* (Donn) Howell). This is found commonly along the tram tracks. From my arrival to mid April.

Cornopus didymus (L.) Smith. Not listed before. I found only one specimen of this plant in front of living quarters #2. It had already gone to seed when I found it in mid June.

Cotula australis (Sieb.) Hook. f. Ornduff added this species to the list. It is commonly found along the tram tracks. From my arrival to mid May.

Crassula erecta (H. & A.) Berger (*Tillaea erecta* H. & A.). This inconspicuous plant is found with *Plagiobothrys reticulatus* where the soil is fine, gravelly, and firm. It is found commonly around the living quarters, on the path to the paint locker, and between the living quarters and the power house and sparsely in the eastern part of the island in such places where these conditions prevail. Throughout my stay.

Cupressus macrocarpa Hartw. Planted. This species was reported by neither Blankenship nor Ornduff. However, there was once a large grove of cypress near the fog horn but at present there are only two on the island: next to living quarters #1. The trees are about 25 feet tall.

Cymbalaria muralis Gaertn., Mey., & Scherb. A new species to the island list. There is one patch of this plant at the back door of living quarters #1. While I found this plant in 1968, I did not find it in 1969, 1970, or 1971. Throughout my stay.

Erigeron glaucus Ker-Gawl. This plant is found sparsely on all the rocky cliffs on the island. Late April to my departure.

Erodium cicutarium (L.) L'Her. This plant is found along the tram tracks between the living quarters and the power house. From my arrival to late April.

Erodium moschatum (L.) L'Her. The distribution and flowering of this species are similar to those of the preceding *Erodium*.

Heliotropium curassavicum L. var. *oculatum* (Heller) Tidestrom. A new plant to the island. There is a small patch of this plant in front of the carpentry shop. Early June to my departure.

Hordum leporinum Link. This grass is common in the south and southeastern portions of the island where it grows thick with *Vulpia bromoides*. From my arrival to mid April.

Juncus bufonius L. I was unable to find this plant which was reported

by both Blankenship and Ornduff.

Lasthenia minor (DC.) Ornduff ssp. *maritima* (Gray) Ornduff (*Baeria minor* (DC.) Ferris ssp. *maritima* (Gray) Ferris). Locally known as Farallon Weed, this composite is the most abundant plant on the Islands. It is found sparsely among the rocks but thickly in the open areas in the northern and southern parts of the island (see map). Throughout my stay.

*Lavatera arborea L. Not previously reported. There was one small shrub of this species just north of Heligoland Hill. It did not bloom in 1968 but when I returned for a day on April 2, 1969, it was blooming. In 1969 there was an additional shrub of this species (not blooming) between the power house and living quarters #1. In 1970 and 1971 I was unable to find any plants of this species.

Phyllospadix torreyi Wats. This marine species was missed by both Ornduff and myself. However, Robert Setzer recently collected a specimen (CAS) on the island.

*Pinus radiata Don. Planted. This species has not previously been reported. There is one representative: just west of Heligoland Hill. The tree is only about 10 feet tall but its branches extend radially to a radius of about 7 feet.

Plagiobothrys reticulatus (Piper) Johnst. var. *rossianorum* Johnst. This small plant is found with *Crassula erecta* where the soil is fine, gravelly and firm. It is found commonly around the living quarters and the power house, and on the path to the paint locker and sparsely in the eastern portion of the island in such places where the soil is as described. From my arrival to the end of April.

*Poa annua L. This small, inconspicuous grass is found sparsely where the soil is thin, fine and gravelly in the south and southeast and around the living quarters. From my arrival to the end of April.

*Polypogon monspeliensis (L.) Desf. This grass recorded by Ornduff is likely the *P. littoralis* of Blankenship. Rare and hard to find, it grows on the path to the lighthouse and in the southeastern part of the island. It is found where the soil is thin. I know nothing about its flowering dates.

Psilocarphus tenellus Nutt. var. *tenellus*. I was unable to find this plant which was listed by both Blankenship and Ornduff.

Sagina occidentalis Wats. I was similarly unable to find this plant which was listed by both Blankenship and Ornduff.

*Senecio vulgaris L. Not previously reported, this composite is found commonly in the southeast: along the tram tracks and sidewalks, among the foundations and near the water in gullies such as that in back of the carpentry shop. Mid April to my departure.

*Sonchus asper L. Previously only this *Sonchus* has been recorded. It is found with the last species in the southeast: along the tram tracks and sidewalks and among the foundations. Mid April to my departure.

*Sonchus oleraceus L. This *Sonchus*, found in the southeast, grows

with the preceding two species among the foundations and along the tram tracks and sidewalks. Mid April to my departure.

Spergularia macrotheca (C. & S.) Heynh. This is found commonly among the rocks and where the soil is thin. It grows in the north, on Lighthouse Hill and in the southwest (west to Jordon Channel and probably on West End). It is found sparsely in the southeast. Throughout my stay.

Spergularia marina (L.) Griseb. Reported by Blankenship, this was probably Ornduff's S.sp. It grows commonly among the rocks and where the soil is thin and in the southern and southeastern portions of the island. Throughout my stay.

*Stellaria media (L.) Vill. This was reported by Blankenship but missed by Ornduff. It grows along the tram tracks, around the carpentry shop and on the slopes above North Landing. From my arrival to the end of April.

*Tetragonia tetragonoides (Pall.) Ktze. This was not recorded earlier. There is one large patch of this species between the living quarters. Throughout my stay.

Trifolium fucatum Lindl. Not reported earlier. There are two patches of this clover on the path between the power house and living quarters #1. From my arrival to mid May.

Trifolium variegatum Nutt. Not found previously. There is one patch of this between the living quarters and another on the path between living quarters #1 and the power house. From my arrival to mid May.

*Urtica urens L. This inconspicuous plant grows around the living quarters and around Heligoland Hill. Throughout my stay.

*Vulpia bromoides (L.) S.F. Gray (*Festuca dertonensis* (All.) Aschers. & Graebn.). It is likely that this species recorded by Ornduff is Blankenship's *F. myuros* L. It grows commonly and thickly with *Hordeum leporinum* in the south and southeast. Smaller plants also grow where the soil is thin and gravelly: around the carpentry shop and around the living quarters.

*Zantedeschia aethiopica (L). Spreng. Obviously an escape from the gardens, this plant still grows among the foundations in the southeast and in front of the carpentry shop where a garden used to be. From my arrival to mid June.

In the above list I have already included those species listed by Ornduff which I did not find. There were ten of Blankenship's species which neither Ornduff nor I were able to find. Most of these have probably disappeared from the island since Blankenship's visit. Blankenship found only one specimen of *Polystichum munitum* (Kaulf.) Presl which he collected. The fern has probably not managed to reestablish itself. Blankenship mentioned six species restricted to the gardens: *Avena fatua* L., *Malva parviflora* L., *Meliotus indica* (L.) All., *Polygonum aviculare* L., *Trifolium bifidum* Gray var. *decipiens* Greene, and *T. microcephalum* Pursh. Ornduff has suggested that after the gardens

were abandoned rabbits destroyed the populations of these plants. Finally, *Medicago hispida* Gaertn., and *Cerastium glomeratum* Thuill. have not been reported since Blankenship.

The flora is a small one. I think this is due, as Ornduff says, to the strong edaphic conditions and the predation of the rabbits which were introduced on the islands during the latter half of the last century. One thing worth noting, however, is the high number and high proportion of nonnative species on the Farallons. This is due to the large amount of human activity. The islands are inhabited by United States Coast Guard servicemen who operate the lighthouse. Until recently a garden was maintained. A mule was kept on the islands from the mid 1800's through the early 1900's. Many plants may have arrived with the animal's feed. Finally, a Coast Guard boat visits the island about once a week.

Literature Cited

Blankenship, J. W., and C. A. Keeler. 1892. On the natural history of the Farallon Islands. Zoe 3:144–165.
Hanna, G D. 1951. *In* O. P. Jenkins (ed.) guidebook Geologic of the San Francisco Bay Counties. Div. of Mines, San Francisco, Calif.
Munz, P. A. 1959. A California flora. Univ. California Press, Berkeley.
Ornduff, R. 1961. The Farallon flora. Leafl. West Bot. 9:139–142.

TRIPLOIDY IN UTAH ASPEN

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The quaking aspen, *Populus tremuloides* Michx., is the most wide-spread tree in North America (Cottam, 1963; Fowels, 1965); a closely related species, *Populus tremula* L., occurs in Europe. The aspen in the western United States is considered by some authors (Sargent, 1961) to be a separate variety, *P. tremuloides* var. *aurea* Daniels, but most taxonomists do not accept the validity of this variety.

Aspen are normally dioecious. The flowers are minute (ca. 2 mm in diameter), unisexual, and wind pollinated. The seeds germinate soon after dispersal; but reproduction is predominantly vegetative, resulting in a clonal population structure. Shoots originate from parent roots producing characteristic "suckers." Baker (1925) and Cottam (1963) report that aspen seedlings are rare or non-existent in the Central Rocky Mountains.

Chromosome numbers reported in aspen (Darlington and Wylie, 1955) are predominantly diploid, $2n = 38$, but a few triploids, $2n = 57$, have been discovered (van Buijtenen, Joranson, and Einspahr, 1957). The same chromosome numbers were noted in the European aspen (Müntzing, 1936a), and a tetraploid, $2n = 76$, was produced experimentally (Bergström, 1940).

The present study was initiated with two principle objectives in mind. First, to determine the extent of variation, if any, of the chromosome numbers in the aspen of Utah, and second, to ascertain if a relationship existed between chromosome number and prevernal leafing patterns (Baker, 1921; Cottam, 1954). Prevernal leafing patterns are the result of differentiation in the time of leaf emergence. In some aspen clones there is a difference in emergence time of several weeks, and the variation is often striking.

MATERIALS AND METHODS

Chromosome numbers were determined primarily from meiotic material because chromosome behavior could also be analyzed, and haploid chromosome associations are easier to count than diploid complements. However, a method of obtaining mitotic chromosome numbers from leaf buds (van Buijtenen, 1957) was a useful and simple alternative to meiotic counts. Voucher specimens of each tree are deposited at the University of Utah Herbarium.

Meiosis. Pollen mother cells (PMC's) from young, developing buds of staminate trees were the source of meiotic counts. Staminate buds swell early in the fall; however, pistillate buds remain dormant until spring. During long, warm autumns, buds of male trees at low elevation may begin to open (if first subjected to an early freeze). Meiosis, how-

Fig. 1. Aspen seedling. Note the lack of rootstock attachment.

ever, appears to be delayed until the buds have undergone a few weeks of freezing temperature. Normally meiosis occurs during March and April, about a month before anthesis.

We attempted to force bud development during the winter under greenhouse conditions. Such attempts were unsuccessful in October, but were almost 100% successful from December through April. This method was also utilized by Müntzing (1936a), and van Buijtenen and Einspahr (1959) to obtain dividing nuclei.

Staminate buds undergoing meiosis varied in length from less than one centimeter to over two centimeters. However, exact bud size was not critical in this study because each inflorescence (ament) contained staminate flowers in various stages of development; the most mature anthers occurred near the base, the least mature near the apex. Because of this condition some anthers undergoing meiosis could usually be found. Whatever the bud size, meiosis appeared to be essentially complete when half the ament had emerged from the bud scales.

Early in the study buds were fixed in acetic alcohol (1:3) for 12–24 hours. However, chromosomes were obscured by what appeared to be oil droplets. This problem was alleviated by changing the fixative to
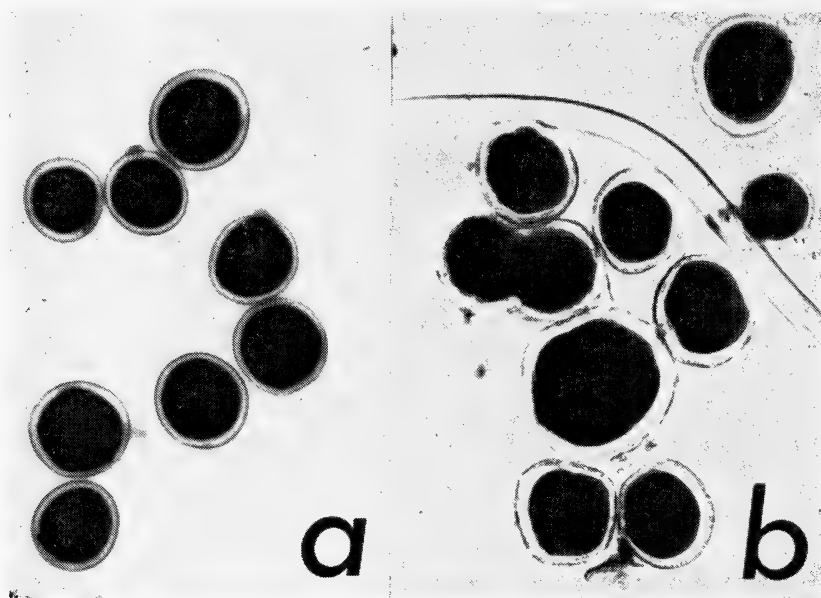
Fig. 2. Aspen pollen, ×400: 2a, single size class; 2b, two size classes.

chloroform, absolute ethyl alcohol, and glacial acetic acid (3:2:1), and then rinsing several times in distilled water and in 70% ethyl alcohol. Buds stored in 70% ethyl alcohol at —10°C remained in workable condition for several months.

A drop of ferric acetate was added to each vial of fixative as a mordant. This procedure noticeably improved chromosomal staining. Anthers were squashed and stained in heated acetocarmine and observed under phase contrast microscope. Chromosome numbers were recorded with the aid of a camera lucida and photomicrographs.

Mitosis. Mitotic chromosome numbers were obtained from young leaves just emerging from the bud. The technique was described by van Buijtenen (1957), but modified in this study. The basis of his technique was a three hour pre-treatment in saturated aqueous paradichlorobenzene (PDB) at 37°F, which we also employed. However, after the pre-treatment in PDB, the leaf buds were treated as previously described for the anthers, except the tissue was softened in 20% HCl for one minute before squashing.

An alternate source of mitotic material was obtained by planting pieces of aspen rootstock three to four inches long. Young shoots usually emerged in a few days, and these were treated in the same manner as leaf buds. This technique extended the period during which mitotic material could be obtained.

Pollen. Whole aments were collected from diploid trees in anthesis,
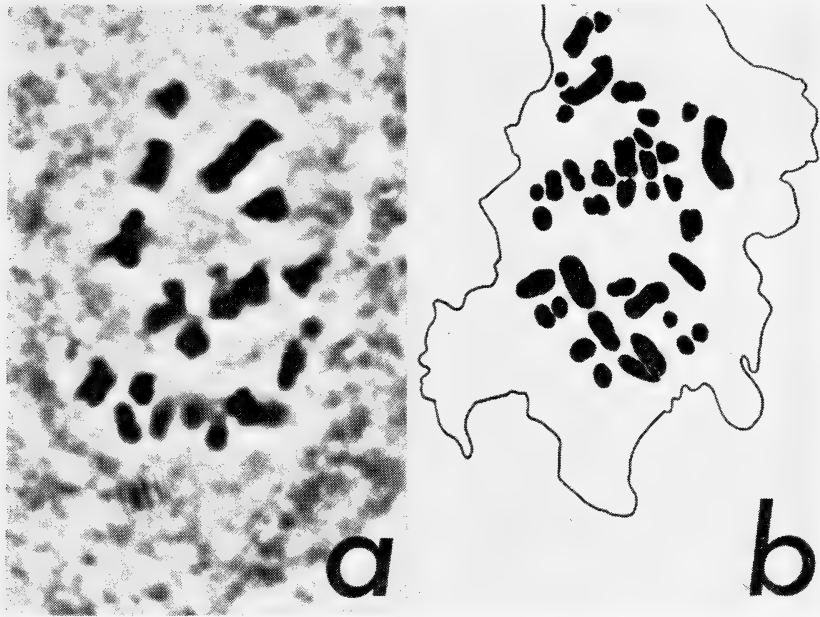
Fig. 3. Diploid aspen: 3a, meiotic metaphase I, $n = 19$, $\times$ 2400; 3b, mitotic metaphase, $2n = 38 \times 4000$.

dried, and stored in envelopes. The diploid pollen was studied to determine if large (unreduced?) pollen grains were produced (Müntzing, 1936a), which might indicate a possible mechanism for the origin of triploidy. Stainability (in Cotton Blue and lactophenol) was used as an indicator of pollen viability (Davis and Heywood, 1963). Observations and photomicrographs were made under bright field microscopy.

RESULTS

Seedlings. While collecting sections of rootstock for mitotic chromosome material, five putative seedlings were found (fig. 1). These came from four widely separated areas and represent about 10% of the saplings studied, suggesting that the occurrence of seedlings is more frequent than previously believed. Even so, most aspen reproduction in this area is still by "suckering" from rootstocks.

Pollen. Pollen from a number of widely separated diploid trees was examined for stainability and size. The variation in both characteristics was similar to that reported in European aspen by Johnsson (1940). Pollen from some trees was relatively uniform. Others contained pollen with a wide range of sizes, and a few appeared to have two size classes. One size class (ca. 30μ) varied around the normal diploid dimensions as established by Johnsson (1940). The other size class (unreduced?) varied around 50μ. Stainability also varied, the percentage of deeply

TABLE 1. CHROMOSOME NUMBERS IN UTAH POPULATIONS OF POPULUS TREMULOIDES. Numbers in parentheses after elevation indicate the number of trees counted.

Cache Co.: Logan Canyon, 6500 ft. (1), n = 19. Carbon Co.: Price Canyon, 6800 ft (2), n = 19. Salt Lake Co.: Alta, 9600 ft (1), n = 28; Alta, 9500 ft (2), 2n = 38; Brighton, 8200 ft (3), n = 19; Brighton, 8400 ft (1), n = ca. 38; Brighton, 8400 ft (2), 2n = 38; Lambs Canyon, 7000 ft (1), n = 19; Lambs Canyon, 7500 ft (1), 2n = 57; Parleys Canyon, 5700 ft (1), n = 29; Parleys Canyon, 5700 ft (4), n = 19; Parleys Canyon, 5700 ft (2), 2n = 38. San Juan Co.: 2 mi N Monticello, 7000 ft (1), n = 19. Tooele Co.: South Willow Creek Canyon, 6000 ft (1), n = 19. Utah Co.: American Fork Canyon, 7000 ft (2), n = 19; American Fork Canyon, 9500 ft (1), 2n = 38; Spanish Fork Canyon 7200 (1), 2n = 38. Wasatch Co.: Soapstone Junction, 8500 ft (1), n = 19.

stained grains ranging from about 30% to about 95%. Because of the small number of pollen grains in the 50μ size class, no meaningful comparisons of stainability between size classes was possible. Many of the pollen grains in the large size class were densely stained, suggesting that they were viable. Figure 2 illustrates these size classes.

Chromosomes. The results of the chromosome studies are presented in Table 1. Chromosome numbers from 28 trees of 18 populations were obtained. Both mitotic (2n) chromosome numbers and meiotic (n) numbers were determined from several populations, but no specific number of counts was necessarily made for any population, although generally the polyploid numbers were better documented than diploid counts. Specific locations for each population are given in Table 1.

Due to the small size and large number of chromosomes, aspen chromosomes are difficult to photograph because some chromosomes are usually out of the plane of focus. Therefore, some of the photographs are accompanied by drawings, and in some cases only drawings are presented (figs. 3, 4, 5). Also for these reasons, the supposed tetraploid is reported only as an approximate count (table 1). Meiosis appeared to be irregular in the putative tetraploid and good chromosome spreads were not obtained. Further efforts to confirm this chromosome number are needed.

DISCUSSION

Triploidy has been reported in quaking aspen, but the incidence is low. Van Buijtenen, et al. (1957) cited only four triploid populations, one from Minnesota, two from Michigan, and one from Colorado. Among the 18 populations we studied (table 1) all were diploid except for three triploids, n = 28, 29; 2n = 57, and an apparent tetraploid, n = ca. 38 (fig. 5).

Therefore, the Wasatch Mountains of Utah may contain a higher proportion of polyploids than areas previously studied. However, because of the relatively small sample the apparent high proportion of triploids could be misleading.

Origin of Polyploidy. The first occurrence of polyploidy (triploidy) in aspen was reported by Müntzing (1936a), who attributed the origin of

triploidy in European aspen to the union of an unreduced (2n) gamete with a normal (n) gamete. Müntzing noticed irregular meiosis in PMC's of triploids, and postulated that in reduced (3n) pollen from this aberrant meiosis could fertilize a normal (n) egg resulting in a tetraploid. Such a tetraploid was produced experimentally (Bergström, 1940).

Pollen from both diploid and triploid European aspen exhibited wide variation in size (Johnsson, 1940). In triploids, two size classes of pollen were reported by Müntzing (1936a), but the pollen from triploids studied by Johnsson (1940) showed continuous variation. However, occasional bimodal distribution of pollen size was not discounted by Johnsson.

The pollen analyzed in the present study (fig. 2) followed the patterns reported for European aspen. Pollen from diploid trees showed wide variation in size, and a few cases exhibited bimodal size distribution. If these criteria are valid the evidence supports the occurrence of unreduced (2n) pollen in Utah aspen. However, pollen from known triploid trees has not been studied as a basis for comparison, nor have pollen grain mitoses been examined to demonstrate the actual occurrence of 2n pollen.

Regardless of these considerations, Müntzing's proposal that polyploids in aspen are of autoploid origin is the most acceptable. However, these are probably inter-populational autoploids. Two additional origins of autoploidy, however, are theoretically possible, viz., somatic mutation and unreduced female gametes. Somatic mutation could feasibly occur during suckering, but triploidy would be difficult to envision by this process. Unreduced eggs are considered by Cheeseman and Dodds (1942) to be responsible for the origin of triploidy in bananas. The same phenomenon may occur in aspen, and that possibility should be examined.

The characteristics of autoploids outlined by Müntzing (1936b) and Stebbins (1950) seem to be applicable to quaking aspen. In meiosis, multivalent formation occurs. One triploid (fig. 4) contains three distinct trivalents at metaphase I. These are similar in shape to those reported by Müntzing (1936a) from European aspen. The presumed tetraploid contains at least one typical quadrivalent (fig. 5).

The morphological differences between polyploid and diploid trees are slight and subtle. Van Buijtenen, et al. (1957) report that triploid aspen are generally larger than comparable diploids, especially the leaves. No such distinction could be attributed to the polyploids in this study due to the extreme leaf variation in adjoining diploid clones (often more than a twofold size difference).

In the European aspen, tetraploid trees were experimentally produced from diploid-triploid crosses (Bergström, 1940). The chances are far greater for the same thing to occur in nature because much larger samples occur. Yet tetraploidy has not been reported. Johnsson (1942) explains the lack of natural tetraploids in *Populus* by suggesting that triploidy may be the optimum level of polypoidy in this genus. But
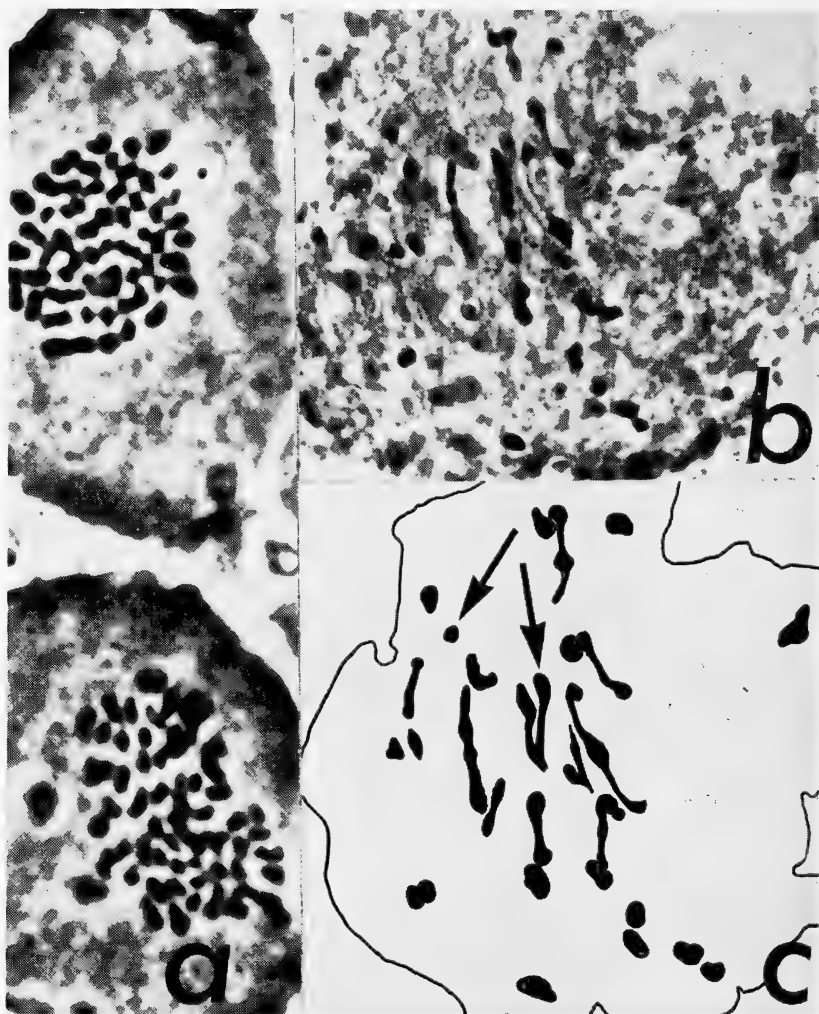
Fig. 4. Triploid aspen: 4a, mitotic metaphase, $2n = 57 \times 2880$; 4b, meiotic metaphase I, $n = 28 \times 1900$; 4c, camera lucida interpretation of 4b, 3 III, 22 II, 3 I, arrows indicate typical trivalent and univalent.

other groups of plants often show much higher levels of optimum polyploidy (Avery, et al., 1959). Often the optimum ploidy level depends on the size of original base chromosome number.

Since tetraploids apparently occur in nature, another natural route to triploidy is possible. The cross between a tetraploid and a diploid would yield a triploid, but this is probably secondary to the origin by unreduced $2n$ pollen. However, if tetraploids exist in an area, then triploids should be more common. This could partially explain the high incidence of triploidy reported in this study.
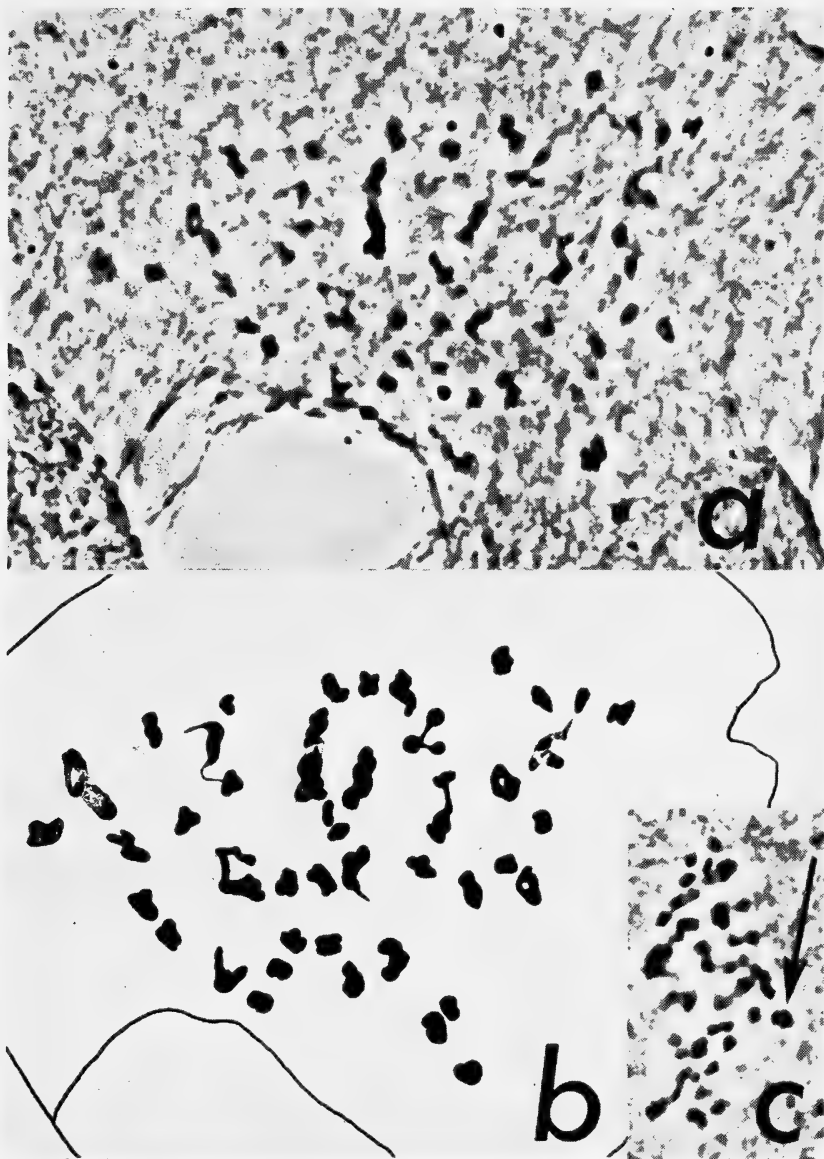
Fig. 5. Putative tetraploid aspen: 5a, meiotic metaphase I, n = ca. 38×2240; 5b, camera lucida interpretation of 5a; 5c, quadrivalent in putative tetraploid denoted by arrow, $\times 2240$.

Seedlings and Ecology. Sexual reproduction is necessary for production of autoploids through unreduced gametes. However, Baker (1918; 1925) and Cottam (1963), after extensive searches, report that they found no aspen seedlings in Utah. Ellison (1943) and Larson (1944)

each report that seedlings occur—but rarely. Kimball Harper (pers. com.) discovered a group of aspen seedlings still in the cotyledon stage. In our study five seedlings were found. We distinguished these as seedlings because of the absence of root attachments to any other aspen.

Baker and Cottam each suggest that the biggest single factor preventing seedling establishment is the early summer drought common to Utah. Perhaps polyploid seedlings are better able to withstand dessication. A study of aspen seedlings combining cytology and ecology might yield an answer to this question. Periodic seedling establishment probably occurs in unusually wet years.

No ecological correlations, other than the above, can be proposed because of the seemingly random distribution of the polyploids. One triploid was found near the lower elevational limits of aspen, one slightly higher, and one very high. Also one triploid and the tetraploid are correlated with the prevernal leafing patterns observed by Cottam (1954). But one prevernal leafing aspen was clearly diploid, and one triploid aspen was definitely late-leafing.

The Parleys Canyon population of aspen has been especially interesting. A single triploid occurred here. However, later collections from nearby trees were diploid with both staminate and pistillate trees present. Several of the trees taken for pistillate at first were obviously hermaphroditic on closer inspection. Unlike the hermaphrodites reported by Pauley and Mennel (1957) and Santamour (1956), these trees contained almost entirely bisexual flowers. One of these was a diploid $2n = 38$. These were the only cases of bisexual flowers found in our collections. Among predominantly staminate trees no bisexual flowers were observed, though Pauley and Santamour each reported a low percentage of hermaphrodites in their studies. This same small area also contained two of the seedlings reported. The aspen occur here about 100 feet above the creek on an east facing slope. Additional moisture from seeps or springs along this hillside may have provided favorable conditions for seedling establishment.

This paper is abstracted from a thesis submitted by the first author in partial fulfillment of the M.S. degree at the University of Utah. His present address is: Department of Botany, University of Washington, Seattle, Washington.

Literature Cited

Avery, A. G., and S. Satina, and J. Rietsema. 1959. Blakeslee: The genus Datura. Ronald Press, New York.

Baker, F. S. 1918. Aspen reproduction in relation to management. J. Forest. (Washington) 16:389–398.

————. 1921. Two races of aspen. J. Forest. (Washington) 19:412–413.

————. 1925. Aspen in the Central Rocky Mountain Region. U. S. D. A. Bull. 1291.

Bergstrom, I. 1940. On the progeny of diploid × triploid Populus tremula. With special reference to the occurrence of tetraploidy. Hereditas 26:191–201.

Cheeseman, E. E., and K. S. Dodds. 1942. Genetical and cytological studies of

Musa IV. Certain triploid clones. J. Genet. 43:337–357.

COTTAM, W. P. 1954. Prevernal leafing aspen in Utah Mountains. J. Arnold Arbor. 35:239–248.

———. 1963. Quaking aspen (Populus tremuloides Michx.). Naturalist 14:3–15.

DARLINGTON, C. D., and A. P. WYLIE. 1955. Chromosome atlas of flowering plants. Allen and Unwin, London.

DAVIS, P. H., and V. H. HEYWOOD. 1963. Principles of angiosperm taxonomy. Van Nostrand, Princeton.

ELLISON, L. 1943. A natural seedling of western aspen. J. Forest. (Washington) 41:767–768.

FOWELS, H. A. 1965. Silvics of forest trees of the United States. U. S. D. A. Handb. 271.

JOHNSSON, H. 1940. Cytological studies of diploid and triploid Populus tremula and of crosses between them. Hereditas 26:321–352.

———. 1942. Cytological studies of triploid progenies of Populus tremula. Hereditas 27:306–312.

LARSON, G. C. 1944. More on seedlings of western aspen. J. Forest. (Washington) 42:452.

MÜNTZING, A. 1936a. The chromosomes of a giant Populus tremula. Hereditas 21: 383–393.

———. 1936b. The evolutionary significance of autopolyploidy. Hereditas 21: 263–378.

PAULEY, S. S., and G. F. MENNEL. 1957. Sex ratio and hermaphroditism in a natural population of quaking aspen. Minnesota Fores. Notes 55.

SANTAMOUR, F. S. 1956. Hermaphroditism in Populus. Proc. Third Northeast Forest Tree Impr. Conf.

SARGENT, C. S. 1961. Manual of the trees of North America. Dover Publications, New York.

STEBBINS, G. L. 1950. Variation and evolution in plants. Columbia Univ. Press, New York.

VAN BUIJTENEN, J. P. 1957. A technique for fixing and staining mitotic chromosomes in aspen. Forest Sci. 5:48.

———, P. N. JORANSON, and D. W. EINSPAHR. 1957. Naturally occurring triploid quaking aspen in the United States. Proc. Soc. Amer. Foresters Ann. Meeting, Syracuse, New York.

———, and D. W. EINSPAHR. 1959. Note on the presence of sex chromosomes in Populus tremuloides. Bot. Gaz. 121:60–61.

NOMENCLATURE AND INTERPRETATION OF A CALIFORNIA SUBSPECIES IN ARCTOSTAPHYLOS (ERICACEAE)

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McMinn (1939), having had access to Adams' specimens and doctoral dissertation (1935), published *Arctostaphylos tomentosa* (Pursh) Lindl. var. *crinita* Adams ex McMinn with a Latin diagnosis ("A specie differt: ramis junioribus tomentosis et albo-divaricate-crinitis; corticis levigatis.") Adams (1940) published the same variety as *A. crustacea* Eastw. var. *tomentosiformis* Adams for which he cited as type *Adams 928* (UC

531720, UC 531721). However, the only epithet written on the type is *A. tomentosa* var. *crinita*, just as McMinn had published it. Munz (1959), interpreted this to be a variety of *A. tomentosa*, overlooking McMinn's Latin diagnosis for var. *crinita*, and accepting Adams' var. *tomentosiformis* instead of McMinn's var. *crinita*, published *A. tomentosa* var. *tomentosiformis* (Adams) Munz. Since var. *crinita* does in fact have a Latin description, it must be the valid name.

Wells (1968) made some important nomenclatural changes in interpreting the *A. tomentosa* alliance and included *A. crustacea* as a subspecies of *A. tomentosa* (*A. tomentosa* ssp. *crustacea* (Eastw.) Wells). If his interpretation is to be considered valid, and the validity of *A. tomentosa* var. *crinita*, described above, is valid, then it is only logical that a new combination be made: *Arctostaphylos tomentosa* (Pursh) Lindl. ssp. **crinita** (Adams ex McMinn) Gankin, comb. nov.

The distribution of *A. tomentosa* ssp. *crinita* is of particular interest. Its northernmost outpost seems to be on Montara Mountain in northern San Mateo Co. where it is sympatric with *A. montaraensis* Roof. It seems to be absent, replaced by ssp. *rosei*, ssp. *tomentosa*, and ssp. reaches its greatest abundance in southern Santa Cruz Co. where it comes in contact with such species as *A. glutinosa* Schreib., *A. silvicola* Jeps. & Wiesl., *A. nummularia* Gray ssp. *sensitiva* (Jeps.) Wells, *A. andersonii* Gray, and *A. canescens* Eastw. in various localities. Throughout the Pajaro Hills and the Santa Lucia Mountains this subspecies seems to be absent, replaced by ssp. *rosei*, ssp. *tomentost*, and ssp. *crustacea*. Wells (1968) described ssp. *insulicola* from Santa Cruz Island. The only distinction between ssp. *crinita* and ssp. *insulicola*, according to Wells, is the apparent lack of setose hairs on ssp. *insulicola*. However, examination of a number of specimens of this subspecies from Santa Cruz Island has shown that there certainly are plenty of specimens with sporadic, non-glandular, setose hairs. In the opinion of this author, the specimens on Santa Cruz Island which have been named ssp. *insulicola* by Wells are insufficiently distinct from and could be considered as relictual forms of ssp. *crinita*, thereby extending the range of ssp. *crinita* to as far south as Santa Cruz Island, Santa Barbara Co.

LITERATURE CITED

ADAMS, J. E. 1935. A systematic study of the genus Arctostaphylos. Ph.D. Thesis, University of California, Berkeley.
————. 1940. A systematic study of the genus Arctostaphylos. J. Elisha Mitchell Sci. Soc. 56:1–62.
McMINN, H. E 1.939. An illustrated manual of California shrubs. Univ. California Press, Berkeley.
MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.
WELLS, P. V. 1968. New taxa, combinations, and chromosome numbers in Arctostaphylos (Ericaceae). Madroño 14:193–210.

VEGETATIVE PROPAGATION OF WOODY SHRUB SPECIES FROM THE NORTHERN MOJAVE AND SOUTHERN GREAT BASIN DESERTS

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Some species of woody desert shrub species have been reported to be successfully propagated by means of stem cuttings. These include: *Fouquieria splendens* Engelm. (Shreve, 1951); *Chiliopsis linearis* Cav. (Everett, 1957; Charles, 1962); *Simmondsia chinesis* Link (Gentry, 1958); *Encelia farinosa* Gray, *Franseria dumosa* Gray, *Hymenoclea salsola* Torr. & Gray, *Peucephyllum schottii* (Gray) Gray, and *Pluchea sericea* (Nutt.) Cav. (Chase and Strain, 1966). Charles (1962) had only partial success with *Vauquelinia california* (Torr.) Sarg. and *Garrya wrightii* Torr. Studies here reported extend the list of such plants which can be vegetatively propagated.

Attempts were made to vegetatively propagate materials from 17 woody perennials from the Nevada Test Site (northern Mojave—southern Great Basin deserts). Stem cuttings were collected in 1966, 1967, and 1968 brought to UCLA. A basic test pattern was established for which each species was subjected. From 5 to 15 cuttings of each of the species were subjected to 15 different treatments. The 15 treatments comprised a 3×5 factorial design. Three growth regulator treatments were a, control; b, dipping cut tips into Hormodin 2 (0.3% IBA in talc); c, and dipping into Hormodin 3 (0.8% IBA in talc preparations). They were then placed into vermiculite in wooden flats with screen bottoms. The cuttings with these three treatments were each placed into five different environmental conditions for rooting. The five were a, a mist house; b, a lathhouse; c, a glasshouse; d, a bottom-heated glasshouse which was open to outside air (low humidity); and e, a closed bottom-heated glasshouse (high humidity). Temperatures in these units reflected ambient conditions and varied from season to season, usually 20 to 30°C in the daytime and 10 to 20°C at night. Later studies involved placing the cuttings directly into Yolo loam soil before rooting. This proved to be a good technique for many species. Procedures selected from the above 15 test procedures except for use of soil are described below:

Larrea divaricata Cav. Stem cuttings taken from mature shoots in the field did not root, but many of those taken from seedlings did root. Within 3 years, however, these clones had decreased ability to root. The most successful technique involved the use of Hormodin 3 powder. Tips 7 to 15 cm in length were dipped in Hormodin 3 and placed in flats in a mist house. Rooting occurred in about a month but some cuttings rooted

and some did not. Precise control with air temperature of 15°C, root temperatures of 20°C and relative humidity of 90% with cuttings in Yolo loam soil has given most uniform results. Two clones representing two different ecotypes were selected for further propagation, and large populations of each have been produced.

Lycium andersonii Gray. Stem cuttings rooted easily, and no special kind of plant material seemed necessary. Stem pieces were dipped into Hormodin 2 powder and then placed into vermiculite in flats which were kept in a mist house until rooted. Cuttings have been the major source of experimental material since viable seeds are difficult to obtain. In the field root pieces from which the shoot and crown have been severed readily develop new shoots.

Lycium pallidum Miers. Stem pieces from the field failed to root. Cuttings from seedlings growing in the glasshouse have rooted under mist with Mormodin 2 or 3. Similar results were obtained with *Lycium shockleyi* Gray.

Franseria dumosa Gray. Stem pieces rooted easily from field or glasshouse. They were dipped in Hormodin 2 powder and placed in vermiculite in a mist house until rooted. Age of clone was not an important factor.

Atriplex canescens (Pursh) Nutt. Stem pieces from seedlings rooted readily. Growth regulator was not used for routine rooting, and use of an open glasshouse was most successful.

Atriplex confertifolia (Torr. & Frem.) Wats. Cuttings from seedlings or from plants in a juvenile form rooted most readily. No growth regulator was used, and the cuttings placed in an open glasshouse with bottom heat rooted readily. Good success was obtained for material placed in soil for rooting.

Atriplex hymenelytra (Torr.) Wats. Cuttings from young seedlings rooted readily under the same conditions as *A. confertifolia*. Somewhat better success has been obtained with cuttings placed in soil than with cuttings in vermiculite. The percentage of rooting seemed to decrease as stock seedlings became older, especially during winter months.

Atriplex lentiformis (Torr.) Wats. Cuttings rooted from a specimen brought into the glasshouse from the field and transplanted into soil. The most successful procedure involved dipping stem pieces in Hormodin 3 powder, placing them in soil (actually in individual cardboard containers for ease in handling), and putting in an open glasshouse until rooted. A large population of plants has been produced from the stock plant.

Eurotia lanata (Pursh) Moq. If vigorous new growing shoots were used, cuttings from old plants rooted as did those from younger seedlings. Use of a lathhouse with Hormodin 2 powder and vermiculite gave best results. Dormancy is a problem with this species in that it prefers a cold root temperature of about 20°C or less.

Grayia spinosa (Hook.) Moq. Some cuttings were made of material

brought from the field; but more success was obtained from material obtained from plants growing in the glasshouse or lathhouse and which had been chilled at about 4°C before cuttings were taken. Dipping stem pieces into Hormodin 2 powder and then placing them in vermiculite in a lathhouse resulted in most successful rooting. Mist also gave very satisfactory results. Good temperature is necessary for vegetative growth of this species.

Ephedra viridis Cov. Stem cuttings from seedlings rooted readily when they were placed in Yolo loam soil (individual cardboard containers) in the open glasshouse with bottom heat. There was no advantage to the IBA treatments. A few cuttings were made from pieces brought in from the field, but none survived after transplanting.

Thamnosma montana Torr. & Frem. Cuttings rooted readily, particularly when dipped with either of the Hormodin powders before being placed in vermiculite in the open glasshouse.

Kochia americana Wats. Cuttings from field-grown stem pieces have been made without IBA in a dry glasshouse and in soil. Only succulent material rooted.

The success so far obtained with vegetative propagation of these species is of interest for two major reasons. Clonal populations of the plants can be prepared for experimental studies for several of the species. Also the 3 × 5 experimental design may be used to test and prepare populations of other species which may be of ecological or economic interest.

The study of vegetative propagation of desert woody plant materials is being continued in that clonal populations are needed for many contemplated biological studies. It can be expected that the techniques described here will be improved and that some of the problems encountered will be solved and that other species will be rooted.

Conclusions

1. Stem cuttings of 14 woody desert perennial shrub species were successfully rooted. At least one of these, *L. divaricata,* is a species for which earlier attempts to root had been unsuccessful (Chase and Strain, 1966).

2. Conditions for successful rooting varied with species. *L. divaricata, A. hymenelytra, A. confertifolia,* and *C. ramosissima* rooted more readily in soil than in vermiculite. IBA was not needed for Atriplex species or *K. americana. L. divaricata, L. andersonii, F. dumosa, A. tridentata* and *G. spinosa* required mist or responded satisfactorily to mist rooting while other species disintegrated rapidly under the same circumstances. Other species rooted equally or better under dry conditions or even in a lathhouse where temperatures are lower. These include *G. spinosa, E. lanata, E. viridis* and *T. montana. E. viridis* responded to bottom heat.

3. The species studied for which stem cuttings have failed to root include *Krameria parvifolia* Benth., and *Juniperus osteosperma* (Torr.) Little.

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LITERATURE CITED

CHARLES, R. F. 1962. Factors effecting the rooting of native desert woody plants. Master's thesis, University of Arizona.

CHASE, V. C., and B. R. STRAIN. 1966. Propagation of some woody desert perennials by stem cuttings. Madroño 18:240–243.

EVERETT, P. C. 1957. A summary of the culture of California plants at the Rancho Santa Ana Botanic Gardens 1927–1950. Abbey Garden Press, Pasadena.

GENTRY, H. S. 1958. Natural history of Jojoba (Simmondsia chinensis) and its cultural aspects. Econ. Bot. 12:261–295.

SHREVE, F. 1951. Vegetation and flora of the Sonoran Desert. Publ. Carnegie Inst. Wash. 591.

YERMANOS, D. M., A. KADISH, C. M. McKELL, and J. R. GOODIN. 1968. Jojoba— a new California crop Calif. Agric. 22(10):2–3.

NOTES AND NEWS

FOXTAIL PINE ON SIRRETTA PEAK, CALIFORNIA.—The distribution of the Foxtail Pine, *Pinus balfouriana* Grev. & Balf. in California is disjunct and confined to two high elevation areas about 300 miles apart. The northern population is in the Klamath Mountains of northwestern California from Lake Mountain (elev. 6,903 ft., 41° 44.9′N. latitude and 123° 7.9′W. longtitude) to South Yolla Bolly Mountains (elev. 8,092 ft.; 40° 2.2′N. latitude and 122° 51.2′W. longitude). The southern population is about 300 air miles south of the South Yolla Bolly Mountains in the southern Sierra Nevada (Critchfield, W. B., 1966. Geographic distribution of the pines of the world. U. S. D. A. Misc. Publ. 991). The northern extent of the southern population is uncertain, but specimens were collected by Peter Raven on the steep south wall of the South Fork of the Kings River about one mile north of Bench Lake (ca. 9,900 ft. at 36° 57.7′N. latitude and 118° 27.1′W. longitude). The southern-most known locality was considered previously to be Olancha Peak (elev. 12,135 ft.; 36° 15′54″ N. lat. and 118° 7′6″ W. longitude).

On August 13, 1967 we encountered foxtail pine on Sirretta Peak (elev. 9,977 ft.; 35° 55.4′ N. latitude and 118° 19.9′ W. longitude). Several specimens were collected and are presently at the herbarium of Humboldt State College, Arcata, California. The above locality is approximately nine miles north of the Tulare-Kern County line. This area was examined for the foxtail pine on the information of its possible occurrence there from Victor Aubin of Kernville, California. Only the Sirretta Peak area and about two miles of the ridge that is oriented in a NW-SE direction were explored.

Ten trees were measured with both diameters and heights being taken. The largest tree measured 54.5 inches in diameter breast high, and 73 ft. in height. A few other tree measurements were as follows: 25.8 inches—53 ft., 28.3 inches—70 ft., 17.3 inches—49 ft., 5.9 inches—20 ft.

All the measured foxtail pines were at elevations ranging from about 8,970 to 9,780 ft., either on the west-facing slope or on the NW-SW ridge of Sirretta Peak.

Two other five-leaved pine associates were *Pinus flexilis* and *P. monticola*. Also present were two other pines, namely *P. jeffreyi* and *P. murrayana*. Another conifer present was *Abies magnifica* var. *shastensis*. The associated shrubs on the shallow decomposing granitic soils were *Castanopsis sempervirens, Arctostaphylos patula,* and *Spiraea* sp. Foxtail pine apparently was of higher density on north-facing slopes and extended to lower elevations on the west-facing slope of the ridge that was sampled.—H. THOMAS HARVEY, Department of Biological Sciences, San Jose State College, San Jose 95114, and RONALD J. MASTROGIUSEPPE, Arcata 95521.

A REVISION OF PHYMOSIA (MALVACEAE)

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Although *Phymosia* Desv. ex Hamilt. was described more than 140 years ago, and includes species that have been cultivated for an even greater time, the systematics of the genus has never been treated comprehensively. Kearney (1951) presented the only previous coherent account of *Phymosia,* and it is very brief.

Bates (1968) dealt with the placement of this genus within the tribe Malveae, and noted an alliance of *Phymosia* with *Malacothamnus* Greene and *Iliamna* Greene that stands distinctly apart from the *Sphaeralcea* alliance. He notes that, "within this alliance . . . *Phymosia* embodies the most primitive character expressions." I agree fully with this view and simply add that the relatively more arboreal habit and montane tropical distribution of *Phymosia* serve to emphasize this more primitive position.

The American Malvaceae are only rarely arborescent and only rarely montane in distribution. In addition to *Phymosia,* only *Wercklea* Pitt. & Standl. and *Abutilon* sect. Tetrasida (Ulbr.) Krap. may be placed in this category, although certain species of *Robinsonella* Rose & Bak. f. may also be regarded as montane (Fryxell, 1972). (The perennial herbs of the high Andes [e.g., *Nototriche* Turcz. and *Tarasa* Phil.] are excluded because of their obviously derivative nature.) It is interesting that these two characteristics are so combined in *Phymosia,* in view of the prevailing opinion (cf. Takhtajan, 1969) that the angiosperms originated under tropical montane conditions, and that relatively more primitive types may be more commonly encountered in such areas. The relatively primitive character expressions of *Phymosia* are thus underscored by the predominantly tropical montane distribution of the genus.

The genus is small and wholly from the tropics. One species is Caribbean, and the remainder are from Mexico and Guatemala. Typically, *Phymosia* occurs at elevations of 2000–3000 m, except that *P. umbellata* is found at somewhat lower elevations, and the Caribbean *P. abutiloides* may be found near sea level. Britton and Millspaugh (1920), who stated that the genus contains about 40 species, some South African, evidently confused *Phymosia* with other genera, including *Anisodontea* Presl. Some of the species are cultivated for their showy flowers in their native areas, and some of these were introduced as ornamentals in colonial days into the gardens and greenhouses of Europe. In fact, many handsome illustrations of these plants are to be found in the botanical literature of the

TABLE 1. PUBLISHED ILLUSTRATIONS OF SPECIES OF PHYMOSIA.
Color plates are marked with an asterisk.

P. abutiloides. Catesby, Nat. Hist. Carol. 1: t. 77. 1731; Dillenius, Hort. Eltham.
t. 1, f. 1. 1732; Cavanilles, Dissert. 2:t.16, f.2. 1786; Jacquin, Pl. Hort. Schoenbr.
3:t. 293. 1798*; Sims, Bot. Mag. 52:t. 2544. 1825*; Don, Garden 48:t. 1023. 1895;
Kearney, Univ. Calif. Publ. Bot. 19: t. 1, f, B, F. 1935.

    P. umbellata. Cavanilles, Icones 1:t.95. 1791; Cavanilles, Icones 5:t. 500bis, f. 104.
1799; Kerner, Hort. Sempervir. t. 459. 1816*; Schrank, Samml. Zierpfl. t. 12. 1817*;
Loddiges, Bot. Cab. 3:t.222. 1818*; Loiseleur Deslongchamps, Herb. Amat. 7:t.439.
1824*; Drapiez, Herb. Amat. Fl. 3:t 169. 1829*; Nees and Sinnig, Samml. Schonbluh
Gew. t. 58. 1829 *; Bot. Reg. 19:t.1608. 1833*; Piccioli, Anotr. Colt. Fiori 2:t. 64.
1834*; Loudon, Fl. Gard. Orn. Gr. Pl. 6: 21. 1848; Jour. Hort. Ser. 3, 10: 63. 1885;
Alexander, Addisonia 17: t. 555. 1932. Kearney, Univ. Calif. Publ. Bot. 19: t. 1, f.
C, D. 1935.

    P. rosea. Zuccarini, Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 2:t. 9. 1837;
Planchon, Fl. des Serres 7:t. 726. 1851–2; Paxton, Fl. Gard. 3:173. 1853; De-
Candolle, Calq. Dess. Fl. Mex. t. 58. 1874; Chancrin & Dumont, Larousee Agric.
Encycl. Ill. 2:t, 1871; Kearney, Univ. Calif. Publ. Bot. 19; t. 1, f. E. 1935.

18th and 19th centuries (Table 1). The earliest such illustration is that
of Catesby, who according to Dillenius (1732), introduced seeds of
P. abutiloides into greenhouse culture.

It is with Catesby's seeds that we must begin in a consideration of the
typification of the generic name. Dillenius grew a plant from these seeds
that became the subject of a plate (t. 1, f. 1) in *Hortus Elthamensis*
(Dillenius, 1732). Schmidt (1965) described a copy of this work from
the library of Linnaeus that contains Linnaeus' marginal notations, and
which definitely verifies that the Dillenian plate is the type of *Malva
abutiloides* L. Schmidt reproduced a portion of this particular Dillenian
plate (Schmidt, 1965, plate XXI) showing the Linnaean binomial in
Linnaeus' own hand. This correspondence is significant, because the two
specimens in the Linnaean herbarium that bear this binomial are of a
different plant [*Anisodontea elegans* (Cav.) Bates from South Africa],
and the annotations they bear are not in Linnaeus' hand but in the hand
of the younger Linnaeus and of Thunberg (Savage, 1945; Bates, 1969).
These specimens, therefore, have no bearing on the typification of *Malva
abutiloides* L. (non L. f.); rather, Dillenius' plate (t. 1, f. 1) typifies
Malva abutiloides L., which in turn is the nomenclatural type of the
genus *Phymosia* Desvaux ex Hamilton. The Linnaean epithet has been
used in the latter sense of Desvaugh by such authors as Persoon (1807),
Grisebach (1859), Britton and Millspaugh (1920), and Barker and
Dardeau (1930).

Chromosome numbers are known ($n = 17$) for three species: *P.
umbellata* (Skovsted, 1935; Webber, 1936; Bates, pers. comm.); *P.
abutiloides* (Webber, 1936); and *P. rosea* (Bates and Blanchard, 1970).

The same chromosome number is found in the related *Malacothamnus*,
but does not occur elsewhere in the tribe Malveae (Bates, 1968). *Ili-*

amna, the third member of the *Malacothamnus* alliance, has $n = 33$, a number most easily interpreted as a polyploid derivative $(2n - 1)$ of a 17-chromosome ancestor, as suggested by Wiggins (1936).

Chaudhuri (1965) described and illustrated the pollen grains of *P. abutiloides* (as *Sphaeralcea abutiloides*), but unfortunately did not cite a voucher specimen. The pollen is reported to be tricolporate, which is a character relatively less advanced than the panaperturate condition found in some other genera of the Malvaceae. Pentacolporate pollen grains characterize *P. rosea* and *P. umbellata* (Elsik & Fryxell, unpublished).

PHYMOSIA Desvaux ex Hamilton, Prodr. Pl. Ind. Occid. 49. 1825. *Malva* section *Sphaeroma* DC. Prodr. 1:435. 1824. *Sphaeralcea* St. Hil. Fl. Bras. Mer. 1:209. 1827, emend. G. Don, Gen. Hist. 1:465. 1831, pro parte. *Sphaeroma* (DC.) Schlecht. Linnaea 11:352. 1837, non Harv. 1866. *Meliphlea* Zucc. Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 2:359. 1837. *Sphaeralcea* sect. *Meliphlea* (Zucc.) Bak. f. J. Bot. 31:367. 1893. *Sphaeralcea* subgen. *Meliphlea* (Zucc.) Kearn. Univ. Calif. Publ. Bot. 19:2. 1935. *Sphaeralcea* subgen. *Phymosia* (Desv. ex Hamilt.) Kearn. Univ. Calif. Publ. Bot. 19:2. 1935.

D. M. Bates (pers. comm.) pointed out the need to designate a lectotype species of section *Sphaeroma* and provided helpful discussion of the nomenclatural considerations involved in the choice. *Malva rosea* DC. is herewith designated as lectotype species of *Malva* section *Sphaeroma* DC. and hence of the genus *Sphaeroma* (DC.) Schlecht.

Type species. *Phymosia abutiloides* (L.) Desv. ex Hamilt.

Shrubs or small trees of neotropical distribution, usually densely invested with stellate tomentum on stems, petioles, and peduncles, the hairs often stipitate and more or less furfureous. Leaves aceriform, cordate, 3–7 lobed (often merely pentagonal), the central lobe predominant, obtuse to acuminate, 5–9 nerved, crenate or crenulate (rarely subentire) or dentate. Petioles half length of lamina to equaling lamina. Stipules subulate, persistent (?). Peduncles solitary in the axils, 1-many flowered, usually exceeding the subtending leaf, the branch sometimes forming a terminal paniculate inflorescence. Involucre trimerous, of 3 distinct involucral bractlets, or forming a gamophyllous tube, sometimes caducous. Calyx gamosepalous, 5-lobed, plicate in bud, tomentose without; inner surface of calyx divided into two regions: the proximal region made up of the calyx tube and the central portion of each lobe, which is glabrous, and the distal region made up of the margin of each lobe (where plicate in bud) which is densely matted with fine hairs. Bractlets of individual flower (when distinct) often positioned asymmetrically, so that the bractlets of the inflorescence (often umbellate) tend to be on the periphery of the umbel. Petals asymmetrically obovate, obtuse or shallowly bifid, glabrous except on claw where densely but locally pubescent (except glabrous throughout in *P. rosea*). Staminal column glab-

rous, pallid, narrowly columnar, abundantly antheriferous on upper portion (or anthers petaloid in certain double-flowered cultigens); anther mass globose to elongate; pollen yellow or orange, spheroidal, echinate. Styles numerous, as many as the carpels (10–20 in the smaller-fruited species, 30–40 in the larger-fruited), distinct where exserted from the androecium, at first glabrous, but often revealing ascending-strigose hairs when fully elongated, at length recurved; stigmas capitate in the smaller-flowered species (sometimes obliquely so) to unilaterally decurrent in the larger-flowered species. Flowers evidently protandrous, the styles emerging from within the staminal column only after anther dehiscence. Fruits globose to oblate, yellowish-tomentose; mericarps numerous (as many as the styles), reniform or oblong, thin, dehiscent to the base, smooth, shedding from a central column at maturity, few-seeded. Seeds reniform, glabrous. Chromosome number **n = 17.**

Key to the Species of Phymosia

Inflorescence an axillary panicle, many-flowered; involucral bractlets 4–7 mm long, 1–2 mm wide, caducous; calyx 8–10 mm long, petals lavender or pink, 18–22 mm long.

Bractlets 6–7 mm long, 1 mm wide, linear; calyx lobes as long as broad.

1. *P. abutiloides*

Bractlets 4–5 mm long, 1½–2 mm wide, lanceolate; calyx lobes longer than broad . . . . 1. *P. floribunda*

Inflorescence an axillary umbel, 1–4 flowered; involucral bractlets 6–30 mm long, lanceolate, ovate, or spatulate, or sometimes forming a gamophyllous tube, caducous or persistent; calyx 10–40 mm long; petals white to burgundy, 20–70 mm long.

Calyx 10–14 mm long; bractlets 6–14 mm long, caducous; flowers lavender.

Peduncles usually uniflorate; involucral bractlets 6–8 mm wide, enclosing bud, ovate-sessile . . . . 3. *P. crenulata*

Peduncles 2–3 flowered; involucral bractlets 1–4 mm wide, lanceolate.

4. *P. pauciflora*

Calyx 15–40 mm long; bractlets 10–30 mm long, caducous or persistent; flowers white to burgundy (including pink, rose, red, etc).

Calyx 15–20 mm long; petals 20–35 mm long; bractlets stipitate or sessile, usually persistent; claw of petal ciliate; filaments 2–3 mm long.

Bractlets stipitate-spatulate; peduncles usually triflorate; petals burgundy.

5. *P. umbellata*

Bractlets ovate-sessile; peduncles usually uniflorate; petals rose; flowers (in cultivation sometimes double . . . . 6. *P. anomala*

Calyx 25–40 mm long; petals 35–70 mm long; bractlets sessile or forming gamophyllous tube, caducous or persistent; claw of petal glabrous or ciliate; filaments 3–6 mm long.

Petals glabrous on claw, white to rose-red; bractlets ovate or forming a gamophyllous tube, often caducous at anthesis; filaments ca. 3 mm long.

7. *P. rosea*

Petals ciliate on claw, deep burgundy; bractlets lanceolate, distinct, persistent; filaments 5–6 mm long . . . . 8. *P. rzedowskii*

1. Phymosia abutiloides (L.) Desvaux ex Hamilton, Prodr. Pl. Ind. Occid. 49. 1825. *Malva abutiloides* L. Sp. Pl. (ed. ii), 971. 1763, non L.

f., 1781. [Type: Dill. Hort. Elth. t. 1, f. 1.] *Sphaeralcea abutiloides* (L.)
G. Don, Gen. Syst. 1:465. 1831. *Abutilon Eggersii* Bak. f. J. Bot. 31:75.
1893. [Type: *Eggers 4288* (BM-seen as photo, US).]

Shrub to ca. 3 m tall. Twigs densely pallid-tomentose, the hairs stellate, $\frac{1}{2}$–$\frac{3}{4}$ mm diameter, 10–20 armed, sometimes stipitate. Leaves up to 13 cm long, cordate, commonly 5-lobed, the larger leaves 7- or even 9-lobed (the central lobe the largest and triangular), acute, 7–9 nerved, densely stellate tomentose below, moderately so above, discolorous; leaf margin dentate, the teeth about as long as wide, rather closely spaced (3–4 per cm), acute or somewhat rounded, clearly differentiated. Petioles densely tomentose (canescent), $\frac{1}{2}$–$\frac{2}{3}$ length of lamina. Stipules tomentose, 5–10 mm long. Peduncles yellowish-tomentose, branched and paniculately multiflorate, the branch forming compound terminal panicles. Involucre of three distinct bractlets inserted at base of calyx; bractlets 6–7 mm long, 1 mm wide, linear, pubescent, caducous in fruit. Calyx 8–10 mm long, densely tomentose; lobes 3 mm wide at base, 3 mm long, triangular, acute, 3-ribbed. Petals 18–22 mm long, glabrous (except densely pubescent on margins of claw), lavender (pink?), often apically bifid. Staminal column narrow ($\frac{1}{2}$ mm diameter), shorter than the petals, antheriferous in upper two-thirds; filaments 1 mm long, numerous; anther mass elongate; pollen yellowish. Styles as many as the carpels (15–20), at first glabrous but revealing strigose hairs when fully elongated; stigmas glabrous, capitate. Fruit 1 cm diameter, globular or slightly obovoid; mericarps 15–20, reniform, 8–11 mm long. Seeds 2 mm long. Chromosome number, $n = 17$. Figs. 1, 9.

Specimens examined. HAITI: Gros Cheval, *Holdridge 1704* (GH, MICH, MO, US); Massif de la Pelle, Groix des Bougquets, Badeau, *Ekman 7723* (F, US). BAHAMAS: *Brace 103* (MO), *104* (MO), *105* (F), *106* (F), *136* (MO); Grand Bahama: Hawk's Bill Creek, *Howe 2554* (F), Eight Mile Rocks, *Brace 3698* (F); New Providence: *Brace 484* (GH), Blue Hills, *Millspaugh 2475* (F), Blue Ridge, *O'Neill 8212* (MICH), Seven Hills, *Eggers 4288* (US) *E. G. Britton 6591* (F), Coppici, *Britton & Brace 414* (F), Abaco, Cherokee Sound, *Brace 1929* (F, US); Eleuthera: Harbor Island to Upper Bogue, *E. G. Britton 6471* (F). In cultivation: *Dillenius* s.n. (OXF).

Phymosia abutiloides occurs near sea level in the Bahamas to elevations as high as 1500 m in Haiti. Although cultivated for its profuse flowers (at least in Europe, where it was introduced, see Table 1), it apparently has received no vernacular names.

2. **Phymosia floribunda** (Schlecht.) Fryxell, comb. nov. *Sphaeroma floribundum* Schlecht. Linnaea 11:353. 1827. [Type: Oaxaca, *Mühlenpfordt* s.n. (B-destroyed). Neotype: Oaxaca: Yavesía, *Galeotti 4088* (BR).] *Sphaeralcea floribunda* (Schlecht.) Walp. Rep. 2:789. 1843, non Philippi, 1864.

TABLE 2. SUMMARY OF DISTINGUISHING CHARACTERS OF SPECIES OF PHYMOSIA.

Species	Type of inflorescence	Flower size*	Flower color	Bracteole form	Leaf size*	Leaf margin**	Fruit size*	Distribution
abutiloides	axillary panicle	small	lavender	linear	large	dentate	small	Caribbean
floribunda	axillary panicle	small	lavender	lanceolate	small	crenate	small	isthmian Mexico
crenulata	flowers solitary in axils	medium	lavender	ovate	small	crenate	....	isthmian Mexico
pauciflora	axillary umbel	medium	lavender	lanceolate	small	crenate	small	eastern Mexico
umbellata	axillary umbel	medium	burgundy	stipitate	large	subentire	moderately large	eastern Mexico
anomala	flowers solitary	medium	rose	ovate	small	crenate	....	eastern Mexico
rosea	axillary umbel	large	rose or white	often gamophyllous	large	dentate	large	western Mexico, Guatemala
rzedowskii	axillary umbel	large	burgundy	lanceolate	large	crenate	large	western Mexico

*See actual descriptions for exact size measurements.

**See Figs. 1–8 for better evaluation of leaf margin descriptions.
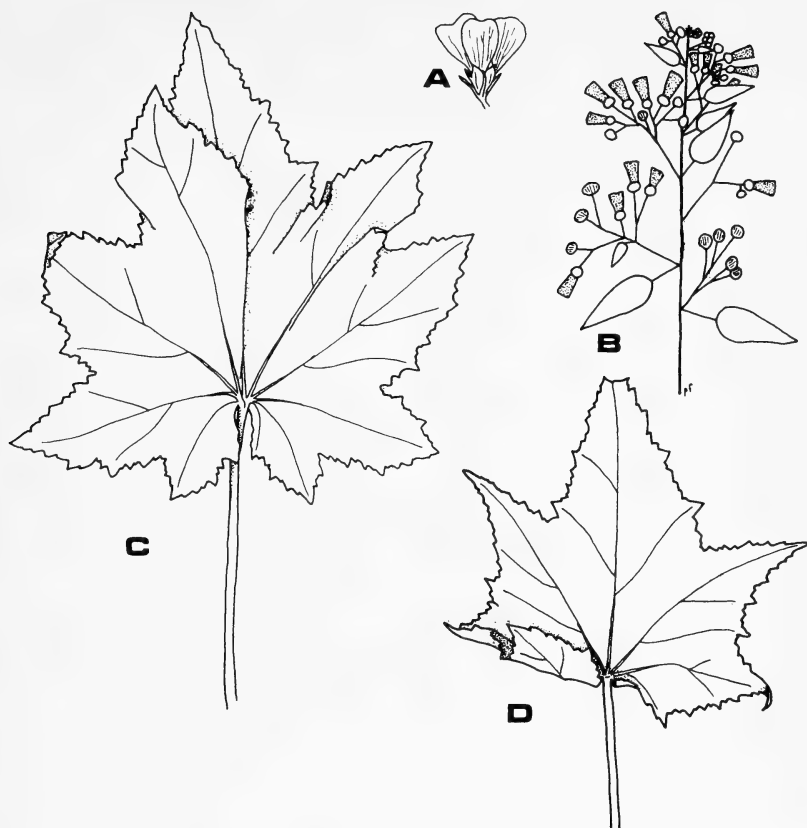
Fig. 1. *Phymosia abutiloides:* A, flower *(Holdridge 1704),* × ½; B, inflorescence diagram *(Holdridge 1704),* ¼; C, leaf *(Holdridge 1704),* × ½ D, leaf *(Mill-spaugh 2476),* × ½.

Shrub. Twigs densely yellowish-tomentose becoming moderately so; the hairs stellate, ½–1 mm diameter, 10–15 armed. Leaves up to 9 cm long, ovate to weakly 3–5 (rarely 7–) lobed, the central lobe predominant, shallowly cordate, acute, usually 7-nerved, densely stellate tomentose below, moderately to sparsely so above; leaf margins crenate, the teeth usually 1 mm long, 2 mm wide, closely spaced (4-4½ per cm), rounded, well differentiated. Petioles densely tomentose, ca. ⅓ length of lamina. Stipules 6-9 mm long, sparsely tomentose. Peduncles yellowish-tomentose, branched and paniculately multiflorate, the branch forming compound terminal panicles. Involucre of three distinct bractlets inserted at base of calyx or (often irregularly so) just below calyx on pedicel; bractlets, 4–5 mm long, 1½–2 mm wide (broadest in middle), lanceolate, moderately tomentose, often caducous. Calyx 7–10 mm long, tomentose; lobes 3 mm wide at base, 5 mm long, triangular, acute, obscurely 3-ribbed. Petals 18–20 mm long, glabrous (except densely

TABLE 3. A COMPARISON OF THREE SPECIES OF PHYMOSIA.

Character	*crenulata*	*anomala*	*umbellata*
Diam. of stellate hairs	1 mm or more	½–¾ mm	½–1 mm
No. arms of stellate hairs	5–10	10–20	10–15
Leaf length	up to 5 cm	up to 9 cm	up to 9 cm
Leaf margin	crenate	crenate	subentire
Petiole length (relative to lamina)	½–1	⅓–⅔	½–1
Inflorescence	uniflorate	uniflorate (rarely paired)	umbellate
Bract form	ovate-sessile	ovate-sessile	stipitate-spatulate
Bract width	6–8 mm	9–12 mm	4–8 mm
Calyx length	10–12 mm	16–22 mm	15–20 mm
Petal color	lavender	rose	burgundy
Petal length	2–3 cm	3–4 cm	2–3½ cm
Filament length	ca. 1 mm	2–3 mm (or petaloid)	ca. 3 mm
Style no.	ca.20	25–30	30–35
Distributor	Puebla	Hidalgo (and cult.)	Tamaulipas to Puebla

pubescent on margins of claw), lavender. Staminal column narrow (⅔ mm diameter), shorter than the petals (ca. 1 cm long), antheriferous in upper half; filaments 1–1½ mm long, numerous; anther mass somewhat elongate. Styles as many as the carpels (10–15), glabrous; stigmas glabrous, capitate. Fruit globular, 8 mm diameter; mericarps 10–15, reniform, 8 mm long. Seeds 2 mm long. Figs. 2, 9.

Specimens examined. MEXICO: Oaxaca: Yavesía, 6500 feet alt., *Galeotti 4088* (BR-3 sheets).

The type of *P. floribunda (Mühlenpfordt,* s.n.) is not among the holdings of the Halle herbarium. Presumably it was kept in Berlin and is now lost. No duplicates of Mühlenpfordt's specimen have yet been located in other herbaria. Schlechtendal's description, however, is ample and matches well the specimen of Galeotti, cited above, on which the preceding description is based. In view of the unlikelihood of discovering additional material of Mühlenpfordt's collection (isotypes), the designation of Galeotti's specimen as neotype is regarded as a satisfactory typification of this name. This view is reinforced by the knowledge that Mühlenpfordt resided in Yavesia for the two years that he was in Mexico while employed at the mining operations in the Ixtepeji region of Oaxaca (Mühlenpfordt, 1839). Since he complained of his inability to visit other parts of Mexico (except for his trip to the Pacific coast, February 2–March 10, 1829), it seems probable that his collection of *P. floribunda* was made in the general vicinity of his residence in Ya-
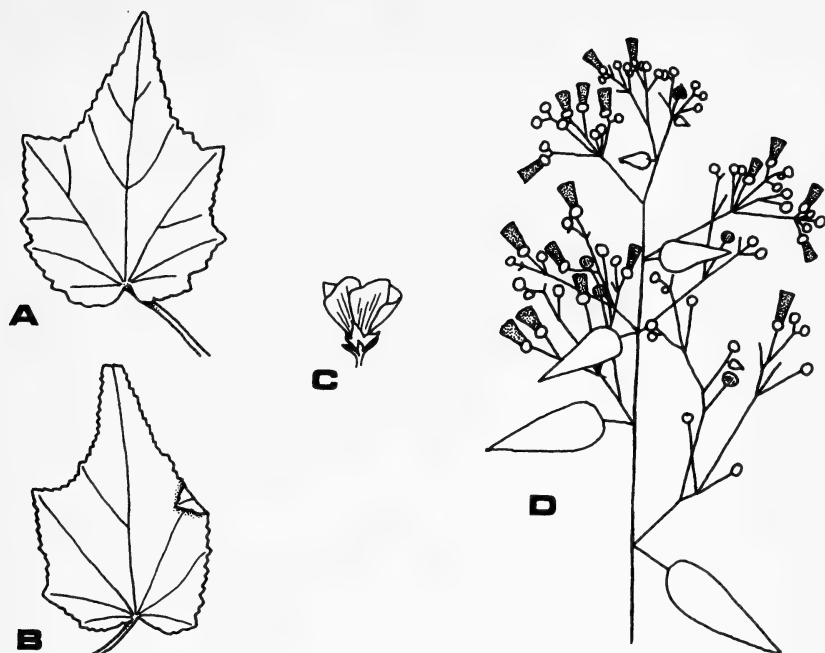
FIG. 2. *Phymosia floribunda:* A-B, leaves *(Galeotti 4088),* × ½; C, flower *(Gale-otti 4088),* × ½; D, inflorescence diagram *(Galeotti 4088),* × ¼.

vesia. The neotype, thus, is from the type locality—and indeed from the only known locality for this species.

Phymosia floribunda is closely allied to *P. abutiloides,* as these two species are the only paniculate-flowered representatives of *Phymosia.* They may be distinguished not only geographically but in several morphological characters as well. *Phymosia floribunda* occurs in north-central Oaxaca rather than in the Caribbean, and at relatively higher elevation (ca. 2000 m) than *P. abutiloides.* Yavesía, the type locality, is approximately 40 km NE of the city of Oaxaca.

Phymosia floribunda appears to have excellent potential as an ornamental shrub, because of the large amount of flowers produced on its abundant panicles. Efforts should be made to recollect this species and bring it into cultivation.

3. **Phymosia crenulata** (Brandg.) Fryxell, comb. nov. *Sphaeralcea crenulata* Brandg. Univ. Calif. Publ. Bot. 3:384. 1909. [Type: MEX-ICO: Puebla: Barranca Cerro de Paxtle, *Purpus 2601* (UC).]

Shrub. Twigs densely yellowish-tomentose becoming glabrate in age; the hairs stellate, 1 mm in diameter or more, 5–10 armed. Leaves up to 5 cm long, about as wide, cordate, 3–5 lobed (or sometimes simply pentagonal), the central lobe the largest, obtuse or sometimes acute, 5–7
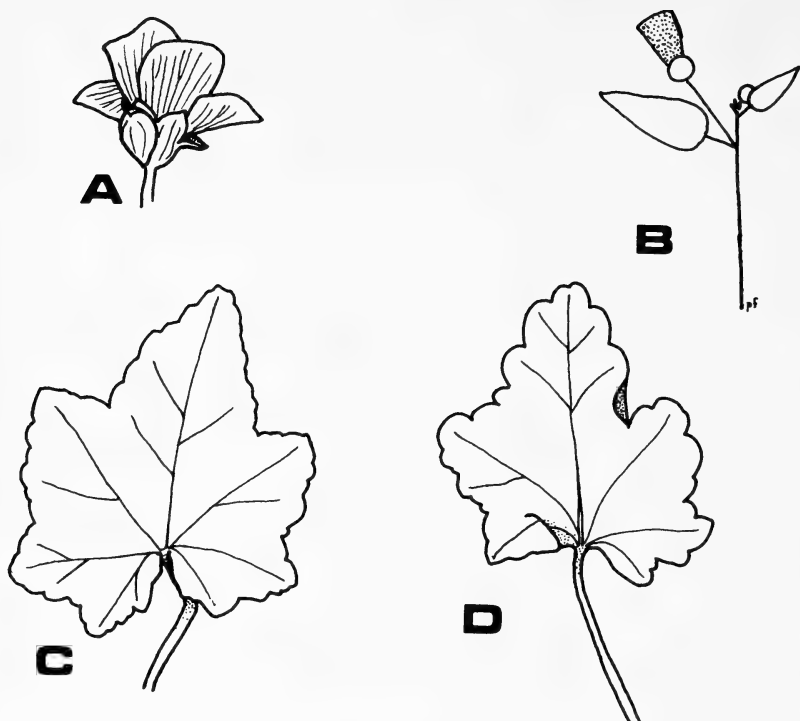
Fig. 3. *Phymosia crenulata:* A, flower *(Purpus 2601a)*, × ½; B, inflorescence diagram *(Purpus 2601a)*, × ¼; C, leaf *(Purpus 2601a)*, × ½; D, leaf *(Purpus 2601)*, × ½.

nerved, moderately tomentose below, sparsely so above, the stellate hairs of the upper surface often with a reduced number of arms; leaf margins coarsely crenate, the teeth rounded or rarely acutish and clearly differentiated, usually 3–4 mm wide (less commonly 2–5 mm wide), 1–2 mm long. Petioles densely yellowish-tomentose, ½ length of lamina to equaling lamina. Stipules 4–9 mm long, sparsely to moderately tomentose (in contrast to adjacent stem and petiole which are densely so). Peduncles 1½–4 cm long, densely yellowish-tomentose, usually (always?) uniflorate, the branch sometimes forming a short terminal raceme; pedicel 1 cm or less. Involucre of 3 bractlets inserted at base of calyx, densely yellowish-tomentose, mostly enclosing bud; bractlets 10–14 mm long, 6–8 mm wide, broadly ovate to lanceolate, sessile, caducous at anthesis. Calyx 10–12 mm long, densely yellowish-tomentose; lobes 4–5 mm wide at base, 6–7 mm long, rounded and slightly apiculate, 3-nerved. Petals 2–3 cm long, glabrous except pubescent at very base of claw where joined to the androecial column, lavender. Staminal column ca. 1 cm long; filaments very short (often <1 mm); pollen yellow-orange. Styles several (ca. 20); stigmas asymmetrically capitate rather than decurrent,
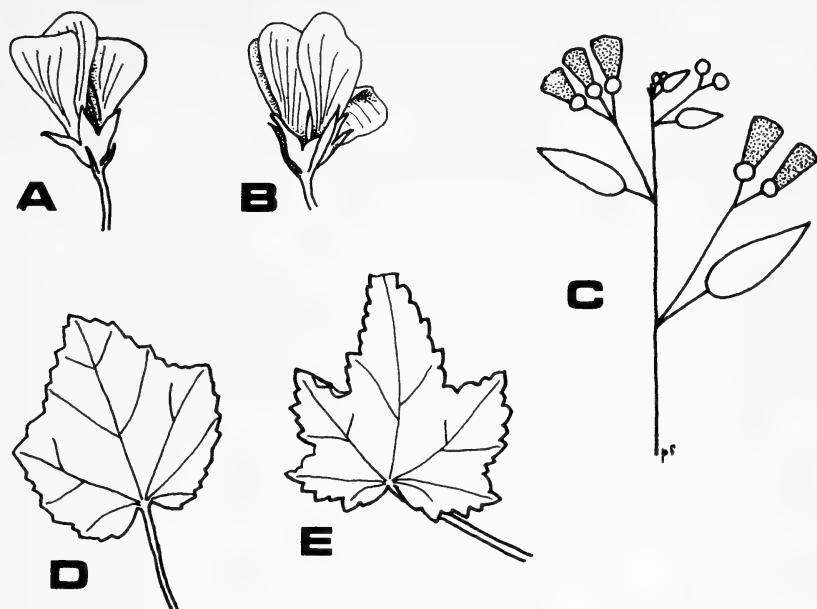
Fig. 4. *Phymosia pauciflora:* A, flower *(Coulter 800)*, × ½; B, flower *(Stanford, et al. 836)*, × ½; C, inflorescence diagram *(Stanford, et al. 836)*, × ¼; D, leaf *(Coulter 800)*, × ½; E, leaf *(Stanford, et al. 836)*, × ½.

pallid. Fruits unknown. Figs. 3, 9.

Specimens examined. MEXICO: Puebla: Barranca Cerro de Paxtle, *Purpus 2601* (UC), vicinity of San Luis Tultitlanapa (near Oaxaca), *Purpus 2601a* (GH, MO).

Phymosia crenulata is poorly known. The two specimens cited were collected from the state of Puebla, Mexico, both in the near vicinity of Tehuacán (Sousa 1969).

4. **Phymosia pauciflora** (Bak. f.) Fryxell, comb. nov. *Sphaeralcea floribunda* (Schlecht.) Walp. var. *pauciflora* Bak. f. J. Bot. 31:365. 1893. [Type: MEXICO: Hidalgo: Zimapan, *Coulter 800.*]

Presumably a shrub; flowering branches slender, densely stellate-canescent on young growth, sparsely pubescent on older twigs. Leaves 4–7 cm long, about as broad, stellate-pubescent, more densely so below than above, cordate, palmately 7-nerved, crenate or dentate, shallowly 3-lobed to moderately 5-lobed (and aceriform), acute. Petiole stellate-pubescent, ½–⅔ length of lamina. Stipules 4–8 mm long, less than 1 mm broad, sparsely pubescent. Inflorescence a 1–3 flowered axillary umbel; peduncles 3–5 cm long; pedicels 1–2 cm long, stellate- pubescent; each flower subtended by 3 distinct involucral bracteoles that are caducous shortly after anthesis; bracteoles 6–11 mm long, 1–4 mm broad, somewhat irregularly inserted below calyx tube, lanceolate, moderately pubescent. Calyx densely pubescent, 10–14 mm long; lobes
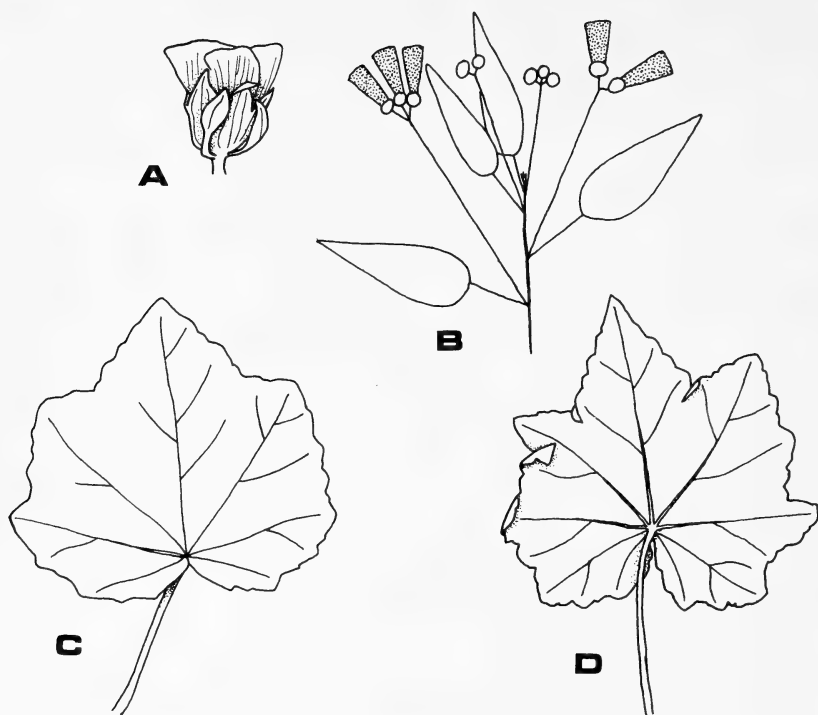
Fig. 5. *Phymosia umbellata:* A, flower, × ½; B, inflorescence diagram *(Pringle 6241),* × ¼; C, leaf *(Pringle 6241)* × ½; D, leaf *(Sessé & Mociño s.n.),* × ½.

weakly costate, acute or slightly acuminate. Petals 2–3 cm long, 1½ cm wide, apically notched, obovate and gradually narrowed below, glabrous except densely pubescent on margin of claw, lavender. Staminal column 7–9 mm long, antheriferous on upper part of column; filaments 1–2 mm long. Styles 12–16, glabrous; stigmas capitate (often obliquely so). Fruit oblate, 8–11 mm long, 12–14 mm diameter; mericarps reniform, stellate-pubescent. Figs. 4, 9.

Specimens examined. MEXICO: Hidalgo: Zimapan, *Coulter 800* (GH, K [as photo, F]); Tamaulipas: in hills 19 km SE of Miquihuana on road to Palmillas in narrow, deep and moist arroyo. Fls. orchid. Elevation 2250 m. Latitude 23°40′ N, 99°41′ W, *L. R. Stanford, K. L. Retherford, & R. D. Northcraft 836,* 11 Aug 1941 (ARIZ, GH, MO).

The two specimens cited above differ appreciably in leaf form, those of *836* being clearly aceriform, while those of *800* are only shallowly lobed. The bracteoles of *800* are also somewhat shorter than those of *836.* In other respects the two are similar.

Number 836 (MO-1221254) bears a manuscript name of a new species in *Sphaeralcea* by I. M. Johnston, but this name was never published to my knowledge.

5. PHYMOSIA UMBELLATA (Cav.) Kearn. Leafl. West. Bot. 5:190. 1949. *Malva umbellata* Cav. Icones 1:64, t. 95. 1791, non Bert., 1829. [Type: *Sessé & Moçiño* s.n. (MA-2 sheets, seen as photo, MO).] *Sphaeralcea umbellata*. (Cav.) G. Don, Gen. Syst. 1:465. 1831. *Sphaeroma umbellatum* (Cav.) Schlecht. Linnaea 11:352. 1837. *Sphaeralcea galeottii* Turcz. Bull. Soc. Nat. Mosc. 31:186. 1858. [Type: Veracruz: Tlachichuca, al pie del Volcán, *Galeotti 4102* (BR-3 sheets).]

Shrub or tree 2–6 m high. Twigs densely yellowish-tomentose, or sometimes sparsely so; the hairs stellate, ½–1 mm diameter, 10–15 armed, often stipitate. Leaves up to 9 cm long (14 cm in *Steyermark 31715*), cordate, 5 (–7) angled or shallowly lobed, acute, 7–9 nerved, densely to moderately tomentose below (rarely glabrate), sparsely tomentose to glabrate above; leaf margins coarsely and shallowly crenate, sometimes undulate to subentire, the teeth typically much broader than long, widely spaced (1–2½ per cm), acute to rounded, often not clearly differentiated. Petioles tomentose, ½ length of lamina to equaling lamina. Stipules tomentose, 4–7 mm long. Peduncles 4–13 cm long, sometimes branching below the articulation of the pedicels, yellowish-tomentose, 1–4 (commonly 3-) flowered, umbellate; pedicels ½–2 cm long. Involucre of 3 distinct bractlets inserted at the base of the calyx; bractlets 1–2 cm long, 4–8 mm wide, spatulate, abruptly narrowed below to form a clearly defined stipe (or rarely sessile and lanceolate), moderately pubescent to glabrate without, usually persistent. Calyx 1½–2 cm long, densely yellow-tomentose; lobes 6–8 mm wide at base, 6–15 mm long, triangular to ovate, acute, 3-ribbed. Petals 2–3½ cm long, glabrous except ciliate on margin of claw, burgundy or rarely paler. Staminal column narrow (2 mm diameter), shorter than the petals, antheriferous only in upper half; filaments ca. 3 mm long, numerous; anther mass subglobose or somewhat elongated; pollen yellow or orange. Styles numerous (30–35), ascending strigose below; stigmas unilaterally decurrent or obliquely capitate. Fruit oblate, 2–2½ cm diameter; mericarps 30–35, reniform, 8–17 mm long. Seeds 3 mm long. Chromosome number, $n = 17$. Figs. 5, 9.

Specimens examined. MEXICO: without locality: *Sessé & Moçiño* s.n. (MA-2 sheets, seen as photo, MO); Tamaulipas: Las Yucas, ca. 40 km NNW of Aldama, *Dressler 1903* (GH, MICH, MO), 10 miles SSW of Ciudad Victoria, *Moran 10039* (UC); Veracruz: Atoyac, *E. Kerber 150* (BR, US), Tlachichuca, *Galeotti 4102* (BR, P-as photo), near Jalapa, *Fryxell 619* (CTES, NY, TAES), cerca de los Baños de Carrizal (=Emiliano Zapata) entre Jalapa y Veracruz, *Paray 2899* (ENCB); San Luis Potosí: 15 km E of Rayón, *Rzedowski 24494* (ENCB, MICH), Tamasopo Canyon, *Pringle 3965* (BR, DS, ENCB, F, GH, MICH, UC, US), *3609* (GH), *Puig 3646* (ENCB), 15–20 km W of Ciudad Valles, *Lukejahr* s.n. 14 Oct 1967 (TAES), near Ciudad del Maiz, *C. & E. Seler 783* (GH); Hidalgo: Zimapan, *Coulter 801* (GH), SW of Tamazunchale (SLP) near state line, *Fryxell 697* (TAES), 20 mi NE of
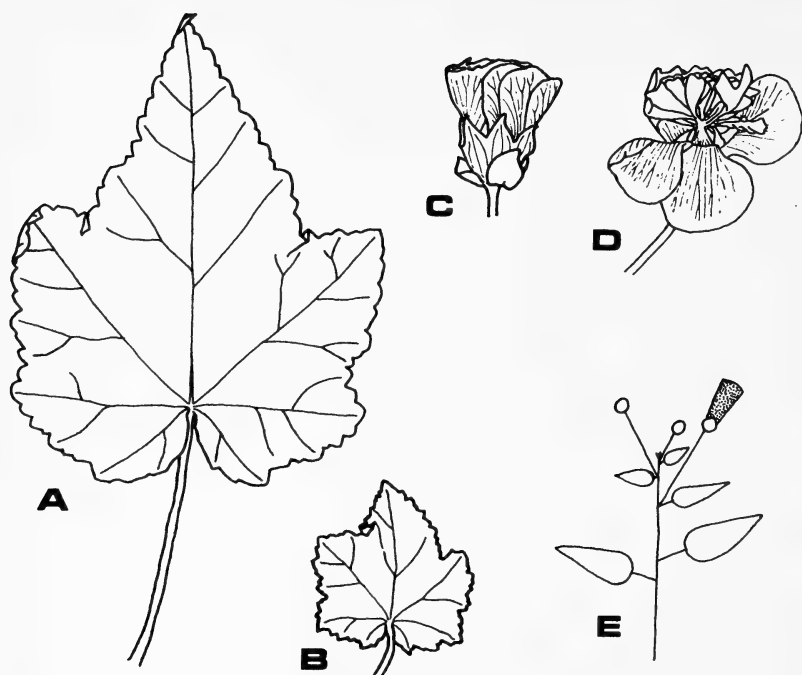
Fig. 6. *Phymosia anomala:* A, leaf *(Bates, Blanchard & Fryxell 1636),* × ½;
B, leaf *(Martinez 15054),* × ½; C, flower *(Martinez 16054),* × ½; D, flower
(showing petaloid staments of double flower) *(Bates, Blanchard, & Fryxell 1636),*
× ½; E, inflorescence diagram *(Bates, Blanchard & Fryxell 1636),* × ¼.

Jacala, *Fryxell 1070* (DS, F, GH, MICH), S of Jacala, *Carlson 2800*
(F), near Zacualtipan, *Moore 5411* (GH, UC); Puebla: near Tehua-
cán, *Rose & Hay 5945* (GH, US) *Rose, Painter & Rose 11244* (GH,
US) *Pringle 6241* (BR, ENCB, F, GH, MICH, MO, UC, US) *Conzatti
2197* (F, GH) *Liebmann 1205* (US) *Fryxell & Bates 920* (BH, OXF),
vicinity of Puebla, *Arsène 7108* (US) *7101* (US) *C. & E. Seler 834*
(ENCB, GH, US); Distrito Federal: Chapultepec [cult.?], *Paray 236*
(ENCB). GUATEMALA: Dept. Chiquimula: montaña Nonja, *Steyer-
mark 31715* (F). In cultivation: Europe, May 1872 (US–11779), Riv-
erside, California, *Kearney 210* (US).

Kearney's specimen, cultivated at Riverside, California, is evidently
the voucher specimen for Webber's (1936) chromosome count of this
species.

The distribution of *P. umbellata* is primarily along the eastern slopes
of central Mexico, except for one anomalous specimen from Guatemala.
The altitudinal range of *P. umbellata,* 800–2100 m altitude, is lower than
that of *P. anomala* or *P. rosea.*

6. **Phymosia anomala** Fryxell, spec. nov. Frutex 3–4 m altus. Ramunculi dense stramini-tomentosi, pilis stellatis ½–¾ mm diam., 10–20 ramosis, saepe stipitatis. Folia usque ad 4 cm longa, circa quam latiora, cordata, 3–5-lobata vel angulata, acuta, 7-nervata, stellato-tomentosa infra, sparse stellato-tomentosa supra; margines foliorum crenati, dentibus latioribus quam longioribus, arcte dispositis (ca. 6 in quoque cm), rotundatis, aliquantim vel valde distinguilibus inter se. Petioli dense tomentosi (canescentes), circa ⅓ longiores quam laminae. Stipulae tomentosae, 4 mm longae, subulatae. Pedunculi stramini-tomentosi, axillares, uniflorentes, usque ad 5 cm longi, incrassati apicem versus, prope centrum bracteola parvula (1–2 mm). Involucra trimera, ad basem calycum inserta; bracteolae involucrorum late ovatae, aliquantum imbricatae, 10–13 mm longae, 9–12 mm latae, sessiles, acutae, sparse tomentosae, per anthesin persistentes. Calyces 16–20 mm longi, dense tomentosi; lobi calycum 6–7 mm lati ad basem, 6–8 mm longi, ovati-acuminati, 3-nervati. Petala 3–3½ cm longa, praeter in unguibus longis ciliatis (pilis 1–2 mm) glabra, rosea vel vinosa in sicca. Columna staminalis quam petala brevior, 2 mm diam., antherifera in dimidio supero; fila 2–3 mm longa, numerosa (in floribus duplicibus excepto, in quibus petaloideis); cumulus antherarum subglobosus; pollen flavum. Styli numerosi (25–30), saltem apicem versus glabri; stigmata secundatim decurrentia vel oblique capitata. Fructus ignotus. Fig. 6.

Holotype. MEXICO: Hidalgo: Real del Monte, *M. Martínez 15054*, Aug 1946 (MO-1313132).

Many of the characters of *Phymosia anomala* recombine or are intermediate between those of *P. crenulata* and *P. umbellata*. I have therefore prepared a detailed comparison of these three species in Table 3.

The type locality, Real del Monte, is about 10 km northeast of Pachuca, Hidalgo, at an elevation of about 2600 meters. For reasons best known to cartographers, this locality appears on most maps as Mineral del Monte. The collection site of the type specimen, a single-flowered plant with normal (not petaloid) stamens, is not known with exactness. I have, however, collected a double-flowered specimen of this species (*1672*), growing as a houseyard cultigen, in the city of Real del Monte. The same double-flowered cultigen has been collected in Pátzcuaro, Michoacán (*1636*), and has been observed (though not collected) in Los Lirios, Coahuila (east of Saltillo). Doubtless, it is widely distributed in cultivation, but curiously has not otherwise been found among the herbarium collections that I have studied.

The double-flowered cultigen produces no fruits and hence must be propagated vegetatively. It has evidently been distributed widely by this means, even beyond the known range of the genus (to Coahuila). It is not possible to say much about the natural distribution of the species, however, or about the origin of the cultivar, since the single-flowered form is known only from a single specimen. The altitudinal range appears to be approximately 2000–2600 meters.

Specimens examined. MEXICO: Hidalgo, Real del Monte, *Martínez 15054* (MO), *Bates, Blanchard & Fryxell 1672* (BH, CTES, MEXU, NA); Michoacán: Pátzcuaro, in houseyard, *Bates, Blanchard, & Fryxell 1636* (BH, CTES, ENCB).

7. Phymosia rosea (DC). Kearn. Leafl. W. Bot. 5:190. 1949. *Malva rosea* DC. Prodr. 1:435. 1824. [Type: Calque des Dessins de la Flore du Mexique de Moçiño et Sessé . . ., No. 58 (F, G, US).] *Sphaeroma roseum* (DC). Schlecht. Linnaea 11:352. 1837. *Malvastrum roseum* (DC). Hemsl. Biol. Centr. Amer. Bot. 1:100. 1879. *Sphaeralcea umbellata* var. *rosea* (DC.) Bak. f. J. Bot. 31:367. 1893. *Sphaeralcea rosea* (DC.) Standl. Contr. U.S. Natl. Herb. 23:767. 1923. *Meliphlea vitifolia* Zucc. Abh. Math.—Phys. Cl. Königl. Bayer. Akad. Wiss. 2:360. 1837. [Type: in caldariis, *Zuccarini* s.n. (BR-3 sheets, M-5 sheets, seen as photo).] *Sphaeralcea vitifolia* (Zucc.) Benth. & Hook. ex Hemsl. Biol. Centr. Amer. Bot. 1:114. 1879. *Sphaeroma vitifolium* (Zucc.) Kuntze, Rev. Gen. Pl. 1:74. 1891. *Sphaeralcea nutans* Scheidw. ex Planch. in Fl. des Serres 7:221. 1851–2. [Type: Planchon, loc. cit., t. 726.] *Sphaeroma nutans* (Scheidw.) Kuntze, Rev. Gen. Pl. 1:74. 1891. *Sphaeralcea schenckii* Ulbr. Notizbl. Bot. Gart. Berlin-Dahlem 11:523. 1932. [Type: *Schenck 97* (B-probably lost).]

Shrub or small tree, $1\frac{1}{2}$–10 m high. Twigs densely (rarely sparsely) tomentose; the hairs stellate, $\frac{1}{4}$–1 mm diameter, 10–35 armed, pallid to yellowish, often stipitate. Leaves up to 14 cm long, cordate, crenate, 3–7 (usually 5-) lobed (the central lobe the largest), acuminate, 7–9 nerved, densely tomentose below (hairs stellate), sparsely so above (hairs sometimes simple and more or less distally oriented) or sometimes glabrate above; leaf margins clearly and distinctly crenate or dentate, the teeth about as broad as long, closely spaced (4–5 per cm), acute to rounded, clearly differentiated. Petioles densely tomentose (sometimes sparsely so), pallid or yellowish, $\frac{1}{2}$ length of lamina to equaling lamina. Stipules sparsely to moderately tomentose, 6–13 mm long. Peduncles 4–17 cm long, sometimes branching below the articulation of the pedicels, yellowish-tomentose, 1–3 flowered, umbellate, the branch sometimes forming few-flowered terminal panicles. Involucre $1\frac{1}{2}$–$2\frac{1}{2}$ cm long, inserted at base of calyx, sometimes enclosing bud as a gamophyllous tube, sometimes of 3 distinct, cuneate, broadly lanceolate bractlets 1–2 cm wide, moderately tomentose to glabrate, the persisting stellate hairs often reduced; involucre often caducous at anthesis. Calyx $2\frac{1}{2}$–4 cm long, splitting in fruit, densely yellow-puberulent; lobes 8–15 mm wide at base, 2–$2\frac{1}{2}$ cm long (rarely shorter), triangular, acute or acuminate, 3–5 ribbed. Petals $3\frac{1}{2}$–7 cm long, glabrous even at base of claw, rose or white. Staminal column narrow (2–3 mm diameter), usually shorter than the petals but sometimes exserted, antheriferous only in upper half; filaments ca. 3 mm long; anther mass elongate; pollen yellow. Styles numerous (30–40), glabrous or sometimes ascending-strigose; stigmas
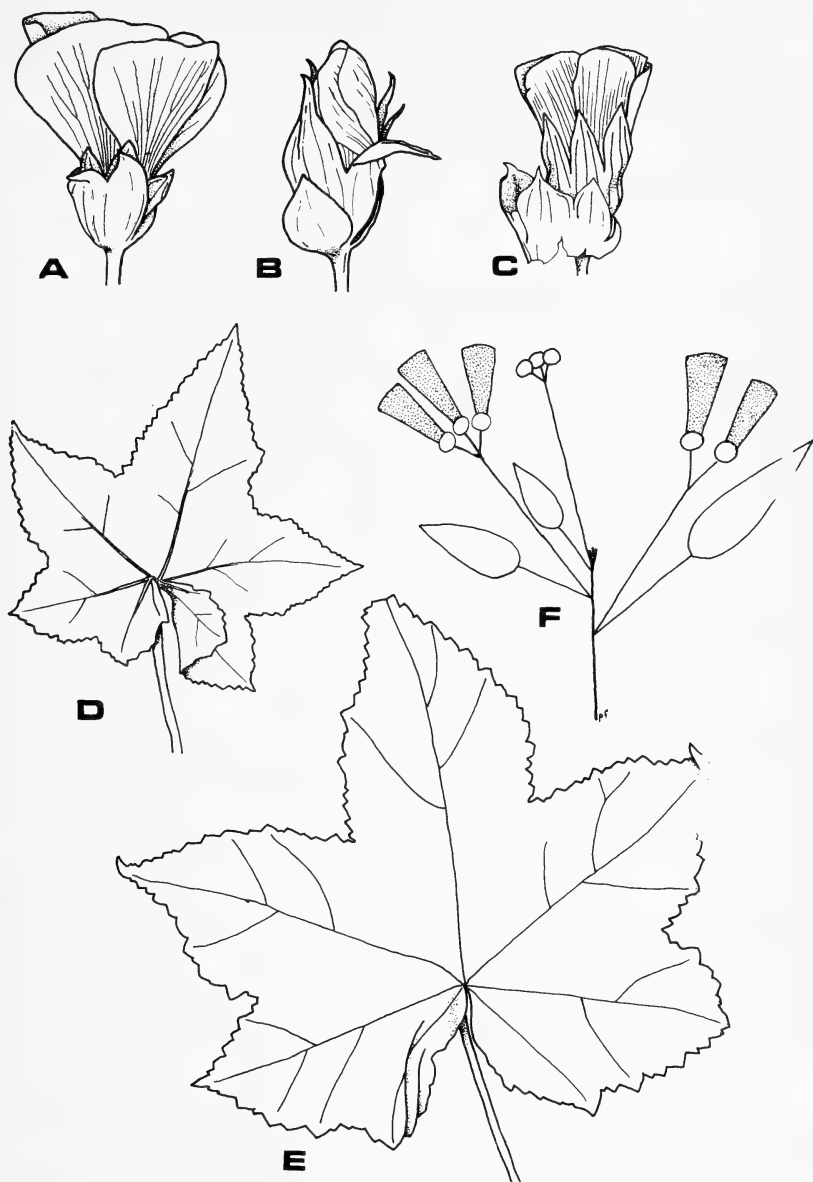
FIG. 7. *Phymosia rosea:* A, flower *(Skutch 1025)*, × ½; B, flower *(Hinton 8946)*, × ½; C, flower *(Hinton 15423)*, × ½; D, leaf *(Matuda 4637)*, × ½; E, leaf *(Zuccarini* s.n.*)*, × ½; F, inflorescence diagram *(Hinton 3800)*, × ¼.

unilaterally decurrent, glabrous. Fruits oblate, 2–3½ cm diameter; mericaps 30–40, 15–32 mm long. Seeds 3 mm long. Figs. 7, 9.

Specimens examined. MEXICO: without locality, *Liebmann 1208* (UC, US), *Sartorius 8000* (US); Veracruz: Orizaba, *Botteri 898* (GH),
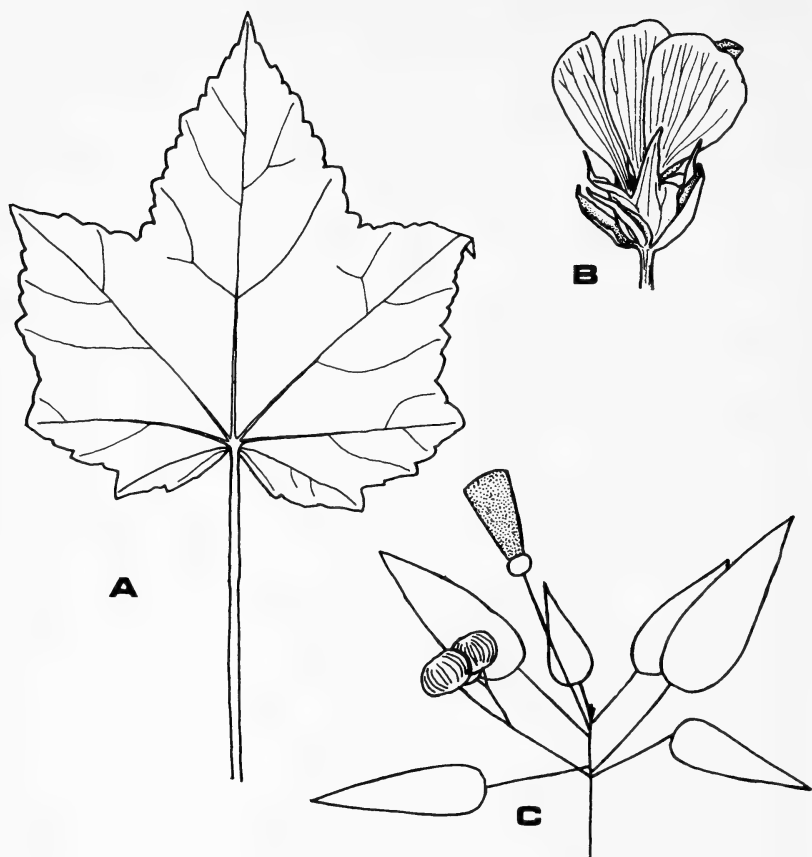
Fig. 8. *Phymosia rzedowskii* (all *Rzedowski 24187*): A, leaf, × ½; B, flower, × ½; C, inflorescence diagram, × ¼.

Lomagrande, Mt. Orizaba, *Balls 5369* (US); Jalisco: near Autlán, *McVaugh 23098* (ENCB, MICH); Michoacan: Tancitaro (Distr. Uruapan), *Hinton 15720* (F, GH, MO, NA, UC, US), Patamban, *Nelson 6553* (GH, US); Guerrero: 3 km SW de Omiltemi (munic. Chilpancingo), *Rzedowski 23602* (ENCB), near Camotla (munic. Chichihualco), *Rzedowski 16459* (ENCB, MICH) *18016* (ENCB, MICH, TEX), Filo de Caballos (munic. Chichihualco), *González Quintero 36* (ENCB); Mexico: Distr. Temascaltepec: Cajones, *Hinton 3035* (US), *5421* (F, GH), *5597* (MICH), *7468* (US), *7469* (GH, US), *7471* (UC, US), *8946* (ARIZ, F, GH, US), *15423* (GH, NA, UC, US), Cumbre *Hinton 5781* (US), *7481* (DS), *8632* (GH, US), San Miguel, *Hinton 5593* (GH), Tequesquipan, *Hinton 3800* (F, GH-2 sheets), Cerro de Sacromonte, cerca de Amecameca, *Hernández* s.n., 5 Aug 1967 (ENCB); Puebla: Alta Luz, *Purpus 2628* (UC); Oaxaca: near Suchixtepec, *Rzedowski 19655* (ENCB), between Juchatengo and San Gabriel Mix-

tepec, *McVaugh 22466* (ENCB, MICH); Chiapas: in cult., Zinacantan, *Laughlin 356* (DS, MICH), Mt. Male near Porvenir, *Matuda 4637* (MO), near San Cristóbal, *Nelson 3236* (US-2 sheets), Chiquihuite, *Matuda 2835* (F, GH, MICH, MO, NA, US); GUATEMALA: Dept. Huehuetenango: near Nentón, *Nelson 3236* (GH), between San Miguel Acatan and Soloma, *Skutch 1025* (F, GH, US), San Mateo Ixtatán, *Breedlove 8710* (DS), *11572* (DS), Todos los Santos, *C. & E. Seler 2733* (GH, US), San Pedro Soloma, *Moncure* s.n., Aug 1950 (F), Huehuetenango, *Standley 65724* (F), La Sierra (Tujimach) across river from San Juan Atitlan, *Steyermark 52008* (F, US); Dept. El Quiché: Sacapulas, *Hawkes* et al. *1745* (F); Dept. San Marcos: NW of San Marcos, *Steyermark 35588* (F); Dept. Totonicapan: between San Francisco El Alto and Momostenango, *Standley 83982* (F, US) *84087* (F); Dept. Chimaltenango: NW of Patzún, *Fryxell 1196* (DS, NA, US), Chichivac, *Skutch 391* (US); Dept Sacatepequez: near Antigua, *Kellerman 7100* (F); Dept. Guatemala: Volcán de Pacaya, *Standley 80500* (F), in cult. *J. Donnell Smith 1902* (US), in cult. Las Calderas, *Standley 58303* (F); Dept. Jalapa: Volcán Jumay, *Steyermark 32393* (F), Montaña Miramundo, *Steyermark 32799* (F); Dept. Alta Verapaz: Purulha, *Cook & Doyle 90* (F, US). In cultivation: *Zuccarini* s.n. (BR, M).

This taxon, as here defined, is a highly variable one. Others may dispute the conservative interpretation I have adopted. However, I was unable to resolve the variation within this taxon into discrete entities, a difficulty that Standley and Steyermark (1949) experienced with the Guatemalan material. Initially I envisioned three taxa, separated principally on the form of the involucre and the relative development of the calyx. This interpretation was found to correlate very poorly, if at all, with geographical distribution; a further search for correlated morphological characters (flower color, fruit size, type of vestiture, form of leaf serration, etc.) proved fruitless. The possibility of defining even infra-specific taxa (one, say, with a gamophyllous involucre, another with three, discrete involucral bractlets), which at first glance seems obvious, cannot be substantiated by closer scrutiny.

This type of variability, where the patterns are not abruptly discontinuous, is in part characteristic of the genus (and of other malvaceous genera) and in the present instance is perhaps accentuated by the history of cultivation of *P. rosea*. This species has the largest, showiest flowers of the genus, more than one flower-color form, and probably a long history of cultivation (cf. Standley and Steyermark, 1949). I have made no intensive study of the history of cultivation of this species, but I suspect it has been grown as an ornamental since pre-Columbian times. A broader range of variability is to be expected in a plant with such a history of cultivation.

The vernacular names that have been recorded for *P. rosea* include "Malvavisco" *(Hinton 4109)* and "Malvon" *(Hinton 3800)* in Mexico;

Fɪɢ. 9. Generalized distribution map of species of *Phymosia,* excepting *P. anomala,* numbered as in text.

and "Aguamecate" *(Steyermark 32799),* "Amapola" *(Standley 58303, 65724, Steyermark 52008),* "Ech" (also *Steyermark 52008),* and "Amanda" (Standley and Steyermark 1949) in Guatemala.

Phymosia rosea is found at relatively high elevations from Guatemala on the south to the Mexican state of Jalisco on the north, primarily on the Pacific watershed. It is only sporadically represented in the intervening regions, possibly because areas that are at sufficiently high elevation for this species have not been as well explored botanically. *P. rosea* has been collected at elevations of 1600 m to over 3000 m.

8. **Phymosia rzedowskii** Fryxell, sp. nov. Frutex usque ad 4 m altus. Ramunculi dense tomentosi; pilis stellatis, ½ mm diam., 15–20 ramosis, pallidis, saepe stipitatis praesertim in petiolis ubi stipites usque ad 1 mm longi sunt. Folia usque ad 12 cm longa, cordata, crenata, plerumque 5-lobata, acuta vel acuminata, 7–9 nervata, moderate tomentosa infra (pilis stellatis), sparse tomentosa supra (pilis numero brachiorum deminutis, brachiis plus minusve ascendens); margines foliorum crenati perspicue, dentibus latioribus quam longioribus, inter se semotis (1–3 in quoque cm), rotundatis, manifeste distinguilibus inter se. Petioli tomentosi, quam laminae ½–⅔ longiori. Stipulae moderate tomentosae, ca. 1 cm longae. Pedunculi 7–13 cm longi, interdum ramificantes infra articulos pedicellorum, stramini-tomentosi, 1–3 florentes, umbellati. Involucra ad basem calycum inserta, persistentia in statu fructendo; bracteolae involucrorum 3, distinctae, 20–30 mm longae, 4–11 mm latae, sessiles, lanceolatae, sparse stellato-tomentosae. Calyces 25–35 mm longi, dense stramini-tomentosi; lobi calycum 8–13 mm lati ad basem, 15–20 mm longi, triangularis, acuti vel acuminati, 3-costati. Petala 5–6 cm longa, 3–3½ cm lata, praeter in margine unguium ciliatis (pilis usque ad 2 mm) glabra, atrovinosa. Columna staminalis quam petala brevior, 2½ mm diam., antherifera in dimidio supero; fila 5–6 mm longa; cumulus antherarum elongatus; antherae vinosae; pollen

flavum. Styli numerosi (30–35), glabri (saltem supra); stigmata secun-
datim decurrentia, glabra. Fructus oblati, 3–4 cm diam.; carpida
30–35, reniformia, complanata, 25–30 mm longa. Semina 3 mm longa.
Figs. 8, 9.

Holotype. MEXICO: México (Estado de): 2 km al SE de San Pablo
Ixayoc, munic. de Texcoco; fondo de cañada con vegetatión de bosque
de *Alnus* con *Abies, Fraxinus,* y *Quercus;* arbusto de 4 m de alto; flores
de color rojo vino obscuro; alt. 2600 m, *Rzedowski 24187,* 3 Aug 1967
(ENCB; isotypes ENCB, MICH).

Phymosia rzedowskii is known only from the type collection. It
recombines certain of the characters of *P. umbellata* and *P. rosea,* but
is evidently distinct from either. It has burgundy petals with ciliate
claws like the former species, but has flowering and fruiting structures
(petals, calyx, carpels) of a size comparable to the latter species. Its
involucral bracteoles are distinctive, as are its long filaments and purple
anthers.

EXCLUDED SPECIES

Phymosia acerifolia (Greene) Rydberg = *Iliamna rivularis* (Dougl.)
Greene
Phymosia crandallii (Rydb.) Rydb. = *Iliamna crandallii* (Rydb.)
Wiggins
Phymosia cuspidata (Britt.) Britt. = *Sphaeralcea cuspidata* Britt.
Phymosia grandiflora (Rydb.) Rydb. = *Iliamna grandiflora* (Rydb.)
Wiggins
Phymosia longisepala (Torr.) Rydb. = *Iliamna longisepala* (Torr.)
Wiggins
Phymosia remota (Greene) Britt. in Britt. & Brown = *Iliamna remota*
Greene
Phymosia rivularis (Dougl.) Rydb. = *Iliamna rivularis* (Dougl.)
Greene

LITERATURE CITED

BARKER, H. D., and W. S. DARDEAU. 1930. Flore d'Haiti. Port-au-Prince.
BATES, D. M. 1968. Generic relationships in the Malvaceae, tribe Malveae. Gentes
    Herb 10:117–135.
————. 1969. Systematics of the South African genus Anisodontea Presl (Mal-
    vaceae). Gentes Herb. 10:215–383.
————., and O. J. BLANCHARD, JR. 1970. Chromosome numbers in the Malvalves.
    II. New and otherwise noteworthy counts relevant to classification in the Mal-

vaceae, tribe Malveae. Amer. J. Bot. 57:927–934.

BRITTON, N. L., and C. F. MILLSPAUGH. 1920. The Bahaman Flora. New York.

CHAUDHURI, S. K. 1965. Pollen morphological studies of the order Malvales. II. Bull. Bot. Soc. Bengal 19:147–158.

DILLENIUS, J. J. 1732. Hortus Elthamensis. London.

FRYXELL, P. A. 1972. A revision of the genus Robinsonella (Malvaceae). Gentes Herb. (in press).

GRISEBACH, A. H. R. 1859. Flora of the British West Indian Islands. London.

HAMILTON, W. 1825. Prodromus Plantarum Indiae Occidentalis. London.

KEARNEY, T. H. 1935. The North American species of Sphaeralcea subgenus Eusphaeralcea. Univ. Calif. Publ. 19:1–128.

————. 1951. The American genera of Malvaceae. Amer. Midl. Naturalist. 46: 93–131.

MUHLENPFORDT, E. A. E. 1839. Ausflug an die Ufer der Südsee in Frühjahr 1829. Ausland 12:361–362; 366–367; 370–371; 374–375; 378–379; 609–610; 614–615; 618–619; 622–623; 625–627; 630–631; 634–635; 637–639; 642–643; 646–648; 673–674; 678–679; 681–683; 685–687; 689–690.

PERSOON, C. H. 1807. Synopsis plantarum. 2:250.

SAVAGE, S. 1945. A catalogue of the Linnaean Herbarium. Taylor & Francis Ltd. London.

SCHMIDT, H. 1965. Der "Hortus Elthamensis" aus der Bibliothek Carl von Linnes. Feddes Repert. Spec. Nov. Regni Veg. 70:69–108.

SKOVSTED, A. 1935. Chromosome numbers in the Malvaceae. I. J. Genet. 31:263–296.

SOUSA SÁNCHEZ, M. 1969. Las colecciones botánicas de C. A. Purpus en México, periodo 1898–1925. Univ. Calif. Publ. Bot. 51:1–36.

STANDLEY, P. C. 1923. Trees and shrubs of Mexico. Contr. U. S. Natl. Herb. 23: 767–768.

————., and J. A. STEYERMARK. 1949. Flora of Guatemala. Fieldiana, Bot. 24(b): 381–383.

TAKHTAJAN, A. 1969. Flowering plants origin and dispersal. Smithsonian Institution Press, Washington.

WEBBER, J. M. 1936. Chromosomes in Sphaeralcea and related genera. Cytologia 7:313–323.

WIGGINS, I. L. 1936. A resurrection and revision of the genus Iliamna Greene. Contr. Dudley Herb. 1:213–229.

REVIEWS

Manual of the Vascular Plants of Texas. By DONOVAN S. CORRELL and MARSHALL C. JOHNSTON. Frontispiece, xvi + 1881 pp., 2 maps. Contributions from Texas Research Foundation, Vol. 6, Texas Research Foundation, Renner, Texas 75079. 1970. $35.00.

The state of Texas has a most strategic position within North American biogeography and this is one especially important reason why the availability of a *Manual of the Vascular Plants of Texas* is welcomed by biologists.

The *Manual* is meritorious, however, for many other reasons, one being that Texas is one of the last major land areas in the United States without a concise flora, despite the fact that Texas is a rich state and has been so for a long time.

But now the *Manual* has been published, it is in our hands, and its comprehension and quality are a fair reward for our patience. The task was certainly not a minor one: it embraces 4839 species plus 540 infraspecific taxa and hybrids, distributed among 1216 genera in 174 families. These figures place Texas as having the second largest state flora, coming close after California with 5675 species in 1075 genera.

The richness of the Texas flora is overwhelmingly due to the diversity of its physiographic and climatic provinces, the distribution of which is closely reflected by the vegetation areas, well represented by Frank W. Gould's map, which has been reproduced. Forests, priaries and different kinds of xerophilous shrubs occupy vast areas, the coastal belt has its characteristic plants and the southern part of the state is strongly influenced by tropical elements.

From a point of view of a Mexican botanist, it was interesting to learn how useful the *Manual* is in the identification of plants of northern and northeastern parts of our country. I purposely delayed the preparation of this review, waiting for an opportunity to use the book with a set of plants collected in some drier areas of Mexico. Such an opportunity came eventually and I must report that out of 150 specimens from eastern Chihuahua and Durango about 85% could be determined by means of the *Manual* without difficulty and these identifications were checked with herbarium specimens. This is certainly a very positive feature of the work.

In general arrangement the *Manual* can be compared in many aspects with P. A. Munz' *A California Flora,* although most of the descriptions are somewhat longer, the sequence of families is different and there are no plant illustrations in the text. Another important difference is the large number of contributed treatments, which amount to 60 different taxonomic groups and almost as many contributors. So many different criteria necessarily disrupt the uniformity of a flora, but this lack of uniformity, especially in details, is also evident in the groups prepared by the two co-authors. On the other hand, the assistance of specialists in many critical taxonomic groups contributes in a very significant way to strengthening the value and usefulness of the work as a whole.

After what has been said, it seems almost superfluous to state that the *Manual* offers keys to all families, genera, species, and distinguished infraspecific taxa. Descriptions include known English and other local names, as well as ecological and economic data. The geographic distribution is detailed for Texas and usually also for neighboring areas. Included is a glossary of technical terms and a list of abbreviated authors' names, including pertinent biographical data, both mostly compiled from *A California Flora.* The introduction discusses main floral features of the different regions of the state.

Some minor aspects of the flora are not free from criticism. In the keys, for instance, undue effort has been made to avoid repeating of a taxon in a given key. This was perhaps an editorial requirement, but it must be kept in mind that the keys are the most essential part of a flora and no effort should be spared to make them as workable and useful as possible. A more practical key to the genera of the Compositae, for instance, could be desired.

On the whole, it must be stated that Correll and Johnston are to be congratulated on their great achievement of providing us with a modern and scholarly *Manual of the Vascular Plants of Texas.* It will constitute one of the fundamental resources for the proposed *Flora North America* and in the somewhat further future, of a *Flora of Mexico.*

The graphic presentation of this *Manual* is pleasant and the text is almost free of errors. The price of the book is unfortunately higher than one would have liked.—J. RZEDOWSKI, Escuela Nacional de Ciencias Biológicas, México, D. F., Mexico.

Botanico-Periodicum-Huntianum. Edited by George H. M. Lawrence, A. F. Günther Buchheim, Gilbert S. Daniels, and Helmut Dolezal. 1063 pp. Hunt Botanical Library, Pittsburgh, Penn. 1968. Available through Stechert-Hafner Service Agency, 31 E. 10th St., New York, N.Y. 10003. $30.00.

Book reviews should probably be more current than this one. However, *Botanico-Periodicum-Huntianum* is not something that one can read quickly and evaluate, much less at bed time. After having used *B-P-H* for three years, I think that I can say something informative about it.

Botanico-Periodicum-Huntianum is a compendium of titles and their unambiguous abbreviations of "information on all periodical (serial) publications that regularly contain . . . articles dealing with the plant sciences and botanical literature . . ." The editors have produced an excellent, accurate, and most helpful reference work. To be sure there are some omissions, for instance, I cannot find *The Blue Bird* listed. In time, though, those who are interested in *B-P-H* will send additions and corrections to the Hunt Library. The beauty of *B-P-H* is that the information in it is also stored in a computer, hence corrections, additions, and new editions, can be accomplished easily. *Botanico-Periodicum-Huntianum* is an excellent example of the intelligent use of computer technology.

The names of many journals are short and one can agree with E. D. Merrill in his essay "One-Name Periodicals" (Brittonia 1:1–5. 1931) on the appropriateness of one-word titles. Certainly for the sake of convenience, briefness, and ease of use, such titles as *Rhodora, Madroño, Castanea, Erythea, Muhlenbergia, Sida, Brittonia, Nemophila, Werdenda, Torreya, Watsonia,* and *Aliso,* to mention only a few, are preferable to longer names. There is nothing wrong with *Bulletin of the Torrey Botanical Club, Annals of the Missouri Botanical Garden,* or *Transactions of the Linnean Society of London,* but they are more cumbersome. By and large, though, it is governments that create the worst bibliographic nightmares. In the United States, the Department of Agriculture, which includes the Forest Service, is a particularly bad offender. Is it any wonder that many librarians do not like to work in "government documents"?

Some may object to the way in which journal titles have been abbreviated. For instance some may object that the *Botanical Gazette* is abbreviated to *Bot. Gaz. (Crawfordsville)*. But this is bound to happen once a system is set up to insure completely unique and unambiguous abbreviations. Consistency has been said to be the hobgoblin of little minds. Perhaps in some situations it is, but in the writing of dictionaries, glossaries, floras, and *B-P-H*'s, consistency is of the utmost importance. Without it why even bother? Consistency is important in such works, and I have yet to hear anyone demand that "n" come before "m."

The editors of *B-P-H* and the Hunt Library, now officially known as the Hunt Institute for Botanical Documentation, are to be congratulated on this fine and most important compendium.—John H. Thomas, Department of Biological Sciences, Stanford University, Stanford, California 94305.

MADROÑO

Contents

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

THE SIGNIFICANCE OF NILES CANYON IN THE PHYTOGEOGRAPHY OF THE COAST RANGES OF CENTRAL CALIFORNIA

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Introduction

Purpose. The purpose of this report is to describe the flora which occur in the Niles Canyon area and to interpret from the observations the significance of the area in the phytogeography of the Coast Ranges of Central California.

Ninety native species which occur on Mount Diablo have not been reported from the Mount Hamilton Range. And at least 100 species of native plants which occur in the Mount Hamilton Range do not occur on Mount Diablo or in the North Coast Ranges. The nature of the barriers which have resulted in this distribution are not understood. Bowerman (1944, p. 71), points out that, ". . . speculation is unprofitable until the exact distribution of the various species in the intermediate areas has been determined in detail." Niles Canyon is one of these intermediate areas.

Because it forms a topographic break in the Diablo range, it has been suggested that Niles Canyon may also represent a physical barrier in the north-south distribution of plants. This could be determined by comparing the plants found in Niles Canyon with those found to the north and south. A barrier or "break" would be found to exist only if the vegetation to the north differed materially from that to the south.

Niles Canyon was chosen as an area for research in the hope it would contribute to understanding some of these problems in the phytogeography of the Coast Ranges.

Location and Topography. Niles Canyon lies within the Diablo Range and is approximately 25 miles south of the city of Oakland on the southeast side of the San Francisco Bay. The canyon connects the Sunol Valley (sometimes referred to as part of the Livermore Valley) with the coastal plain and forms a topographic break between two subdivisions of the Diablo Range, the Contra Costa Hills (sometimes called the Oakland or Berkeley Hills) to the north and the Mount Hamilton Range to the south.

Niles Canyon is approximately five miles long. At Sunol Valley the elevation is 200 feet. The average slope through Niles Canyon is 24 feet per mile (U.S. Army Corps of Engineers, 1961). The area discussed in this report extends to the top of the ridge on the south, an elevation of 1,200 feet and up the Walpert and Sunol Ridges on the north to an elevation of 1,400 feet (fig. 1).
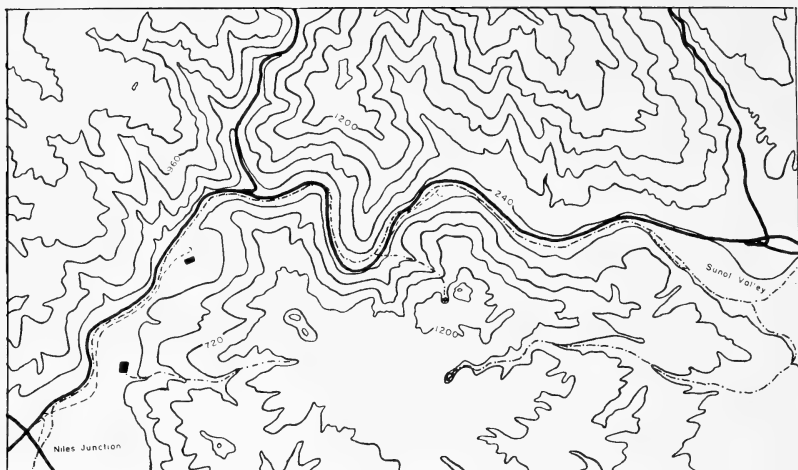
Fig. 1. Map of Niles Canyon.

Climate. Niles Canyon has a Mediterranean climate. Rain is concentrated in the winter months and the summers are dry. The major storms occur between December and March (U.S. Army Corps of Engineers, 1961). No temperature records for Niles Canyon are available, but it is the investigator's impression that the temperature extremes are less severe than those which occur in the Livermore Valley, where mean temperatures range from 32 to 55 degrees Fahrenheit during the winter months and from 70 to 100 degrees Fahrenheit during the summer months (Hall, 1958).

Geology. Most of the surface area in Niles Canyon is composed of Lower Cretaceous rocks, alternating sandstone, sandy shale, shale, and some conglomerate lenses for which the name "Niles Canyon formation" has been proposed (Hall, 1958). Niles Canyon has been selected as the type section because of accessibility and the excellent exposures which occur there. The thickest section has been measured in Niles Canyon. A 7,500 foot section lies between the eastern branch of the Mission fault and Stonybrook fault.

Recent alluvium covers the floor of the canyon at the western end. Recent terrace deposits occur above the present stream course in this same area.

The following account of the geologic history of the area is given by Hall (1958). During the Mesozoic, Franciscan rocks of Jurassic age were uplifted and deformed. This was followed by a time of erosion and deposition of the Lowest Cretaceous massive coarse Oakland conglomerate. With the wearing down of the terrain, the sediments became finer, and several thousand feet of strata of the Niles Canyon formation were de-

posited. During the Cenozoic, from the Eocene to the Upper Miocene, the seas transgressed and regressed several times as erosion, deposition, and uplift occurred. In the Late Miocene, nearby uplift caused the slow regression of the San Pablo seas. By the Late Pliocene, intense folding and faulting had occurred which destroyed the Piocene basins, and resulted in tight or overturned folds. Faulting, erosion, and alluviation continue to the present. Headward growth of the stream valleys and canyon cutting are now the dominant processes.

The strike-slip feaults in the Pleasanton area developed in response to north-south maximum stress (Hall, 1958). The Mission fault parallels the base of the hills that rise from the coastal plain. Two branches of the fault occur 3,250 feet and 4,750 feet northeast of the Niles Canyon-Mission Boulevard intersection. The trace of the Stonybrook fault follows the course of the stream in Stonybrook Canyon.

Drainage. Alameda Creek is the major stream which flows through Niles Canyon. It drains 695 square miles of the Coast Ranges. Alameda Creek arises in Santa Clara County at an elevation of 3,200 feet and flows northwesterly about 25 miles to enter Niles Canyon. It then flows westerly five miles to the west end of the canyon and discharges across the coastal plain into the bay. The principal tributaries are Calaveras Creek and San Antonio Creek, which flow from the south and join upstream from Sunol and Arroyo de la Laguna, which flows from the north and joins Alameda Creek near the head of Niles Canyon. The valley at the eastern end of the canyon was once a shallow lake bordered by marsh land. This was drained by deepening the outlet and constructing a channel across the old lake bed. The artesian wells which occurred on the drained lake bed were once an important source of water for the Spring Valley Water Company. Although the water table in this area has dropped, the Niles Canyon formation is still one of the area's most important aquifers.

Method of Investigation. The field work upon which this report is based was done between June of 1967 and May of 1970. Over 1000 collections of plants from the Niles Canyon area were made. These specimens have been mounted and are deposited in the Dudley Herbarium of Stanford University. Aerial photographs taken in 1968 and a topographic map of Niles Quadrangle (7½ minute series) were invaluable aids in carrying out this field work.

Initially, a card catalogue of the plants which occur north and south of Niles Canyon was assembled. The references used were Bowerman's *The Flowering Plants and Ferns of Mount Diablo, California* and Sharsmith's *Flora of the Mount Hamilton Range of California.* As plants were collected in Niles Canyon, the information was incorporated into the catalogue. Ultimately, it was possible to interpret from the observations the significance of Niles Canyon in the phytogeography of the Coast Ranges.

The Plant Communities

The term "plant community" as used in this report is defined as a characteristic assemblage of plants. It is not to be confused with the term as used in an ecological sense nor as it is used by other writers. The four plant communities recognized in Niles Canyon are: a grassland community, a riparian community, an oak-woodland community, and a sagebrush community. Plants tolerant of greater environmental diversity may occur in more than one community, while less tolerant plants will be restricted to one.

The Grassland Community. Grasslands cover the crests of the hills and extend down the slopes on either side of the canyon. On the more mesophytic north-facing slopes, the grassland gives way to brush and oak-woodland. On the drier south-facing slopes, it may extend to the canyon bottom where it meets the riparian community or it may give way to patches of the sage community. These grasslands have been heavily grazed by sheep and cattle. This has favored the spread of introduced species at the expense of the native plants. The greatest number of species occurs in the grassland community.

A list follows: *Avena fatua, Briza minor, Bromus carinatus, B. mollis, B. rigidus, B. rubens, Festuca dertonensis, F. idahoensis, F. myuros, Hordeum vulgare, H. leporinum, Lolium multiflorum, Calochortus albus, Chlorogalum pomeridianum, Brassica geniculata, Capsella, bursa-pastoris, Lepidium nitidum, Sisymbrium officinale, Lotus subpinnatus, L. purshianus, Lupinus bicolor, L. succulentus, Medicago sativa, Trifolium hirtum, T. incarnatum, T. subterraneum, T. tridentatum, Vicia sativa, Erodium botrys, E. circutarium, E. moschatum, Geranium dissectum, G. molle, Sidalcea malvaeflora, Viola pedunculata, Camissonia ovata, Clarkia purpurea, C. unguiculata, Brodiaea congesta, B. laxa, B. pulchella, Muilla maritima, Sysyrinchium bellum, Eriogonum nudum, Rumex acetosella, Calandrinia ciliata, Montia perfoliata, Cerastium viscosum, Silene gallica, Stellaria media, Ranunculus californicus, Eschscholzia californica, Lomatium utriculatum, Sanicula bipinnata, S. bipinnatifida, Convolvulus arvensis, Amsinckia intermedia, A. menziesii, Plagiobothrys canescens, Collinsia heterophylla, Orthocarpus purpurascens, O. pusillus, Plantago erecta, Achyrachaena mollis, Agoseris grandiflora, A. heterophylla, Carduus tenuiflorus, Centaurea melitensis, Hemizonia luzulifolia, Hypochaeris glabra, Lagophylla ramosissima, Madia sativa, Microseris douglasii, Silybum marianum, Wyethia angustifolia,* and *W. helenioides.*

The Riparian Community. Alameda Creek, which flows through Niles Canyon supports a highly developed riparian community. Many species are restricted to this perennial stream, but others, such as *Acer macrophyllum,* may extend far up the north-facing slopes. The character of

the vegetation changes along intermittent streams and gullies and is dependent upon the amount of water available throughout the year.

The trees and shrubs which occur in the riparian community are: *Populus fremontii, P. trichocarpa, Salix ssp., Alnus rhombifolia, Juglans hindsii, Plantanus racemosa, Ailanthus altissima, Acer negundo californicum, A. macrophyllum, Umbellularia californica, Schinus molle, Rhamnus californica, Rhus diversiloba, Aesculus californica, Sambucus mexicana, Vitis californica, Cornus glabrata, Buddleia davidii,* and *Nicotiana glauca.*

The herbaceous species include the following: *Equisetum hiemale* var. *affine, Typha angustifolia, T. domingensis, Echinochloa cruz-galli, Gastridium ventricosum, Paspalum distichum, Polypogon interruptus, Carex nudata, Cyperus eragrostis, Scirpus olneyi, S. microcarpus, Juncus ssp., Urtica holosericea, Polygonum lapathifolium, P. punctatum, Chenopodium ambrosioides, Clematis ligusticifolia, Rorippa nasturtium-aquaticum, Rubus procerus, Lotus strigosus, Melilotus albus, M. indica, Smilacina racemosa amplexicaulis, S. stellata sessifolia, Epilobium adenocaulon, Ludwigia peploides peploides, Berula erecta, Plantago major, Marah fabaceus, Aster exilis, Baccharis glutinosa, B. viminea, Solidago occidentalis, Vinca major, Cynoglossum grande, Lippia nodiflora rosea, Verbena lasiostachys, Stachys pycnantha, Solanum nodiflorum, Kickxia spuria, Mimulus pilosa, Cotula coronopifolia, Erigeron philadelphicus, Gnaphalium luteo-album, Helenium puberulum, Senecio mikanioides,* and *Xanthium strumarium.*

The Oak-Woodland Community. This community is characteristic of the nower north-facing slopes and is also present in the gullies and ravines of the south-facing slopes. *Quercus agrifolia* is the dominant tree of this community. Commonly associated with it is *Aesculus californica.* In the moister areas, *Umbellularia californica* is an important constituent. *Quercus lobata, Arbutus menziesii* and *Acer macrophyllum* are present in the dense woodland area which occurs on the north-facing slopes at the eastern end of the canyon.

The trees and shrubs of this community are: *Quercus agrifolia, Q. lobata, Umbellularia californica, Acer macrophyllum, Aesculus californica, Eucalyptus globulus, Arbutus menziesii, Lonicera hispidula, Holodiscus discolor, Osmaronia cersiformis, Rhamnus californica, Symphoriocarpus albus laevigatus, S. mollis, Grossularia californica, Photinia arbutifolia, Rhus diversiloba,* and *Rosa gymnocarpa.*

The herbaceous species include the following: *Adiantum jordanii, Pellaea andromedifolia, Melica torreyana, Lithophragma affinis, L. heterophylla, Saxifraga californica, Fragaria californica, Bowlesia incana, Heracleum maximum, Sanicula crassicaulis, Dodecatheon hendersonii, Eucrypta chrysanthemifolia, Nemophila heterophylla, Phacelia nemoralis, Pholistoma auritum, Satureja douglasii, Solanum umbelliferum, Galium*

aparine, G. nuttallii, Aster chilensis, Montia perfoliata, Ranunculus hebecarpus, Lathyrus vestitus puberulus, Achillea millefolium, Osmorrhiza chilensis, Polypodium californicum, Dryopteris arguta, Pteridium aquilinum pubescens, Chlorogalum pomeridianum, Fritillaria lanceolata, and *Calochortus albus.*

The Sage Community. Patches of a sage community are present on the dry, rocky, south-facing slopes. *Artemisia californica* is the dominant plant in this community and in places forms almost pure stands. *Photinia arbutifolia* and *Diplacus aurantiacus* are common associates. In the gullies, *Quercus agrifolia* and *Umbellularia californica* may be present. *Eriodictyon californicum* is rare. Although closely related, the sage community is more open than that of the chaparral. The least number of species occurs in the sage community.

A list follows: *Artemisia californica, Photinia arbutifolia, Diplacus aurantiacus, Eriophyllum confertiflorum, Lotus scoparious, Eriogonum nudum, Mentzelia lindeyi, Quercus agrifolia, Umbellularia californica, Rhus diversiloba, Rhamnus californica, Eriodictyon californicum,* and *Zauschneria californica.*

Content and Geographical Relationships of the Flora

The vascular plants of Niles Canyon comprise 361 species. The following summary indicates their taxonomic position.

	Family	Genus	Total	Species Native	Introduced
Pteridophyta	2	8	8	8	0
Monocotyledonae	7	36	63	37	26
Dicotyledonae	57	191	290	190	100
Totals	66	235	361	235	126

Twenty native species were collected in Niles Canyon which are reported from Mount Diablo but not from the Mount Hamilton Range.

A list follows: *Acer negundo californicum, Artemisia douglasiana, Berula erecta, Brickellia californica, Bromus laevipes, Clematis ligustifolia, *Convolvulus occidentalis, Conyza canadensis, *Equisetum hiemale affine, Fragaria californica, Clarkia purpurea viminea, *Gnaphalium purpureum, *G. microcephalum, Heracleum maximum, *Lythrum californicum, Madia gracilis, *Oenothera hookeri, Perideridia kelloggii, Pteridium aquilinum, Scirpus microcarpus,* and *Solanum nodiflorum.*

All except those with asterisks occur south of Alameda Creek. It should be noted that at least five of the six species which are restricted to the north side of Alameda Creek are sun loving plants which prefer a southern exposure and this fact possibly accounts for their not being collected on the north-facing slopes. Sharsmith (1945, p. 293) established Alameda Creek as the northern boundary for the Mount Hamilton Range. Therefore, at least those plants occurring south of Alameda Creek must be considered as belonging to the flora of Mount Hamilton.

The following is a list of the twenty-one native species collected in Niles Canyon that have been reported from the Mount Hamilton Range but not from Mount Diablo: *Amsinckia menziesii, *Aster chilensis, Calochortus albus, *Carex nudata, *Castilleja affinis, *Chrysopsis oregona, Corethrogyne filaginifolia, Distichlis spcata stricta, Heliotropium curassavicum oculatum, Hemizonia pungens, Lotus strigosus, *Mentzelia laevicaulis, M. lindleyi, *Mimulus pilosa, Muilla maritima, Plagiobothrys canescens, *Polystitchum munitum, Populus trichocarpa, *Salix melanopsis, Sidalcea malvaeflora, *Stachys ajugoides, *Verbena lasiostachys,* and *Wyethia angustifolia.*

Those with asterisks are species which Bowerman (1944, p. 71) indicates are to be expected on Mount Diablo. The remaining ten species must be considered in terms of their general distribution and the kinds of habitats they occupy to determine if Niles Canyon does indeed represent any sort of a break. Unless otherwise noted the habitats and ranges given will be those recorded by Munz (1959; 1968).

Amsinckia menziesii occurs occasionally in dry grassy areas away from the immediate coast from San Diego Co. to Washington, Idaho, and Utah. *Heliotropium curvassavicum oculatum* is common in saline or alkaline soils below 6,700 feet throughout California to Oregon, Utah, and Nevada. *Lotus strigosus* commonly occurs in dry disturbed places below 5,000 feet in many plant communities from Marin, Sutter, and Tuolumne counties south to Lower California. *Plagiobothrys canescens* is found on grassy slopes and flats below 4,500 feet from Siskiyou Co. south along the west base of the Sierras, the Central Valley, and the South Coast Ranges. *Populus trichocarpa* occurs along streams below 9,000 feet from San Diego Co. to Alaska and western Nevada. *Muilla maritima* is present in many plant communities from Glenn to San Diego counties. Niles Canyon does not appear to create a barrier to the north-south distribution of these six species. Mount Diablo affords the proper habitats and lies within the normal range of distribution. It is possible these species do occur on Mount Diablo and that their presence has been overlooked.

Corethrogyne filaginifolia is restricted to slopes below 1,000 feet and occurs most frequently along the coast. *Sidalcea malvaeflora* is another species commonly restricted to coastal areas. It has been observed on the northwest end of Shell Ridge although not on Mount Diablo proper (Bowerman, 1944, p. 70). Apparently these two species do not have a sufficiently broad range of climatic tolerance to allow them to reach as far inland as Mount Diablo.

Mentzelia lindleyi occurs in the Sage and Foothill-Woodland Communities of the South Coast Ranges from Alameda County to Santa Clara County and Stanislaus and Fresno counties. This species reaches its highest development in the Mount Hamilton Range, its type locality (Sharsmith 1945, p. 347). No specimens of *M. lindleyi* deposited in the Dudley Herbarium at Stanford University were collected from localities north of the Mount Hamilton Range. *Hemizonia pungens* occurs in the

interior dry valleys and foothills below 1,000 feet from the San Joaquin Valley to Kern County. It reaches its northern limit in the Mount Hamilton Range (Sharsmith 1945, p. 317). Niles Canyon is apparently the northernmost area reached by these two species.

To summarize: Twenty native species were collected in Niles Canyon that are reported from Mount Diablo but not from the Mount Hamilton Range. At least fourteen of these species must be considered as part of the Mount Hamilton flora. Twenty-one species of native plants were collected in Niles Canyon which also occur in the Mount Hamilton Range but are not reported on Mount Diablo. Eleven of these are expected to occur on Mount Diablo and six others could possibly occur there. Niles Canyon does not create a barrier to the north-south distribution of these species. Two species are restricted to more coastal areas and do not reach so far inland. *Hemizonia pungens* and *Mentzelia lindleyi* apparently reach the northern limit of their distribution in Niles Canyon, and are the only native species which occur to the south and not to the north of Niles Canyon. The vegetation to the north does not differ significantly from that to the south. Therefore, Niles Canyon does not represent a break in the phytogeography of the Coast Ranges of Central California.

Annotated Catalogue of the Vascular Plants

On the following pages is a list of the vascular plants which occur in Niles Canyon. The habitat or locality is given for each species. All the specimens upon which this study is based are deposited in the Dudley Herbarium at Stanford University. The references used in this case are Sharsmith's *Flora of the Mount Hamilton Range of California* (1945) and Bowerman's *The Flowering Plants and Ferns of Mount Diablo, California* (1944).

Care in making the determinations, was considered essential. Munz's *A California Flora* (1959; 1968) and Thomas' *Flora of the Santa Cruz Mountains* (1961) were the manuals most often consulted. These were supplemented by other floras and, occasionally, by monographs. In addition, herbarium specimens were consulted and in many cases the determinations were verified by other taxonomists.

EQUISETACEAE

Equisetum hiemale L. var. *affine* (Engelm.) Eaton. Occasional along banks of Alameda Creek.

POLYPODIACEAE

Adiantum jordanii Muell. Wooded shady slopes, all exposures.

Dryopteris arguta (Kaulf.) Watt. Common on wooded slopes.

Pellaea andromedifolia (Kaulf.) Fee. Oak-madrone forest, northern exposure.

Polypodium californicum Kaulf. A common fern of Niles Canyon growing in a variety of habitats, ranging from rocky banks to shaded canyon areas.

Polystichum munitum (Kaulf.) Presl. Moist shaded places, side canyons.

Pteridium aquilinum (L.) Kunh. var. *pubescens* Underw. Embankment between Niles Boulevard and Alameda Creek, north exposure.

Woodwardia fimbriata Smith. Shady side canyon, dry during the summer months.

TYPHACEAE

Typha angustifolia L. Occasionally in ditches where water collects and stands, banks of Alameda Creek where water is slow moving.

T. domingensis Pers. Banks of Alameda Creek where water is slow moving.

POACEAE

Agrostis avenaceae Gmel. Occasional in disturbed areas.

A. semiverticillata (Forsk.) Christ. Margins of Alameda Creek, and in ditches.

Avena fatua L. In grassland, disturbed areas, sometimes in open woodland, all exposures, frequent.

Briza minor L. Open grassy hillsides.

Bromus carinatus H. & A. Brush covered areas, and on grassy slopes.

B. laevipes Shear. Brush covered areas, mostly northern exposures.

B. mollis L. Common species of grassland, and roadsides, all exposures.

B. rigidus Roth. Grasslands, and disturbed areas, widespread.

B. rubens L. Disturbed areas, and on grassy slopes.

B. willdenowii Kunth. Along Alameda Creek, infrequent.

Cynodon dactylon (L.) Pers. Edges of streams and in disturbed habitats.

Distichlis spicata (L.) Green var. *stricta* (Torr.) Bettle. Alkaline areas.

Echinochloa cruz-galli (L.) Beauv. Along margins of Alameda Creek, and other moist areas.

Elymus glaucus Buckl. Frequent along streams, and on woody slopes.

E. triticoides Buckl. Moist and alkaline places.

Festuca dertonensis (All.) Aschers. & Graebn. Common grass of open slopes, and disturbed habitats, all exposures.

F. elmeri Scribn. & Merr. Wooded slopes.

F. idahoensis Elmer. Grasslands.

F. megalura L. Brush covered slopes, infrequent.

F. myuros L. Open slopes.

Gastridium ventricosum (Gouan) Schinz & Thell. Along stream bed, and probably in grasslands.

Hordeum leporinum Link. Occasional in grasslands, and in disturbed areas.

H. vulgare L. Grasslands, and disturbed areas.

Koeleria macrantha (Ledeb.) Spreng. North hillside, Sunol.

Lolium multiflorum Lam. A very common species of grasslands, and road sides.

L. temulentum L. var. *leptochaeton* A. Br. Road embankments, rare.

Melica californica Scribn. Rocky slopes, and to be expected elsewhere.

M. imperfecta Trin. Grassy slopes, and wooded hillsides, frequent.

M. torreyana Scribn. Wooded hillsides, mostly northerly exposure.

Paspalum distichum L. Margins of Alameda Creek, and in ditches.

Phalaris minor Retz. Occasional in disturbed areas.

Poa annua L. Occasional in grasslands, and more commonly in disturbed habitats.

P. scabrella (Thurb.) Benth. South facing grassy slopes, and probably elsewhere.

Polypogon interruptus HBK. Occasional along margins of Alameda Creek, and other moist places.

P. monspeliensis (L.) Desf. Common about the margins of Alameda Creek, in ditches, and other moist areas.

Pseudosasa japonica (Sieb. & Zucc.) Makino. Several clumps along Alameda Creek at Mission Boulevard, cut back at various times and still persisting.

Sorghum halepense (L.) Pers. Occasional in low, wet places.

S. sudanense (Piper) Stapf. Road embankments, escaped from cultivation as a pasture grass.

S. vulgare Pers. Grassy areas, escape from cultivation.

CYPERACEAE

Carex athrostachya Olney. Drainage ditch.

C. nudata Boott. Banks of Alameda Creek, frequent.

Cyperus eragrotis Lam. Common along the banks of Alameda Creek.

Scirpus microcarpus Presl. Occasional along the banks of Alameda Creek.

S. olneyi Gray. Infrequent along Alameda Creek.

JUNCACEAE

Juncus patens Meyer. Road embankments, north exposure, ditches where water collects and stands, shady side canyon, and grasslands.

J. xiphioides Meyer. Along streams, in ditches where water collects and stands, and at alkaline seeps.

Luzula multiflora (Retz.) Lejuene. Wooded slopes, north exposure.

LILIACEAE

Asparagus asparagoides Wight. Riparian community, escape from cultivation.

Calochortus albus (Benth.) Dougl. Common in Niles Canyon found in a variety of habitats, grassy or brush covered slopes, rocky banks, all exposures.

C. luteus Lindl. Collected at Sunol.

Chlorogalum pomeridianum (DC). Kunth. Widespread and tolerant of a wide range of conditions, in grasslands, brush-covered and rocky ground, even woodland, all exposures.

Fritillaria lanceolata Pursh. Brushy slopes of side canyon, infrequent, north exposure.

Smilacina racemosa (L.) Desf. var. *amplexicaulis* (Nutt.) Wats. Shady side canyon, north exposure, infrequent.

S. stellata (L.) Desf. var. *sessilifolia* (Baker) Henders. Shady side canyons, north exposure, both species often occurring together.

Trillium chloropetalum (Torr.) Howell var. *giganteum* (H. & A.) Munz. Under *Quercus agrifolia* at edge of grasslands, shady side canyon, north exposure, infrequent.

AMARYLLIDACEAE

Allium triquetrum L. Embankment between Old Niles Canyon Road and Alameda Creek.

Brodiaea congesta Smith. Grassy slopes, infrequent.

B. laxa (Benth.) Wats. Grassy slopes, occasional.

B. pulchella (Salisb.) Greene. Grassy slopes, the most common species of *Brodiaea* in Niles Canyon, all exposures.

Muilla maritima (Torr.) Wats. Grassy slopes, south exposure, infrequent.

IRIDACEAE

Sisyrinchium bellum Wats. A common plant of grasslands in Niles Canyon, and along roads and railroad tracks, all exposures.

SALICACEAE

Populus fremontii Wats. A common species of the riparian community throughout Niles Canyon.

P. trichocarpa T. & G. Occasional along Alameda Creek.

Salix hindsiana Benth. A fairly common species along Alameda Creek.

S. laevigata Bebb. Frequent along Alameda Creek.

S. lasiandra Benth. Occasional along Alameda Creek.

S. lasiolepis Benth. The most common species of willow in Niles Canyon, along stream margins and in side canyons.

S. melanopsis Nutt. Margins of Alameda Creek, infrequent.

BETULACEAE

Alnus rhombifolia Nutt. Occasional to abundant along Alameda Creek.

FAGACEAE

Quercus agrifolia Nee. The most common tree in Niles Canyon, occurring along Alameda Creek, along roads, on brush covered slopes, as single trees or in relatively pure stands, and in oak-madrone woodland, all exposures.

Q. lobata Nee. Occurring as individual trees, and in oak-madrone woodland. Restricted to eastern end of Niles Canyon.

JUGLANDACEAE

Juglands hindsii Jepson. Occasional tree of riparian community.

URTICEAE

Urtica holosericea Nutt. Along Alameda Creek, and side canyons where it remains moist all year.

U. urens L. Disturbed areas.

POLYGONACEAE

Eriogonum nudum Dougl. ex. Benth. Common plant of dry slopes, all exposures.

Polygonum aviculare L. Plant of disturbed areas.

P. lapathifolium L. Common along stream margins throughout Niles Canyon.

P. punctatum Ell. Stream margins of Alameda Creek.

Rumex acetosella L. Grasslands, all exposures.

R. conglomeratus Murr. Fairly common in low moist areas.

R. crispus L. Stream margins, and ditches.

R. pulcher L. Road embankment.

R. salicifolius Weinm. Along stream margins, and in ditches.

CHENOPODIACEAE

Atriplex patula L. ssp. *hastata* (L.) Hall & Clements. Stream margins, and in alkaline seep.

A. rosea L. Weed of disturbed areas.

Beta vulgaris L. Occasional in ditches.

Chenopodium ambrosioides L. var. *suffruticosum* (Willd.) Aellen. Fairly common along Alameda Creek.

C. murale L. Weed of disturbed places.

Salsola kali L. var. *tenuifolia* Tausch. Common weed of disturbed areas.

AMARANTHACEAE

Amaranthus albus L. A weed of disturbed areas.

A. retroflexus L. A weed of disturbed areas.

AIZOACEAE

Mesembryanthemum edule L. Naturalized in one area along Niles Boulevard.

M. floribundum Haw. Naturalized in one area along sand bag levee.

PORTULACACEAE

Calandrinia ciliata (R. & P.) DC. var. *menziesii* (Hook.) Macbr. Grasslands, fairly common.

Montia perfoliata (Willd.) Howell. Very common plant of moist habitats.

CARYOPHYLLACEAE

Cerastium viscosum L. Common on grassy slopes.

Silene gallica L. Common plant on grassy slopes.

Spergula arvensis L. Grasslands.

Stellaria media (L.) Cyr. A common weed of moist disturbed areas, and grassland.

RANUNCULACEAE

Clematis lasiantha Nutt. Brush covered slopes.

C. ligusticifolia Nutt. Common along banks of Alameda Creek.

Delphinium patens Benth. Edge of grasslands, north exposure.

Ranunculus californicus Benth. var. *californicus*. A common species of grasslands, open slopes, and shady canyon slopes.

R. hebecarpus H. & A. Oak woodland, north exposure.

R. muricatus L. In moist ravines, infrequent.

LAURACEAE

Umbellularia californica Nutt. A very common tree tolerant of a variety of habitats, along creek banks, in the open, in oak woodland.

PAPAVERACEAE

Eschscholzia californica Cham. Common on grassy slopes, road embankments, fields.

BRASSICACEAE

Brassica campestris L. Road embankments, and a common species of open fields, and slopes.

B. geniculata (Desf.) Ball. Road embankments, open slopes.

B. kaber (DC.) Wheeler. Weed of disturbed areas.

B. nigra Koch. Occasional in disturbed areas.

Capsella bursa-pastoris (L.) Medic. Open grassy slopes, and disturbed areas.

Cardamine oligosperma Nutt. Grassy slopes, and disturbed areas.

Dentaria californica Nutt. Shady slopes, common.

Lepidium nitidum Nutt. Grassy slopes.

L. strictum (Wats.) Rattan. Grassy slopes.

Raphanus sativus L. Along margins of streams, road embankments, open fields and grasslands.

Rorippa nasturtium-aquaticum (L.) Brit. & Rendle. Common along stream margins.

Sisymbrium officinale (L.) Scop. Common weed along road sides, and in grasslands.

Streptanthus glandulosus Hook. Dry south hillside at Sunol. Not reported from Mount Diablo.

Thelypodium lasiophyllum (H. & A.) Greene, north hillside at Sunol.

Thysanocarpus laciniatus Nutt. Brush covered slopes.

SAXIFRAGACEAE

Grossularia californica (H. & A.) Cov. & Britt. Open and partly woody slopes, north exposure.

Lithophragma affinis Gray. Moist slopes, north exposure.

L. heterophylla (H. & A.) T. & G. Moist slopes. This and the preceding species occurring together.

Saxifraga californica Greene. Rocky slopes, north exposure.

PLANTANACEAE

Plantanus racemosa Nutt. Fairly common along Alameda Creek.

ROSACEAE

Cotoneaster pannosa Franchet. Along road sides, and on brush covered slopes, infrequent.

Fragaria californica C. & S. Shady north facing slopes.

Holodiscus discolor (Pursh) Maxim. Shady wooded slopes, road embankments, north exposure mostly.

Osmaronia cerasiformis (T. & G. ex H. & A.) Greene. On wooded hillsides, and shady slopes, mostly north exposure.

Photinia arbutifolia (Ait.) Lindl. A very common shrub of Niles Canyon occurring on brush covered slopes, as member of the understory in oak-madrone woodland, and less commonly as isolated shrubs, all exposures.

Prunus amygdalus Batsch. Common along Alameda Creek, along road sides, and on open hillsides.

P. cerasifera Ehrh. Occasional on wooded north facing slopes.

Rosa californica C. & S. Along stream beds and gullies, and wooded hills.

R. gymnocarpa T. & G. Wooded, shady slopes, north exposure.

Rubus procerus Muell. ex Boulay. Common along stream banks, and road sides.

R. ursinus C. & S. Common along shady canyon bottom, and sometimes on shady north facing slopes.

FABACEAE

Cassia tomentosa L. Known from one station between Old Niles Canyon Road and Alameda Creek.

Cytissus monspessulanus L. Canyon bottom at western end.

Glycyrrhiza lepidota Pursh. var. *glutinosa* (Nutt.) Wats. Drainage ditches, and grassy flats.

Lathyrus jepsonii Greene ssp. *californicus* (Wats.) Hitchc. Infrequent along Alameda Creek.

Lathyrus vestitus Nutt. ssp. *puberulus* (Greene) Hitchc. The most common subspecies of *Lathyrus* in Niles Canyon; on brush covered slopes, road embankments, and wooded areas. Subspecies *L. v.* ssp. *bolanderi* Wats is reported from Mount Hamilton and Mount Diablo.

Lotus purshianus (Benth.) Clem. & Clem. Along stream banks, and grassy slopes.

L. scoparius (Nutt.) Ottley. A common species of dry, open places.

L. strigosus (Nutt.) Greene. Stream banks.

L. subpinnatus Lag. Common in grasslands, and occasional on wooded slopes.

Lupinus albifrons Benth. A very common species of brush covered slopes, and road embankments.

L. bicolor Lind. Frequent in grasslands, commonly observed in disturbed areas.

L. densiflorus Benth. Quite common on grassy hillsides, in side canyons, and on road sides.

L. succulentus Koch. Grassy slopes.

Medicago arabica (L.) Huds. Grassy slopes.

M. polymorpha L. var. *vulgaris* (Benth.) Shinners f. *vulgaris*. Grassy slopes, and disturbed areas.

M. polymorpha L. var. *vulgaris* (Benth.) Shinners f. *tuberculata* (Gordon) Shinners. Grassy slopes, and disturbed areas.

M. sativa L. Grassy slopes.

Melilotus albus Desr. ex Lam. Common along stream banks, and in disturbed areas.

M. indica (L.) All. Common along Alameda Creek, and in disturbed areas.

Trifolium hirtum All. Grasslands, and road sides.

T. incarnatum L. Grassy slopes.

T. subterraneum L. Grasslands.

T. tridentatum Lindl. Common clover of grassy slopes.

Vicia americana Willd. var. *oregana* (Nutt.) Nels. Brush covered areas. However, *V. americana* var. *trucata* Brew. has been reported by both Sharsmith and Bowerman.

V. dasycarpa Tenore. Occasional in disturbed areas.

V. sativa L. Frequent on grassy slopes, and in disturbed areas.

GERANIACEAE

Erodium botrys (Cav.) Bertol. Grassy slopes, very common.

E. circutarium (L.) L'Her. Grassy slopes, and disturbed areas, all exposures.

E. moschatum (L.) L'Her. Grasslands, and disturbed areas.

Geranium dissectum L. Canyon bottoms, common.

G. molle L. Canyon bottoms, grasslands.

OXALIDACEAE

Oxalis pes-caprae L. Common in disturbed areas.

O. pilosa Nutt. Grassy slopes, and road embankments.

ZYGOPHYLLACEAE

Tribulus terrestris L. Disturbed areas where the ground is hard packed.

SIMAROUBACEAE

Ailanthus altissima (Mill.) Swingle. A very common tree of the canyon bottom, especially at the western end of the canyon.

EUPHORBIACEAE

Eremocarpus setigerus (Hook.) Benth. Common plant of disturbed areas.

Euphorbia crenulata Engelm. Shady side canyon, infrequent.

E. lathyrus L. Shady north facing slopes.

E. peplus L. Disturbed areas.

E. serpyllifolia Pers. Low areas where water has stood during the spring.

ANACARDIACEAE

Rhus diversiloba T. & G. Forming an understory in oak-madrone woodlands, often forming colonies in canyon bottoms, and also in grasslands, and on rocky slopes. Tolerant of a wide range of conditions.

Schinus molle. L. Common along canyon bottom.

ACERACEAE

Acer macrophyllum Pursh. An important tree of the riparian community, also on moist wooded slopes.

A. negundo L. var. *californicum* (T. & G.) Sarg. Occasional along the margins of Alameda Creek.

HIPPOCASTANACEAE

Aesculus californica (Spach) Nutt. Canyon bottoms, and wooded hillsides, all exposures, but mostly north.

RHAMNACEAE

Rhamnus californica Esch. Brush covered slopes, and wooded areas, mostly north exposure.

VITACEAE

Vitis californica Benth. Clambering over ground, telephone poles, and other vegetation in canyon bottom and gullies, very common.

Malvaceae

Lavatera cretica L. Common along road sides.

Malva nicaeensis All. Stream banks, and in disturbed areas.

M. parviflora L. grassy slopes.

Sida leprosa (Ort.) K. Schum. var. *hederacea* (Hook.) K. Schum. Occasional in alkaline soils.

Sidalcea malvaeflora (DC.) Benth. ssp. *laciniata* Hitchc. Occasional on grassy slopes.

Violaceae

Viola pedunculata T. & G. Open grassy slopes.

Loasaceae

Mentzelia laevicaulis (Dougl.) T. & G. Occasional on south facing slopes.

M. lindleyi T. & G. A very common species of dry south facing slopes, especially east of Palomares Road.

Lythraceae

Lythrum californicum T. & G. In moist seepage area.

Myrtaceae

Eucalyptus globulus Labill. Frequent along roads, and up side canyons, seedlings common.

Onagraceae

Camissonia ovata (Nutt.) Raven. Common species of grasslands.

Clarkia concinna (F. & M.) Greene. North slope 2.5 miles west of Sunol.

C. purpurea (Curtis.) Nels. & Macbr. ssp. *viminea* (Dougl.) Lewis & Lewis. Grassy hillsides, north and west exposure.

C. unguiculata Lindl. The most common species of *Clarkia* in Niles Canyon. Brushy or grassy hillsides.

Epilobium adenocaulon Hausskn. var. *occidentale* Trel. Stream margins.

E. paniculatum Nutt. Stream banks, and grassy hillsides.

Ludwigia peploides (HBK.) Raven. ssp. *peploides*. Common in Alameda Creek.

Oenothera hookeri T. & G. Wet ground, south exposure, infrequent.

Zauschneria californica Presl. Dry hillsides and rocky banks, common. all exposures.

Apiaceae

Anthriscus scandicina (Weber) Mansf. Moist areas along stream banks.

Berula erecta (Huds.) Cov. At edges of Alameda Creek. Not reported from Mount Hamilton.

Bowlesia incana R. & P. In oak woodland, and probably elsewhere.

Conium maculatum L. Common along road sides.

Foeniculum vulgare Mill. Common in disturbed areas. Not reported from Mount Hamilton.

Heracleum maximum Bartr. Common on moist slopes, and wooded slopes.

Lomatium californicum (Nutt.) Math. & Const. On shaded slopes, north exposure.

L. utriculatum (Nutt.) C. & R. Grassy slopes, and edge of oak woodland.

Osmorhiza chilensis H. & A. In deep shade of side canyon, infrequent.

Perideridia kelloggii (Gray) Mathias. Occasional on brush covered slopes.

Sanicula bipinnata H. & A. Occasional on open grassy hillsides, all exposures.

S. bipinnatifida Dougl. Common on grassy slopes, all exposures.

S. crassicaulis Poepp. A frequent species of woodland areas, mostly northerly exposure.

Scandix pecten-veneris L. Moist areas.

Torilis nodosa (L.) Gaertn. Shady areas, and grassy slopes.

CORNACEAE

Cornus glabrata Benth. Collected at a branch of Alameda Creek, Sunol.

ERICACEAE

Arbutus menziesii Pursh. North facing wooded slopes at eastern sector of canyon in association with *Quercus, Umbellularia californica,* and *Holodiscus discolor.*

PRIMULACEAE

Anagallis arvensis L. Common in disturbed areas.

Dodecatheon hendersonii Gray. Wooded north facing slopes.

OLEACEAE

Olea europa L. Known from one station, a large grove probably cultivated in the past and still persisting.

LOGANIACEAE

Buddleia davidii Franchet. Common along road and banks of Alameda Creek.

APOCYNACEAE

Vinca major L. Common along banks of Alameda Creek.

ASCLEPIADACEAE

Asclepias fascicularis Decne. Dry slopes, and disturbed areas, all exposures.

CONVOLVULACEAE

Convolvulus arvensis L. Disturbed areas, a common weed of fields and grasslands.

C. occidentalis Gray. Very common on moist slopes and road embankments.

Cuscuta subinclusa Dur. & Hilg. Brush covered slopes, parasitic on *Rhus diversiloba*.

POLEMONIACEAE

Polemonium carneum Gray. Known from one specimen collected at summit in Stonybrook Canyon.

HYDROPHYLLACEAE

Eucrypta chrysanthemifolia (Benth.) Greene. Occasional in moist areas, mostly north exposure.

Eriodictyon californicum (H. & A.) Torr. Rare. Dry south facing slopes.

Nemophila heterophylla F. & M. Common woodland species, especially on shady north slopes, and in shady side canyons.

Phacelia imbricata Greene. Rocky slopes, and road embankments, frequent.

P. nemoralis Greene. The most common species of *Phacelia* in Niles Canyon, on wooded, shady slopes.

Pholistoma auritum (Lindl.) Lilja. Moist shady areas.

BORAGINACEAE

Allocarya bracteata Howell. Grasslands.

Amsinckia intermedia F. & M. Grassy slopes.

A. menziesii (Lehm.) Nels. & Macbr. Grasslands.

Cynoglossum grande Dougl. Shady side canyon, infrequent.

Heliotropium curassavicum L. var. *oculatum* (Heller) Tidestrom. Common plant of creek banks, and disturbed areas.

Plagiobothrys canescens Benth. Open grasslands, all exposures.

VERBENACEAE

Lippia nodiflora Michx. var. *rosea* (D. Don) Munz. Well established in moist areas along Alameda Creek.

Verbena lasiostachys Link. Fairly common along margins of Alameda Creek.

LAMIACEAE

Marrubium vulgare L. Common along road sides.

Melissa officinalis L. Shady slopes.

Monardella villosa Benth. Quite common on brush covered slopes, all exposures.

Satureja douglasii (Benth.) Brig. Shrubby areas, and oak woodland.

Stachy ajugoides Benth. Moist places. Not reported from Mount Diablo by Bowerman.

S. pycnantha Benth. Dry creek bed in Stonybrook Canyon.

S. rigida Benth. ssp. *quercetorum* (Heller) Epling. Very common species along road embankments, on brushy slopes, and open grassy areas, all exposures.

Trichostema lanceolatum Benth. Dry open fields.

SOLANACEAE

Nicotiana glauca Graham.. Along Alameda Creek and road sides.

Solanum nodiflorum Jacq. A very common species of moist areas along Alameda Creek.

S. umbelliferum Esch. A common species of brush covered slopes.

SCROPHULARIACEAE

Antirrhinum majus L. Known from one station on south facing slope just east of bridge. This colony has persisted here for at least four years.

A. vexillo-calyculatum Kell. Dry open areas, mostly south exposure.

Castilleja affinis H. & A. Brush covered slopes and edge of oak woodland, mostly northerly exposure.

C. foliolosa H. & A. Rocky slopes.

C. wightii Elmer. A common species on west facing slopes in Stonybrook Canyon.

Collinsia heterophylla Grah. Shady, grassy slopes, mostly north exposure.

Cymbalaria muralis Gaertn., Mey. & Scherb. Growing in shade around concrete railroad abutment.

Diplacus aurantiacus Jepson. Common shrub of dry brushy or wooded hillsides, all exposures.

Kickxia spuria (L.) Dumort. Fairly common along banks of Alameda Creek.

Mimulus cardinalis Dougl. In side canyons, rare.

M. pilosa (Benth.) Greene. Occasional in dry stream beds.

Orthocarpus purpurascens Benth. Common species of grasslands, all exposures.

O. pusillus Benth. Common in grasslands.

Scrophularia californica C. & S. Common along Alameda Creek, and shrubby slopes.

Verbascum thapsus L. Disturbed habitats, especially common at the eastern end of the canyon.

Veronica persica Poir. Shady areas, grasslands, and road embankments.

PLANTAGINACEAE

Plantago erecta Morris. Grasslands.

P. lanceolata L. Road sides, and grassy areas.

P. major L. Moist areas along Alameda Creek.

RUBIACEAE

Galium aparine L. Brush covered slopes, and side canyons, mostly northerly exposure.

G. nuttallii Gray. Very common species inhabiting road embankments, brush covered slopes.

CAPRIFOLIACEAE

Lonicera hispidula Lindl. A common plant of wooded areas, north exposure.

Sambucus mexicana DC. Very common along road sides, and on brush covered slopes.

Symphoricarpos albus (L.) Blake var. *laevigatus* (Fern.) Blake. Along canyon bottoms, and on wooded hillsides, mostly northerly exposure.

S. mollis Nutt. Wooded or brushy hillsides, north exposure, common.

VALERIANACEAE

Centranthus ruber (L.) DC. Well established in disturbed areas, especially in western end of canyon.

CUCURBITACEAE

Marah fabaceus (Naud.) Greene. Common along Alameda Creek.

ASTERACEAE

Achillea millefolium L. var. *californica* (Pollard) Jeps. Open grassy slopes, and wooded hillsides, common, all exposures.

Achyrachaena mollis Schauer. Common on grassy slopes.

Agoseris grandiflora (Nutt.) Greene. Common in grassland, and along road sides.

A. heterophylla (Nutt.) Greene. Grasslands.

Ambrosia pilostachya DC. Fairly common in low, moist places.

Anthemis cotula L. Open grassy hillsides.

Artemisia californica Less. Frequent on exposed slopes, occasional on brushy north facing slopes, mostly south exposure.

A. douglasiana Bess. Along stream bed, and occasionally on north facing slopes.

Aster chilensis Nees. Wooded or brush covered slopes.

A. exilis Ell. Alameda Creek at western end of canyon.

Baccharis douglasii DC. In moist seepage areas, occasional.

B. glutinosa Pers. Along banks of Alameda Creek.

B. pilularis DC. ssp. *consanguinea* (DC.) Kuntze. A very common shrub in Niles Canyon, often at the edges of woodland areas, along roads, and in disturbed areas.

B. viminea DC. Fairly common along the banks of Alameda Creek.

Brickellia californica T. & G. Occasional along stream margins, or dry ditches.

Calendula officinalis L. Known from one station along bank between road and creek at west end of canyon, an escape from cultivation which has persisted in this location for at least four years.

Carduus tenuiflorus Curt. A widespread plant of grasslands, road embankments, and disturbed areas.

Centaurea melitensis L. Common on grassy slopes, and in disturbed areas, all exposures.

C. solstitialis L. Occasional in disturbed areas.

Chrysopsis oregona (Nutt.) Gray var. *rudis* (Greene) Jeps. Occasional in dry flood plains.

Cichorium intybus L. Occasional along road sides.

Cirsium vulgare (Savi) Tenore. Grasslands, and disturbed areas, occasional.

C. proteanum Howell. Open slopes.

Conyza bonariensis (L.) Cronquist. Disturbed areas, and open slopes.

C. canadensis (L.) Cronquist. Common along Alameda Creek and roadsides.

Corethrogyne filaginifolia (H. & A.) Nutt. Frequent on open slopes.

Cotula coronopifolia L. Occasional along the banks of Alameda Creek.

Erigeron philadelphicus L. Infrequent along banks of Alameda Creek.

Eriophyllum confertiflorum Gray. Common along rocky slopes, and road embankments.

Gnaphalium californicum DC. Wooded hillsides, and dry, open banks, fairly common.

G. luteo-album L. Fairly common along banks of Alameda Creek.

G. microcephalum Nutt. Dry slopes and open places, south exposure.

G. purpureum L. Grassy slopes, south exposure, rare.

Grindelia camporum Greene. Dry slopes, and road embankments, all exposures.

Helenium puberulum DC. At the edges of stream beds.

Hemizonia luzulifolia DC. Common in grasslands.

H. pungens (H. & A.) T. & G. Open hillside.

Heterotheca grandiflora Nutt. Dry bank at east end of canyon, south exposure.

Hypochaeris glabra L. Open grasslands, all exposures.

H. radicata L. Grassy slopes.

Lactuca saligna L. Disturbed areas.

L. serriola L. Grasslands, and disturbed areas. A varient, *Lactuca serriola* L. f. *integrifolia* Bogenh. has been collected on the northeast side of the canyon, and on Mount Diablo.

Lagophylla ramosissima Nutt. Grasslands, occasional.

Madia gracilis (Smith) Keck. Grassy slopes, and moist banks along Alameda Creek.

M. sativa Molina. Grasslands.

Matricaria matricarioides (Less.) Porter. Grasslands, and to be expected elsewhere in disturbed habitats.

Microseris douglasii (DC.) Sch.-Bip. Grassy slopes.

Picris echioides L. Grassy slopes, and disturbed habitats, common.

Rafinesquia californica Nutt. On shady, brush covered slopes, mostly north exposure.

Scolymus hispanicus L. Known from hills just north of Niles Canyon, and suspected to be in range land. This plant is under state-wide eradication.

Senecio mikanioides Otto. A common plant of the stream bank vegetation.

S. vulgaris L. Disturbed areas and in grasslands.

Silybum marianum (L.) Gaertn. A common weed along road sides, and in overgrazed pasture land.

Solidago californica Nutt. Grasslands, and in moist gullies, all exposures.

S. occidentalis (Nutt.) T. & G. In moist places along Alameda Creek.

Sonchus asper L. Occasional in disturbed areas, and moist places.

S. oleraceus L. Common on grassy slopes, at edges of streams, and by road sides.

Stephanomeria virgata Benth. Open slopes, south exposure.

Taraxacum officinale Weber. Shady slopes, and in disturbed habitats.

Tragopogon dubius Scop. Flat grassy areas.

T. porrifolius L. Roadsides.

Wyethia angustifolia (DC.) Nutt. Grassy south facing slopes.

W. helenioides Nutt. Moist grassy slopes, mostly north exposure.

Xanthium strumarium L. Along Alameda Creek and other moist areas.

LITERATURE CITED

BOWERMAN, M. L. 1944. The flowering plants and ferns of Mount Diablo, California. Gillick Press, Berkeley.

HALL, C. A. 1958. The geology and paleontology of the Pleasanton area, Alameda and Contra Costa counties, California. Univ. Calif. Publ. Geol. Sci. 34:1–90.

MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.

————. 1968. Supplement to a California flora. Univ. California Press, Berkeley.

SHARSMITH, H. K. 1945. Flora of the Mount Hamilton Range of California. Amer. Midl. Nat. 34:289–367.

THOMAS, J. H. 1961. Flora of the Santa Cruz Mountains of California. Stanford Univ. Press, Stanford.

U. S. ARMY CORPS OF ENGINEERS. 1961. Review report for flood control and allied purposes, Alameda Creek, Alameda County, California. San Francisco, California.

NOTES AND NEWS

NOTEWORTHY RECORDS OF WESTERN PLANTS.—The following records are based upon plants deposited in the University of Idaho Herbarium. The collections were made by the author and others, as cited below. Some of these are new state records. For assistance in making critical determinations, appreciattion is expressed to Rupert C. Barneby, David D. Keck, John Thomas Howell, and Jason R. Swallen.

Agrostis lepida Hitchc. Moist slopes near the summit of Lake Mountain *(Baker & Ruhle 483)*; meadow at Upper Biglow Lake, Oregon Caves National Monument, Josephine Co., Oregon *(Baker & Ruhle 620)*. This is apparently the first record of this species in Oregon. It ranges southward to southern California.

Corynephorus canescens (L.) Beauv. West bank of the Duwamish River, on a sandy flat, South Seattle, King Co., Washington *(Eyerdam 6678)*. This is the first record for Washington. It has been collected on waste ground and ballast in New England and the central Atlantic coastal states. It is introduced from Europe.

Poa laxiflora Buckl. Slopes near summit of Lake Mountain, Oregon Caves National Monument, Josephine Co., Oregon *(Baker & Ruhle 263)*. This species has not been collected south of the Columbia River previously. It ranges northward to southeastern Alaska.

Alisma gramineum Gmel. Growing in a pond on the shore of the Rogue River at Cherry Flat, 4 mi north of Agness, Curry Co., Oregon *(Baker 15434)*. Peck (Manual higher plants Oregon, 1941) lists this species as occurring in shallow water and mud along the Columbia River east of the Cascades and in the Harney Valley of Oregon.

Eleocharis ovata (Roth) R. & S. Sandy shore at edge of Rogue River at Cherry Flat, 4 mi north of Agness, Curry Co., Oregon *(Baker 16555)*. This widespread but local species, occurring mainly in eastern United States, is known from several localities in western Washington. Peck (loc. cit.) noted that its status in Oregon was uncertain and that it had not been collected recently.

Carex paucicostata Mack. Moist soil, edge of Lower Biglow Lake, Oregon Caves National Monument, Josephine Co., Oregon *(Baker & Ruhle 600)*; marshy ground along Trapper Creek *(Baker 7250)*; edge of Vidae Falls *(Baker 7106)*, Crater Lake National Park, Klamath Co., Oregon. An addition collections from eastern Oregon is from near the summit of Lookout Mountain, Crook Co. *(Cronquist 7483,* ID). These are additional records to the one published by Peck from near the summit of Mt. Ashland, Jackson Co. This species is otherwise known from the Sierra Nevada of California.

Reseda alba L. Common in vacant lots, sandy soil along the coast at Gold Beach, Curry Co., Oregon *(Baker* s. n.). Native of Europe and possibly introduced with ballast.

Astragalus advordensis Jones. Roadside, south of the Oregon-Nevada line, just south of Denio, in Humboldt Co., Nevada *(Baker 1750)*. An extremely rare and local species, this being the first record for Nevada, although it was cited in the mimeographed Flora of Nevada.

Tellima grandiflora (Pursh) Dougl. Fish Creek, north fork of the Flathead River, Glacier National Park, Montana *(McMullen 1017)*. This is the first record for Montana, although the author has collected it at Hope, Bonner Co., Idaho. This species is fairly common in Idaho and probably not uncommon in Montana. It is found on rocky cliffs, along shady stream banks, and in moist woods from southern Alaska and British Columbia to central California.

Asclepias cryptoceras Wats. Talus slope at Tibbet Ranch, east side of Joseph Creek, Asotin Co., Washington *(Mohan 133)*. This is the first record of this species from Washington and is the basis of the locality record reported by Hitchcock (Vascular Plants Pacific Northwest, 1959).

Sphenosciadium capitellatum Gray. Rocky streambank at Dry Gulch, 5 miles south of Jarbidge, Elko Co., Nevada *(Baker 8641)*. This species has been collected on Mt. Rose, Washoe Co., *(Allen 39A18,* ID), although Holmgren (Handbook vascular plants northeastern Nevada, 1941) does not record it.

Gentiana heterosepala Englem. Occasional, marshy ground, upper Bear Creek Meadows, 8400 ft., Elko Co., Nevada *(Baker 8648)*. This first record from Nevada is not listed by Holmgren (loc. cit.).

Penstemon humilus Gray. Rocky slope, Five Mile View Point, Wallowa Mountains, Wallowa Co., Oregon *(Baker 9049)*. Peck (loc. cit.) did not record this species—WILLIAM H. BAKER, University of Idaho, Moscow 83843.

ARENARIA, SECTION EREMOGONE (CARYOPHYLLACEAE) IN THE PACIFIC NORTHWEST: A KEY AND DISCUSSION

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Arenaria is one of the taxonomically most difficult genera in western North America. Members of Section *Eremogone* (the filiform-leaved cespitose perennials) are commonly encountered in the drier regions of the western United States. Although only 13 American species are normally recognized in this section, the group presents a vast and confusing array of morphological types. The present paper is an attempt to sort out and more completely describe the forms which occur in the Pacific Northwest and the ways in which they intergrade. An attempt is also made to summarize the evolutionary mechanisms by which such a species complex might originate. The study is an offshoot of a more comprehensive continuing investigation of the ecology and evolutionary history of species in the Cascade Mountains of Oregon (Hickman, 1968; Hickman and Johnson, 1969).

I have examined over 1000 specimens of eremogones from ORE, OSC, DS, and WSC. The fact that over 40 percent of these specimens were mislabeled or misfiled indicates the amount of taxonomic and nomenclatural confusion within the group. Specimens of all currently recognized North American species have been studied, but with minor exceptions type material has not been available. Strictly nomenclatural problems which would necessitate reference to types appear to be lacking. In addition to herbarium studies, all Pacific Northwest species, with the exception of typical *A. kingii* (Wats.) Jones, have been studied in the field.

All currently available treatments of this group (Maguire, 1947; 1951; Munz, 1959; Peck, 1961; St. John, 1963; Hitchcock, *et al.*, 1964) have some internal and mutual inconsistencies. Detail of treatment varies greatly, but only Maguire (1947) includes all five currently recognized Pacific Northwest species. In many cases the diagnostic characters cited by Maguire have proved too variable to be consistently useful.

The difficulties in arriving at a definitive treatment of the group include the fact that taxa of *Eremogone* are fully polythetic classes in the sense of Beckner (1959): they are sufficiently variable that no single set of characters will completely delimit them. Each population may have a large number of common characteristics, and every such character may be possessed by many members of the population but no single character is found in every individual. Each taxon represents a new combination of states of the numerous, widely-varying characters to-

gether with one or a few traits which are less widely distributed but which are nevertheless not always diagnostic. For example, the most definite character in this group of species is the sharply-pungent leaf tip of *A. aculeata* Wats. However, occasional specimens which on other grounds must be considered to be *A. capillaris, A. pumicola,* or *A. kingii* also have sharply-pungent leaf tips which are virtually indistinguishable from those of *A. aculeata.*

A taxonomic scheme for such a polythetic group based on the presence or absence of one or a few characters would be highly artificial, and natural separations must therefore depend on as large a number of characteristics as possible. There are so many intermediate forms that it is difficult, but necessary, to describe more fully material typical of the various species populations. The simple recognition of intermediate forms as such will be a great aid in working with this group floristically and taxonomically. For these reasons, a more completely descriptive key to these species is presented here. No new names or combinations are proposed at this time, but these will inevitably result from continued work with this complex genus. References for the original descriptions are available from standard taxonomic works, especially Hitchcock, *et al.* (1964).

Section *Eremogone* Fenzl. Plants perennial, frequently suffrutescent and more or less cespitose; capsule dehiscing by six teeth, each valve thus bidentate; leaves narrowly linear, obtuse to apiculate or acicular-pungent; glands at the base of the stamens conspicuous or occasionally obsolete.

Key to Pacific Northwest Species

Infl. congested, the fls. borne in one to several more or less captitate cymes, glabrous; anthers white or yellowish; lvs. straight, thin, obtuse to apiculate, mostly 4–6 cm long; stems typically tall and leafy. Range: through e Oregon and Washington, e to Montana and Wyoming, s to southern Colorado, Nevada, and the s Sierra Nevada. The most widespread and variable taxon.

A. congesta Nutt.

Infl. an open cyme, normally glandular (rarely glabrous); lvs. various, but if straight under 3 cm long.

Basal lvs. persistent, recurved (in material from Nevada, lvs. often straight and strictly ascending); herbage, at least in dried specimens, appearing permanently dusty from the translucent cuticle and occasional very short eglandular hairs; infl. glabrous to densely but minutely glandular. Range: in pure form, from Harney and Malheur cos., Oregon, e across s Idaho to sw Wyoming, and s through the Great Basin; in forms intermediate to *A. capillaris americana* at least as far north as Gilliam and Morrow cos., Oregon. . . *A. kingii* (Wats.) Jones (in the Pacific NW var. *glabrescens* Mag. = *A. aculeata* Wats. var. *uintahensis* (Nels.) Peck).

Basal lvs. persistent or falling in age, rigidly ascending, lax, or curved
in the same direction; not recurved; herbage glaucous (es-
pecially the basal lvs.) or glabrous; infl. glandular-pubescent.
Lvs. with long-subulate, yellow, pungent tips; basal lvs. rigid-
ascending in youth, arcuate-spreading in age, strongly per-
sistent, normally under 2 cm long; cauline lvs. above the
lowest pair abruptly reduced and mostly scarious; stems
strongly matted. Range: the Wallowa Mts. e through c Idaho
to sw Montana, s and w to ne California, n Nevada, and nw
Utah. . . . . *A. aculeata* Wats.
Lvs. with green, acute to apiculate, non-pungent tips.
Basal lvs. thick, rigid-ascending, glaucous, never spreading or
curved, falling after one or two years leaving a naked,
incompletely lignified caudex that branches just below the
soil surface; cauline lvs. markedly wider than the basal,
somewhat fleshy, of equal size up to the many-flowered
infl. Range: in pure form, from Marion Co., Oregon, s in
the Cascades to Crater Lake, occasional in the Siskiyou
Mts. as far w as Curry Co., Oregon. Intermediates be-
tween this and *A. capillaris americana* are found from the
Three Sisters, Lane Co., n to Whatcom and Okanogan
cos., Washington. (The variety *californica* Maguire, with
less fleshy lvs. and woodier caudex, is found in the Sierra
Nevada from Sierra to Mono cos. It is transitional to
A. kingii). . . . . . . *A. pumicola* Cov. & Leib.
Basal lvs. thin and somewhat lax, all lvs. of one vegetative stem
curved slightly to markedly in the same direction, gla-
brous, toothed along the margins, persistent at the base,
2.5–4 cm long except for alpine ecotypes, where shorter;
stems somewhat matted; cauline lvs. of same shape as
basal, not fleshy, reduced gradually to the relatively few-
flowered infl.; anthers purple. Range: Alberta and British
Columbia s in the Cascades to the Three Sisters, Oregon,
and in the Rockies to Montana and c Idaho. Found occa-
sionally in the Columbia Basin in forms transitional to
A. congesta. A. capillaris Poir. subsp. *americana* Maguire
(=*A. formosa* of American authors, not *A. formosa* Fisch.)

The present treatment has a number of limitations. Although the
diagnostic character sets have been made as large as possible, the char-
acters (as previously noted) are not always faithfully associated. It will
remain unclear which characteristics can be considered most nearly
diagnostic until exhaustive experimental work is undertaken.
Sepal shape, a character heavily weighted by most workers in this
genus, has not been included in the present key because of the great
variability within single flowers and more importantly because of the
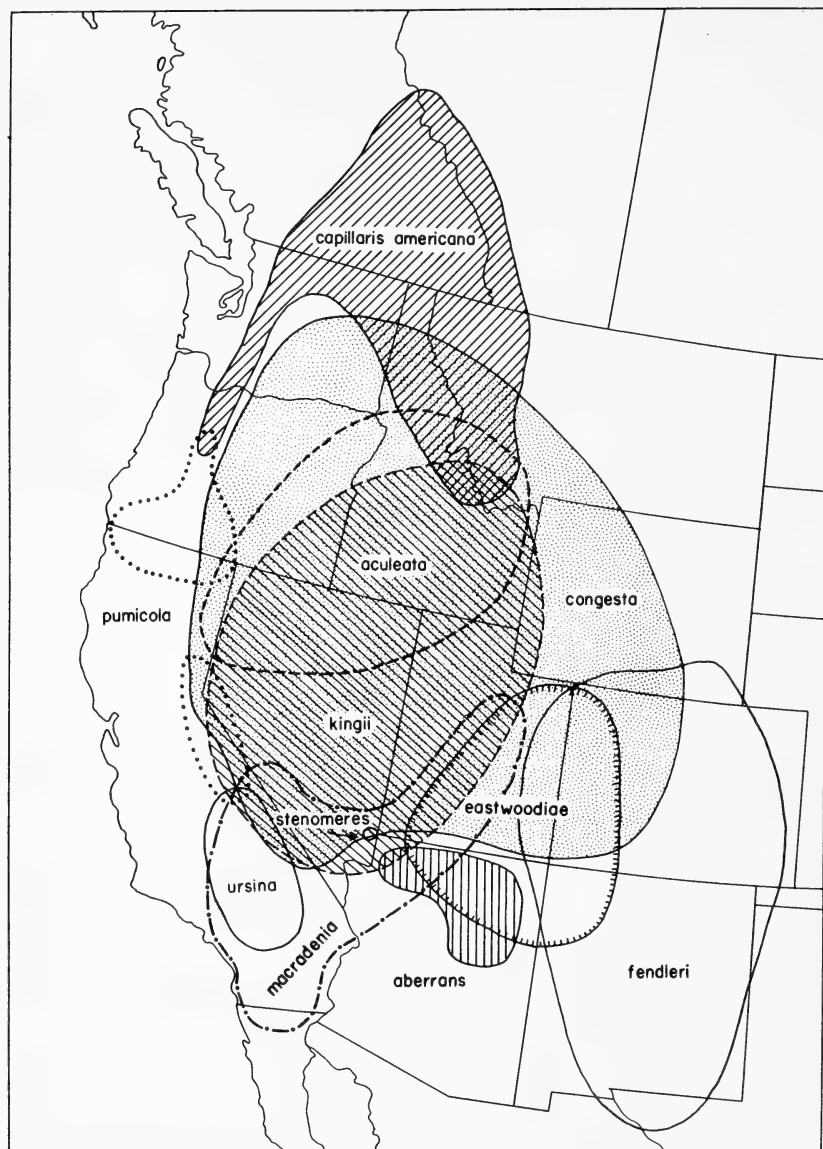
Fig. 1. Geographical distributions of eleven taxa of *Arenaria (Eremogone)* in western North America.

lack of any discontinuities in the clines of this character. There is no doubt a correlation between sepal shape and some of the characteristics used above, but the relationship is too complex to be incorporated usefully into a key. In general, *A. capillaris, A. aculeata,* and *A. pumicola* have obtuse or barely acute sepals; the sepals of *A. congesta* vary from
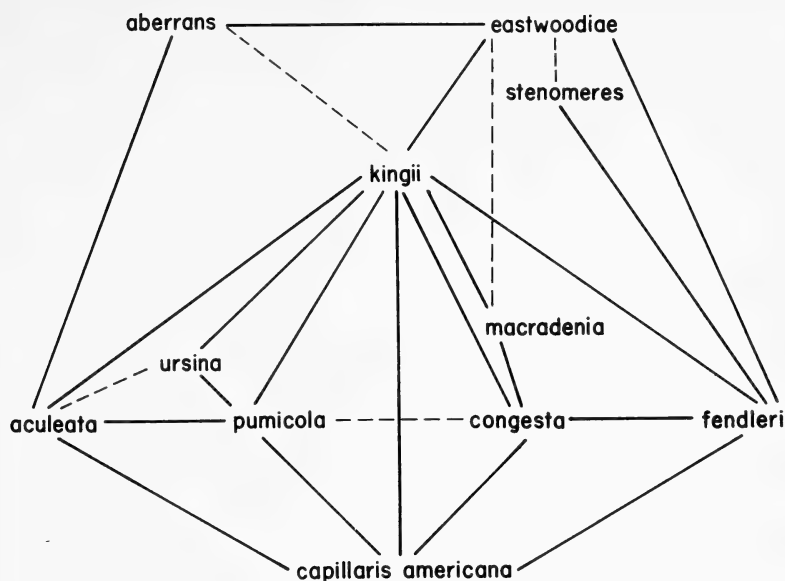
FIG. 2. Morphologically derived patterns of intergradation among eleven taxa of *Arenaria (Eremogone)*. Dotted lines indicate less obvious affinities.

obtuse to acuminate; and *A. kingii,* throughout most of its range, but not in Oregon or western Idaho, has definitely acute sepals.

While I have studied some material of all 13 American species of *Eremogone,* most was collected from the Pacific Northwest. Due to the gradually shifting nature of the diagnostic features of all the taxa when they are considered throughout their ranges, the present key will decrease in value with distance from this region. However, for all of Oregon, Washington, Idaho, Montana, and large portions of California, Nevada, Utah, and Wyoming, the five species treated here are the only ones encountered (fig. 1).

Arenaria franklinii Dougl. and *A. hookeri* Nutt. have been excluded from this study because they seem intermediate between Sections *Eremogone* and *Alsine,* having the capitate inflorescence of *A. congesta* and the prostrate habit of *A. nuttallii* Pax. *A. franklinii* is found throughout eastern Oregon and in adjacent Washington, Idaho, and Nevada; and *A. hookeri* occurs primarily east of the continental divide in Montana, Wyoming, and Colorado.

Arenaria capillaris americana intergrades morphologically with all of the other species treated here (fig. 2, which shows morphologically derived estimates of present or past gene flow among the 11 species). The only character that is reliable in separating this species from *A. congesta* is the congested inflorescence. Six Pacific Northwest varieties of *A. congesta* have been characterized by more open inflorescences and combinations of other highly variable characters. It is my opinion that these

"varieties" represent intermediate forms with *A. capillaris americana* in our range, and elsewhere with other taxa—especially *A. fendleri* in Wyoming and Colorado and *A. macradenia* in southern California, Nevada, and Utah. It is also possible that a very small number of genes is involved in producing a congested inflorescence in this genus and that this characteristic has arisen numerous times in various parts of the section.

Other intermediates are also common. Robust forms of *A. capillaris americana* from lower elevations between the Three Sisters and Mt. Hood, and highly reduced alpine forms from Mt. Hood to northern Washington exhibit the wide, somewhat fleshy cauline leaves characteristic of *A. pumicola*. *Arenaria capillaris americana* partially intergrades with *A. aculeata,* since many sharply pungent-leaved specimens show some signs of leaf length and laxness characteristics of the former species. It also merges completely with *A. kingii glabrescens,* resulting in the occurrence of *capillaris*-like morphological characters as far south as White Pine Co., Nevada. Occasional intermediates between *A. aculeata* and *A. kingii* have been collected in southeastern Oregon; and one population from Gearhart Mt., Lake Co., Oregon, is intermediate between *A. aculeata* and *A. pumicola*. As mentioned in the key, *A. pumicola* var. *californica* appears to be derived from typical *A. pumicola* and *A. kingii*.

The diversity of intermediate forms suggests that barriers to gene exchange in these species are incomplete. In addition, there is considerable evidence here for a complex pattern of reticulate evolution. *A. capillaris americana* is apparently the most primitive member of the section discussed here, providing the North American connection between the circumboreal *A. capillaris* subsp. *capillaris* and the more southerly derived species. *Arenaria capillaris* is the only American species found north of the southern limit of Pleistocene continental glaciation. With considerable recombination possible, there has been great potential for local differentiation as the migrating complex has come into contact with new environments. Fluctuating climates from the late Tertiary to the present have no doubt had the following three important and recurring effects: 1, isolation of relatively small populations; 2, re-establishment of contacts between formerly isolated populations; 3, re-isolation of local populations following gene exchange with other types. Such processes could easily have led to the observed widespread complex of interrelated forms, the larger units varying gradually with geographic locality. These mechanisms could also explain the broad areas of "specific" overlap shown in Fig. 1. At present there are virtually no ecological data from which one might deduce the importance of character displacement in functionally separating populations of *Eremogone* in areas of sympatry, but this must be considered as an alternative suggestion.

Arenaria kingii seems to comprise the central portion of the complex,

both morphologically and geographically. This species also contains the most diverse and incongruous forms and is partially sympatric or parapatric with all other American eremogones. It seems likely to me, by means of the evolutionary-migrational mechanisms outlined above, that this species has been a "genetic dumping ground" for all the closely related taxa. It may either represent the parental stock or be derived by recombination from many of the more localized entities. Probably both hypotheses are in part correct, but verification of this will prove difficult. If only the latter is correct, the biological validity of *A. kingii* as a species could be questioned, but, as pointed out by Maguire (1947), to discard the name would cause insurmountable problems in the taxonomy of the section. The central morphological tendencies of *A. kingii* are illustrated in Fig. 2.

This discussion of evolutionary patterns is highly speculative, but is suggested by the trends of various morphological characters. Work by others is beginning to elucidate genetic and chromosomal patterns in some portions of the section. Extensive experimental studies are needed to assess the biological significance of the described morphological patterns and to support or contradict the derivative evolutionary hypotheses presented here. Until such studies are completed, these impressions will be of value to those who wish to understand eremogones from the Pacific Northwest as the species are presently constituted.

LITERATURE CITED

BECKNER, M. 1959. The biological way of thought. Columbia Univ. Press, New York.
HICKMAN, J. C. 1968. Disjunction and endemism in the central Western Cascades of Oregon: An historical and ecological approach to plant distributions. Ph.D. dissertion, Univ. Oregon, Eugene.
HICKMAN, J. C., and M. P. JOHNSON. 1969. An analysis of geographical variation in western North American Menziesia (Ericaceae). Madroño 20:1–11.
HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY, and J. W. THOMPSON. 1964. Vascular plants of the Pacific Northwest. Vol. II. Univ. Wash. Press, Seattle.
MAGUIRE, B. 1947. Studies in the Caryophyllaceae. III. A synopsis of the North American species of Arenaria, Section Eremogone Fenzl. Bull. Torrey Bot. Club 74:38–56.
————. 1951. Studies in the Caryophyllaceae. V. Arenaria in America north of Mexico. A conspectus. Amer. Midl. Nat. 46:493–511.
MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.
PECK, M. E. 1961. A manual of the higher plants of Oregon. 2nd ed. Binfords and Mort, Portland.
ST. JOHN, H. 1963. Flora of southeastern Washington and of adjacent Idaho. 3rd ed. Outdoor Pictures, Anacortes, Washington.

STUDIES IN THE AGAVACEAE. I.
CHROMOSOME MORPHOLOGY AND
NUMBER OF SEVEN SPECIES

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Programa de Genética, Comisión Nacional de Energía Nuclear

Introduction

The position of the family Agavaceae has long been controversial. Hutchinson (1934), considering inflorescence type and habit more stable characters than ovary position, assigned to this group the most highly evolved tribes of the Liliaceae and Amaryllidaceae. This amounted to a resurrection of the old family Agavaceae (Endlicher, 1841; Lotsy, 1911), the nomenclatural type of which is the genus *Agave*. Hutchinson's decision has provoked much discussion among botanists. His arguments in refutation of the classical position are not numerous and may be quoted here: "In tracing out the relationships of Monocotyledons amongst themselves I have come to the conclusion that the character of the superior or inferior ovary has often been stressed too much and has led to artificial classification." He thus eliminated from consideration the single character separating the Liliaceae and Amaryllidaceae and continued, "To my mind the type of inflorescence is of much more importance than the superior or inferior ovary, and the result is a nearer approximation of allied genera." On this basis, he proposed an arrangement which transfers several genera from the two families and places them in others, for example, Agavaceae, Smilacaceae, Ruscaceae, and Trilliaceae. Characters cited by Hutchinson to separate the Amaryllidaceae from the Liliaceae include the presence of a scapose umbellate inflorescence, and involucres of two or more membranous bracts (rarely but one), true umbels being unknown in the Liliaceae.

To be sure, differences between these families are not profound; in many cases the primary distinction is one of habit. With respect to the family Agavaceae, Hutchinson wrote, "It is not clearly marked by any one character from the Liliaceae and is based mainly on habit."

The family Agavaceae includes plants with subterranean rhizomes, long or short stems which are usually arborescent with leaves in a basal rosette, the leaves narrow, thick, and fleshy, and entire or with a spinescent margin; inflorescence racemose or paniculate, the branches of the inflorescence with large bracts at their bases. Members of the family lack bulbs of the kind found among the Liliaceae and their inflorescences are never true umbels as in the Amaryllidaceae.

Fig. 1. A general view of the *Agave* section at the Jardín Botánico, UNAM.

Contemporary with Hutchinson's work was the publication of the observations of McKelvey and Sax (1933) on the morphological and cytological affinities of *Yucca, Hesperaloë, Hesperoyucca, Cleistoyucca,* and *Samuela* (Liliaceae), and *Agave* and *Fourcraea* (Amaryllidaceae). Whitaker (1934) and Sato (1935) believed that *Yucca, Agave,* and related genera should be referred to a single group, since all possessed similar chromosomal patterns: **25** large and **5** small chromosomes. Thus, from a different point of attack, Hutchinson's thesis was corroborated.

On the basis of cytological evidence, most taxonomists are agreed on the necessity of a re-evaluation of the systematics of these groups. Some have suggested the erection of a greater number of families (Sato, 1942), other writers have considered the unification of the Amaryllidaceae and Liliaceae into a single family (Gómez-Pompa, 1963; Thorne, 1968), or the union of the two families while maintaining the family Agavaceae
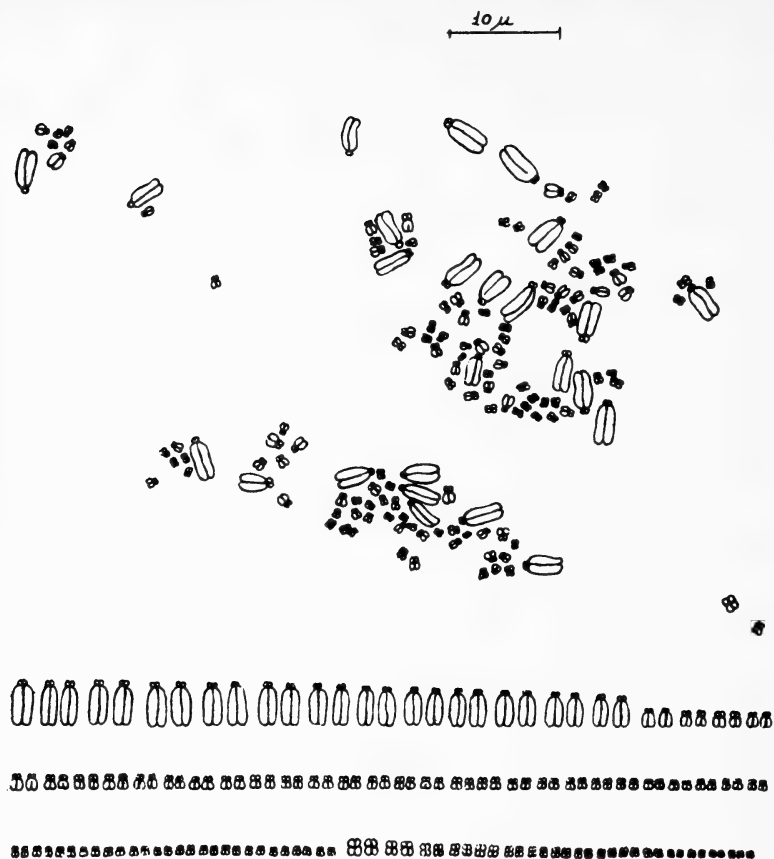
Fig. 2. Camera lucida drawings of the mitotic chromosomes of *Agave mapisaga,* 2n = 150.

(Cronquist, 1968).

Cytological evidence enabling us to take a position is meager. In *Agave,* for example, chromosomal data are available for less than 20% of the species; moreover, several genera have yet to be analyzed (table 1). Equally important, however, is the development of study in other fields which will provide more information on these groups. For this reason, it was decided to begin work with the plants of the Botanical Garden of the Universidad Nacional Autónoma de México. The Garden possesses one of the richest collections of Agavaceae in the world (fig. 1), with nearly all Mexican genera and more than 100 species of the family in cultivation. The plants have been collected by the personnel of the Garden and careful records concerning origin have been maintained.

This paper presents the preliminary results of our work. We plan to

Fig. 3. Camera lucida drawings of the mitotic chromosomes of: A (left), *A. nizandensis*, 2n = 60; B (right), *A. xalapensis*, 2n = 60.

TABLE 1. A SUMMARY OF CHROMOSOMAL STUDIES
OF THE GENERA OF AGAVACEAE FROM DIFFERENT AUTHORS.

L = long chromosomes, M = medium chromosomes, and S = short chromosomes.

Tribe	Genus	Karyotype
Hosteae	*Hosta* (Japan, China)	30 ... 3n(4L + 1M + 25S)
Yucceae	*Yucca* (America)	30(5L + 25S)
	Hesperaloe (America)	30(5L + 25S)
	Clistoyucca (America)	30(5L + 25S)
	Samuela (America)	30(5L + 25S)
Dracaeneae	*Cordyline* (Tropics except Africa)	19 ... 4n(2L + 17S)
	Cohnia (Madagasc. I., N. Caled.)	....
	Dracaena (Tropics)	19 ... 5n(2L + 17S)
	Sansevieria (Africa, Asia)	20 ... 6n(2L + 18S)
Phormiae	*Phormium* (N. Zealand)	16(4L + 12S)
Nolineae	*Nolina* (America)	18–19(6L + 13S)
	Calibanus (America)	....
	Dasylirion (America)	19(6L + 13S)
	Beaucarnea (America)	19 (?L + ?S)
Agaveae	*Agave* (America)	30 ... 6n(5L + 25S)
	Furcraea (America)	30(5L + 25S)
	Beschorneria (America)	30(5L + 25S)
	Doryanthes (Australia)	24(2L + 22S)
Polyantheae	*Polianthes* (Trop. Amer.)	30(5L + 25S)
	Prochnyanthes (Mexico)	....
	Pseudobravoa (Mexico)	....
	Bravoa (Mexico)	30(5L + 25S)
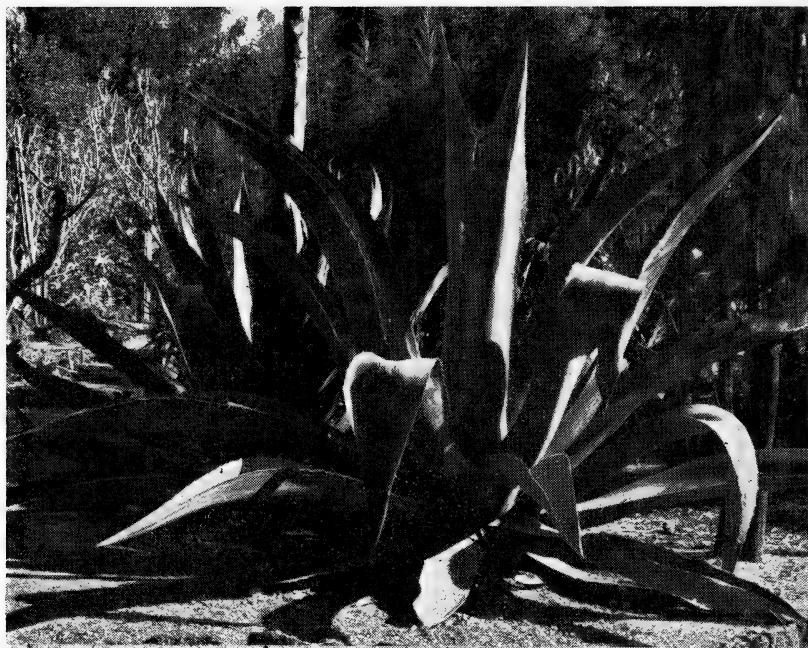
Fig. 4. *Agave mapisaga,* this species is the most common species cultivated for "pulque" in the Valley of Mexico.

assemble more data to facilitate a resolution of problems related to evolution and classification in this group.

On the basis of karyotype, it is possible to divide all genera included in the Agavaceae into two groups. In the first, including *Yucca* and *Agave,* somatic cells are characterized by 30 pairs of chromosomes, 5 of which are very large and 25 very small. The second group, with *Nolina, Dasylirion,* and allied genera, includes plants whose somatic cells contain 19 pairs of chromosomes without marked difference in size.

The study of the possible relationships between the two karyotypes of the family is especially interesting. Although the similarity of the karyotypes of *Yucca* and *Agave* supports the view that these genera are allied, the distinct karyotypes of the genera of the *Nolina* group seem to furnish a rationale for their segregation.

In the present paper the chromosomal complements of seven species are described, six of which were hitherto unstudied.

MATERIALS AND METHODS

Two sorts of mitotic tissue were examined: stamen filaments and roots from adult plants cultivated in the Botanical Garden of the Insti-
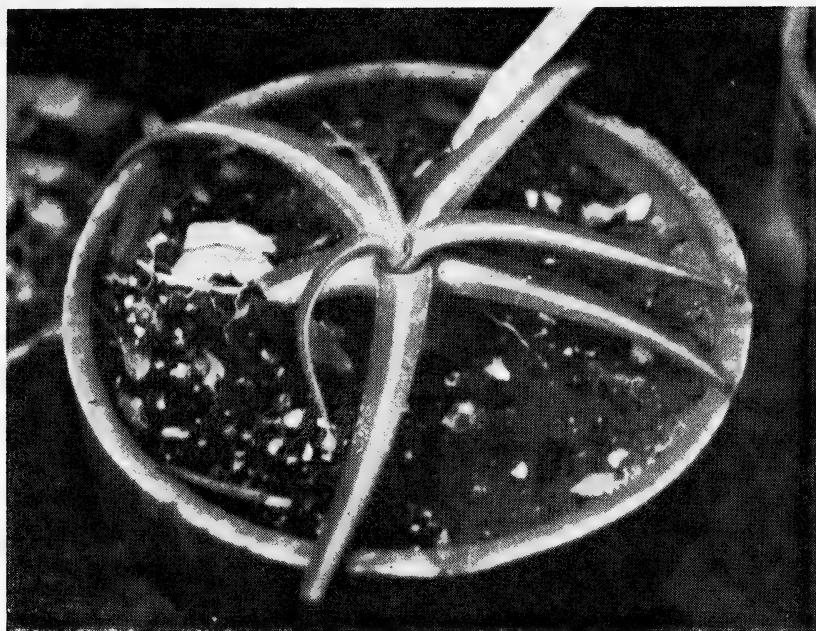
Fig. 5. *Agave nizandeniss* (from the type locality) growing in the Jardin Botánico, UNAM.

tuto de Biología of the Universidad Nacional Autónoma de México. Voucher specimens have been deposited in the Herbario Nacional del Instituto de Biología (MEXU). With both materials the Acetic-orcein-Janus green technique (Villalobos-Pietrini, 1965) was employed, making possible permanent preparations of cells held in metaphase by means of colchicine (C-metaphases).

RESULTS

Agave mapisaga Trel. **2n = 150 (25L + 125S).** *Chimal 65,* Naucalpan, State of Mexico. The chromosomal complex of this species identifies it as a pentaploid with 25 large submetacentric and 125 small metacentric and submetacentric, chromosomes (fig. 2). The plant is cultivated in the Valley of Mexico for the production of pulque (fig. 4).

This represents the second described pentaploid in the genus, the first being *Agave sisalana* (Sato, 1935). In *A. atrovirens*, Sato (1938) found 180 chromosomes (of which 30 were large and 150 small), corresponding to a hexaploid.

Agave nizandensis Cutak. **2n = 60 (10L + 50S).** *Chimal 29,* Nizanda, Oaxaca. The large chromosomes are submetacentric, one pair exhibiting secondary constriction. The small chromosomes are metacentric and submetacentric (fig. 3). This rather rare and infrequent species is from Nizanda, Oax. (fig. 5).

Fig. 6. *Agave verschaffeltii* (from Tehuacán, Pue.) growing in the Jardin Botánico, UNAM.

Agave verschaffeltii Lem. **2n = 60 (10L + 50S)**. *Chimal 37*, Tehuacán, Puebla. The large chromosomes are submetacentric; one pair exhibits secondary constriction. The small chromosomes are metacentric and submetacentric. This species is abundant in the State of Puebla, near Tehuacán (fig. 6).

Agave xalapensis Roezl. **2n = 60 (10L + 50S)**. *Chimal 2*, Xalapa, Veracruz, Botanical Garden No. *5363*. As in the preceding species, the large chromosomes are submetacentric, one pair with secondary constriction, and the small metacentric and submetacentric (fig. 3). These results agree with those obtained by Granick (1944) for the same species. The plant was collected on the basalt flow east of Xalapa (fig. 7).

Dasylirion serratifolium (Schult.) Zucc. **2n = 38 (12L + 26M)**. *Chimal 36*, Oaxaca. There are 12 large submetacentric chromosomes and 26 metacentric and submetacentric and metacentric medium-sized chromosomes present (fig. 9).

The same chromosome number was reported for *Dasylirion longissimum* (Whitaker, 1934; Sato, 1942), *D. taxanum* and *D. wheeleri* (Sato,

FIG. 7. *Agave xalapensis* (from the lava beds near Xalapa) growing in the Jardin Botánico, UNAM.

1936), and *D. acrotriche* (Sato, 1942). The species is native in the state of Oaxaca (fig. 8).

Yucca lacandonica Gómez-Pompa & Valdés. **2n = 60 (10L + 50S).** *Chimal 74,* Botanical Garden No. *6929.* The 10 large chromosomes are submetacentric; the 50 small chromosomes are metacentric and submetacentric (fig. 10). This is the only representatives of the genus in the humid tropics known as an epiphyte (Gómez-Pompa and Valdés, 1962) (fig. 12).

Other authors, McKelvey and Sax (1933), Whitaker (1934), Sato (1935), and Watkins (1936), in examining different species of *Yucca,* encountered the normal somatic chromosome number of **2n = 60.** On the other hand, Sharma and Sarkar (1964), in a study of the karyotypes of five species of *Yucca,* some of which had been described, reported a variation of **42** to **52** chromosomes in somatic cells. Although Sharma and Sarkar reported secondary constrictions in one of two pairs of chro-
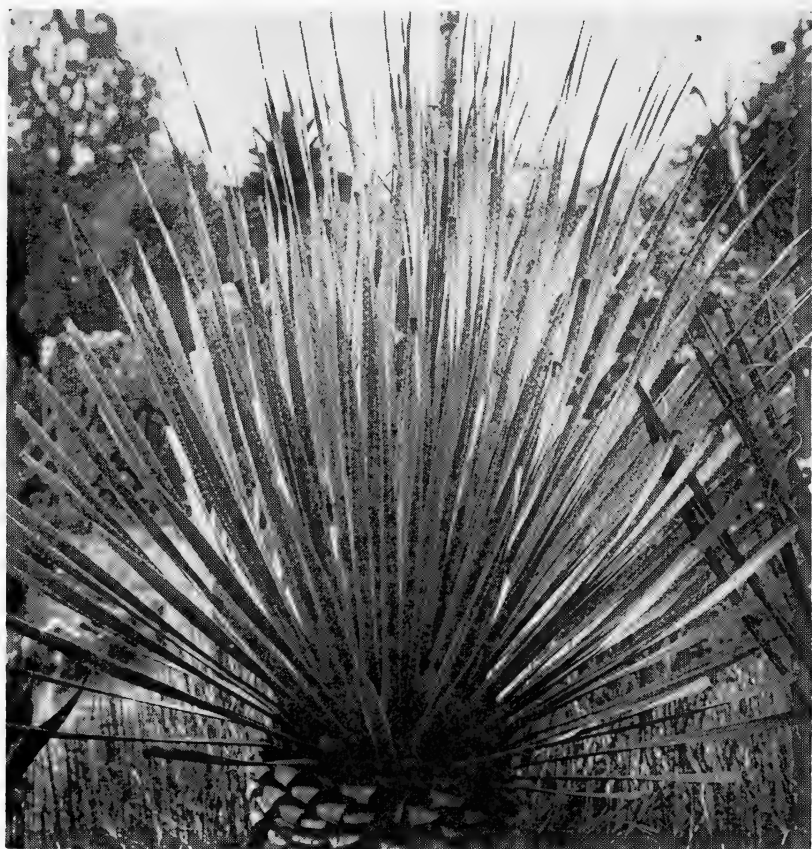
Fig. 8. *Dasylirion serratifolium* (from Oaxaca) growing in the Jardín Botánico, UNAM.

mosomes, in our examination of *Yucca lacandonica* no secondary constrictions were located, a fact which may prove to be of great interest in an understanding of the karyotype evolution of *Yucca*. The plants studied originated in Teapa, Tabasco.

Hesperaloë funifera (Koch) Trel. **2n = 60 (10L + 50S).** The large chromosomes are submetacentric, and the small chromosomes are metacentric and submetacentric (fig. 11). The same chromosome number was reported by McKelvey and Sax (1933) for *H. parviflora*. The plants studied were collected in San Luis Potosí (fig. 13).

DISCUSSION

On the basis of the chromosomal analyses performed, we can corroborate the presence of a very asymmetric karyotype with the uniform chromosome number of **2n = 60** in the genera *Agave, Yucca* and *Hesperaloë*, confirming their close relationship. On the other hand, we have
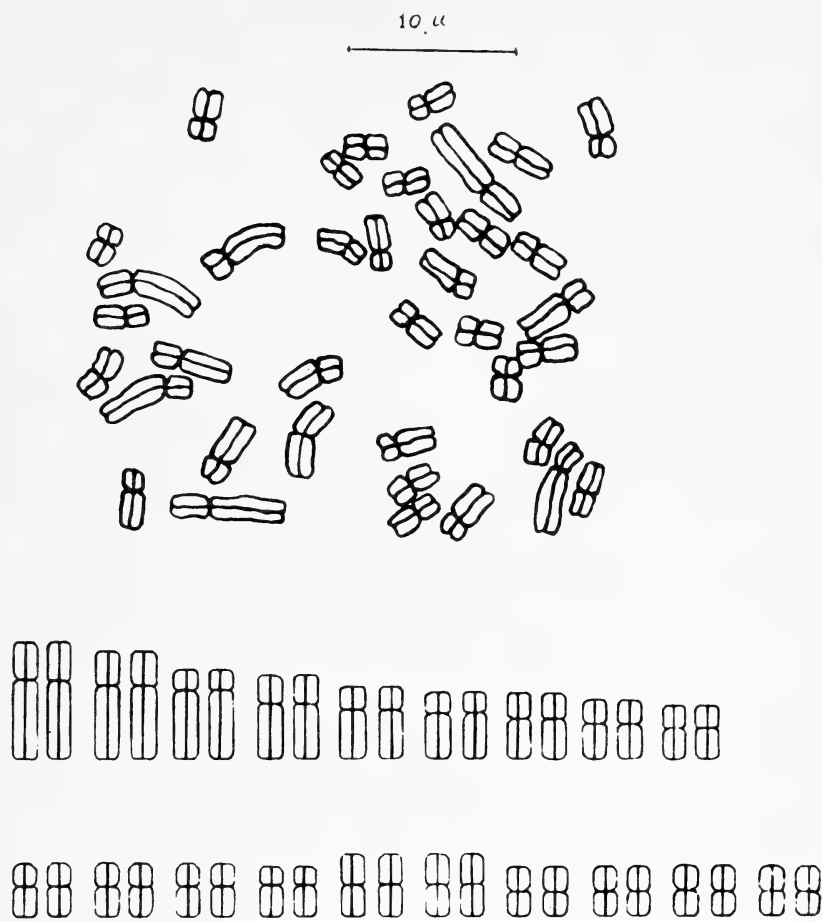
FIG. 9. Camera lucida drawings of the mitotic chromosome of *Dasylirion serrati-folium*, 2n = 38.

in the genus *Dasylirion* with 2n = 38 a number similar to that of other genera in the tribe Nolineae such as *Nolina* (Cave, 1964) and *Beaucarnea* (Flory and Varma, 1960).

The information obtained during our research and from a survey of the literature does not support the circumscription of the family Agavaceae proposed by Hutchinson. The family includes two groups which are well defined chromosomally and with little apparent phylogenetic relationship. Further, they are morphologically and geographically diverse, indicating a long independent evolutionary history.

From a taxonomic point of view, this conclusion seems to weaken the already weak case for maintaining the Agavaceae as a distinct family, especially since it shares many characters with the Liliaceae and Ama-
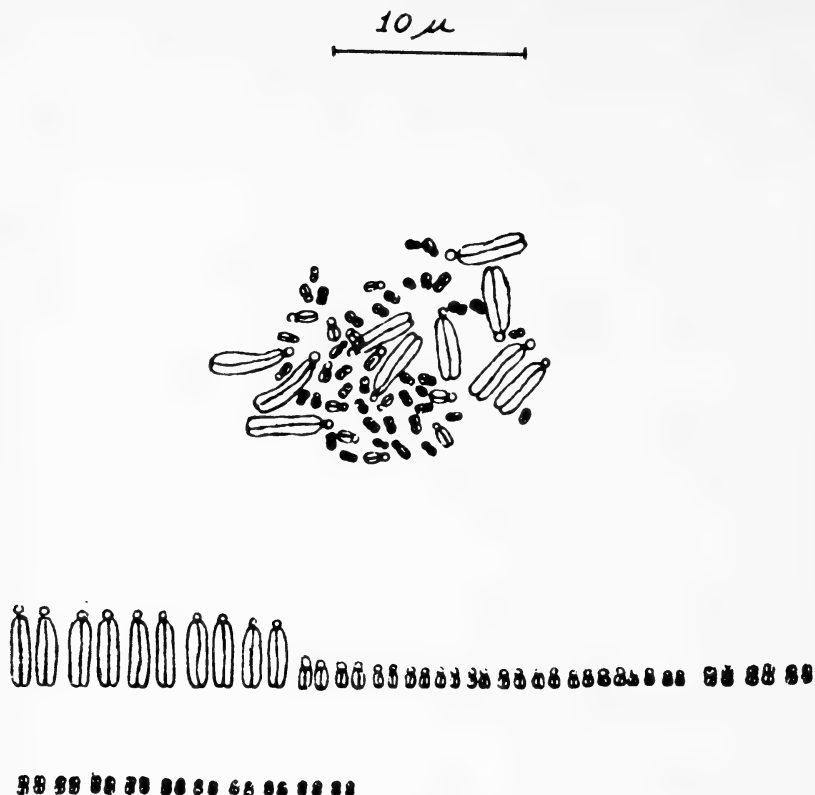
Fig. 10. Camera lucida drawings of the mitotic chromosomes of *Yucca lacandonica*, 2n = 60.

ryllidaceae and is thus not easily separable from them. We are inclined to support Thorne (1968) in a unification of the three families in one, although we are aware of the difficulties engendered by such an arrangement, and to make a separation into subfamilies. Without doubt, it will be necessary to have more information from other sources (morphology, genetics, biochemistry) to achieve an arrangement of subfamilies which best reflects the phylogenetic relationships of the included groups.

ABSTRACT

A chromosomal study of the following species is presented: *Agave mapisaga, A. nizandensis, A. verschaffeltii, A. xalapensis, Dasylirion serratifolium, Hesperaloë junifera,* and *Yucca lacandonica.* Some observations concerning the systematics of the Agavaceae in the light of chromosomal studies are made. The union of the Amaryllidaceae and Liliaceae is discussed.
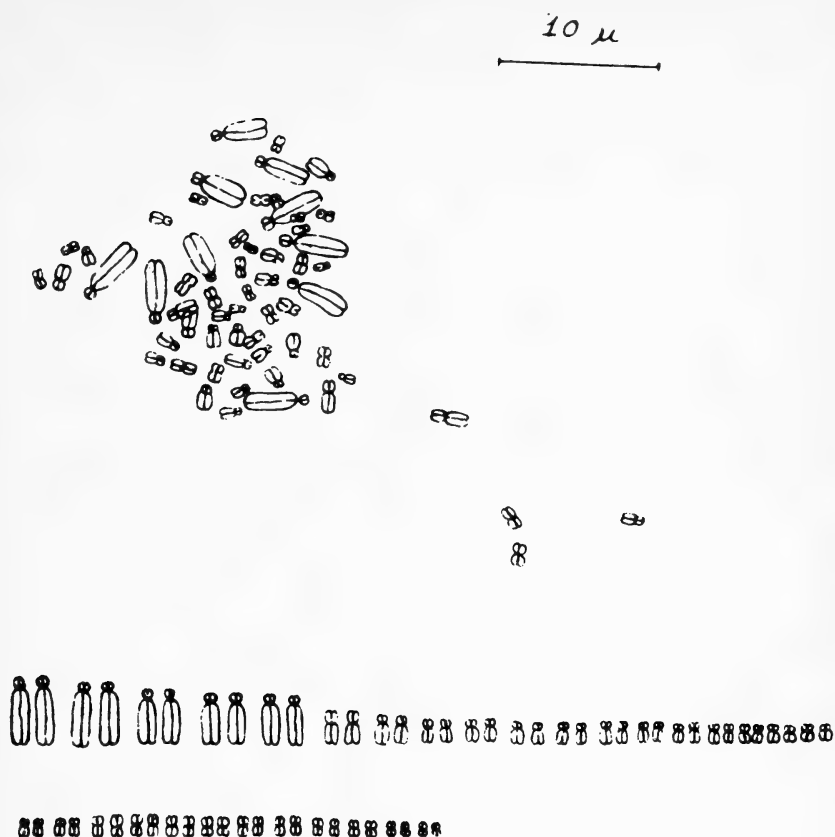
Fig. 11. Camera lucida drawings of themitotic chromosomes of *Hesperaloe funifera*, 2n = 60.

Literature Cited

Cave, M. S. 1964. Cytological observations on some genera of the Agavaceae. Madroño 17:163–170.

Cronquist, A. 1968. The evolution and classification of flowering plants. Houghton Mifflin, Boston.

Endlicher, S. 1841. Agaveae. Enchiridion Botanicum. . . . Engelman, Leipzig.

Flory, W. S., ad R. Varma. 1960. The genus Beaucarnea. Virginia J. Sci. 11:178.

Gómez-Pompa, A. 1963. El género Agave. Cact. Suc. Mex. 8:3–28.

————., and J. Valdés. 1962. Una especie epífita de Yucca de la Selva Lacandónica. Bol. Soc. Bot. México 27:43–45.

Fig. 12. *Yucca lacandonica* in its natural habitat in the state of Chiapas.

Granick, E. B. 1944. A karyosystematic study of genus Agave. Amer. J. Bot. 31:283–298.

Hutchinson, J. 1934. The families of flowering plants. Vol. II Monocotyledons. Macmillan, London.

Lotsy, P. 1911. Agavaceae. *Vortr. Stammesgesch.* III:806.

McKelvey, D., and K. Sax. 1933. Taxonomic and cytological relationships of Yucca and Agave. J. Arnold Arbor. 14:76–81.

Sato, D. 1935. Analysis of the karyotypes in Yucca, Agave and the related genera with special reference to the phylogenetic significance. Jap. J. Genet. 11:272–278.

————. 1938. Karyotype alteration and phylogeny. IV. Karyotypes in Amaryllidaceae with special reference to the sat-chromosome. Cytologia 9:203–242.

Fig. 13. *Hesperaloe funifera* (from San Luis Potosí) growing in the Jardin Botánico, UNAM.

————. 1942. Karyotype alteration and phylogeny in Liliaceae and allied families. Jap. J. Bot. 12:57–161.

SHARMA, A. K., and A. K. SARKAR. 1964. A study on the structure and behaviour of chromosomes in different species of Yucca. Bot. Tidsskr. 60:180–190.

THORNE, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. Aliso 6:57–66.

VILLALOBOS-PIETRINI, R. 1965. Alteraciones inducidas por los rayos X en los cromosomas de las células meristemáticas de la raíz de Vicia faba. I. Aspectos técnicos. Bol. Soc. Bot. México. 29:178–183.

WATKINS, G. M. 1936. Chromosome numbers and species characters in Yucca. Amer. J. Bot. 23:128–333.

WHITAKER, T. W. 1934. Chromosome constitution in certain monocotyledons. J. Arnold. Arbor. 15:135–143.

GENETICS OF LUPINUS. III. EVIDENCE FOR GENETIC DIFFERENTIATION AND COLONIZATION IN LUPINUS SUCCULENTUS (FABACEAE)

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Many species of higher plants occupy a diversity of habitats which results in the formation of localized races or ecotypes. The concept that genetic differentiation exists among natural populations of a species is well established and it is no longer necessary to review the evidence. It is clearly not enough to acknowledge that variation exists. It is necessary to understand the ecological factors which have contributed to genetic differentiation between populations. Why is a gene in high frequency in one population and in lower frequency or absent in another population? It is equally important to understand the genetic differences in greater detail. For example, are differences between populations the result of fixed-gene differences, gene frequncy differences, or chromosomal differences? In cases where evidence is available on genetic differences (e.g., Epling, Lewis and Ball, 1960; Jain and Joshi, 1962; Weil and Allard, 1965) evidence on ecological differences is lacking. Where ecological evidence is available (e.g., Bradshaw, 1959; 1960) genetic differences are not understood. Both genetic and ecological differences have been studied in *Ricinus communis* (Harland, 1947) and *Trifolium repens* (Daday, 1958), In these cases the resulting genetic structure could be related to ecological variables.

Comparative studies of colonizing and non-colonizing species have also received the attention of geneticists and ecologists. Genetic variability has been studied in the following, recently introduced, species: *Bromus mollis* (Knowles, 1943), *Ricinus communis* (Harland, 1947), *Trifolium subterraneum* (Morley, 1958), *Avena fatua* (Imam and Allard, 1965), and *Avena fatua* and *A. barbata* (Jain and Marshall, 1967). The results of these investigations can be compared to those obtained from investigations of the following, relatively non-colonizing species: *Linanthus parryae* (Epling and Dobzhansky, 1942), *Collinsia heterophylla* (Weil and Allard, 1965) and *Festuca microstachys* (Kannenberg and Allard, 1967). Comparisons between colonizing and non-colonizing species are discussed throughout the symposium *The Genetics of Colonizing Species*. In that symposium Lewontin (1965) suggests that emphasis should be placed on colonizing episodes rather than on the a posteriori study of colonizing species. Harper (1965) advises the creation of colonizing episodes by experimental introduction and states that such experiments may "reveal quite simple and fundamental properties of plant populations which classical descriptive ecology cannot uncover."

The introduction of founders into a new habitat does not always result in successful colonization, as shown by Sagar and Harper (1960). The advantages offered by California natives, which have become weedy (colonizing) since the agricultural revolution so drastically changed the ecology of the Central Valley of California, have been pointed out by Stebbins (1965). These species can be studied in their natural (original) habitats as well as in agricultural habitats where they have become colonizing agrestals. Colonizing episodes can be followed from their inceptions by both geneticists and ecologists.

Another possibility is the study of natural popuations and their descendant roadside (ruderal) popuations which are abundant throughout the foothills and mountains of California. *Lupinus succulentus* Dougl. is an annual California native which has become ruderal in many areas (Stebbins, 1965). There are now many more roadside populations than natural populations. Natural populations tend to occur in habitats with a considerable degree of disturbance suggesting that this species may have been preadapted for colonization. Since road-building is continuing, colonizing episodes are constantly initiated. In some cases, founders can be traced to their parental natural population. Some populations may be available for long-term studies, but many are transient and available for only a few years. Nevertheless, such populations offer unique opportunities for both ecological and genetical studies on population differentiation during the early stages of colonization.

The paper reports the results of an investigation concerning four loci in *L. succulentus*. Surveys of genotypic frequencies in natural and ruderal populations were made over a large geographic area and genetic polymorphism is related to seasonal fluctuations and to differences in the degree of disturbance of the habitat.

GENETICS

The papilionaceous flowers of *L. succulentus* are predominantly dark blue except for the white sulcus of the banner. Rarely, there occurs an entirely white flowered variant. Crosses between wild-type (blue) and white gave an F_2 segregation ratio of 53:24, wildtype: white. Pink flowered plants occur rarely and when crossed to wild-type gave an F_2 ratio of 81:27, wild-type: pink. These results are in accord with the inheritance of white and pink in *Lupinus nanus* Dougl. (Harding and Mankinen, 1967) and analogous genetic symbols will be assigned, viz. bb for white and pp for pink. Light blue flowered plants are observed more frequently and crosses to wild-type gave an F_2 ratio of 89:26, wild-type: light blue (designated dd). The presence or absence of a band of dark pigmentation across the seed coat was found to segregate 85:30, band: no band. The recessive, lacking the band, is designated ss. Chi-square tests indicate that none of these ratios depart significantly from the 3:1 Mendelian expectation.
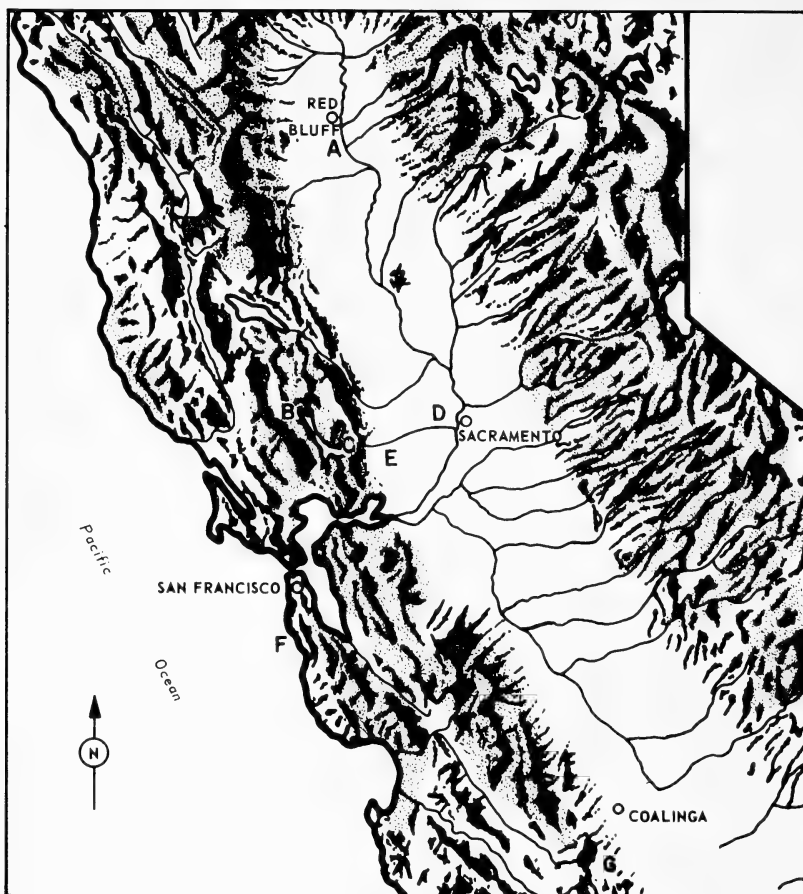
Fig. 1. Northern half of California showing collection areas A through G.

Since some populations are polymorphic for D/d and S/s, the linkage relationship is of interest. The F_2 coupling phase dihybrid ratio was 85:4:0:26 for D–S–:D–ss:ddS–:ddss, which deviates significantly from the expected 9:3:3:1. The maximum likelihood estimate of the recombination fraction, r, is given by the solution of

$$85 \frac{2r-2}{r^2-2r+3} + 4 \frac{2r-2}{r^2-2r} + 26 \frac{2}{r-1} = 0.$$

Use of Allard's tables (Allard, 1956) results in an estimate of $r = .04$ with a standard error of .02. Thus, D/d and S/s are very closely linked.

GEOGRAPHIC VARIATION

The distribution of *L. succulentus* is disjunct with the largest concentration along the Pacific Coast of California. This coastal group is represented by many populations from Mendocino County, California,
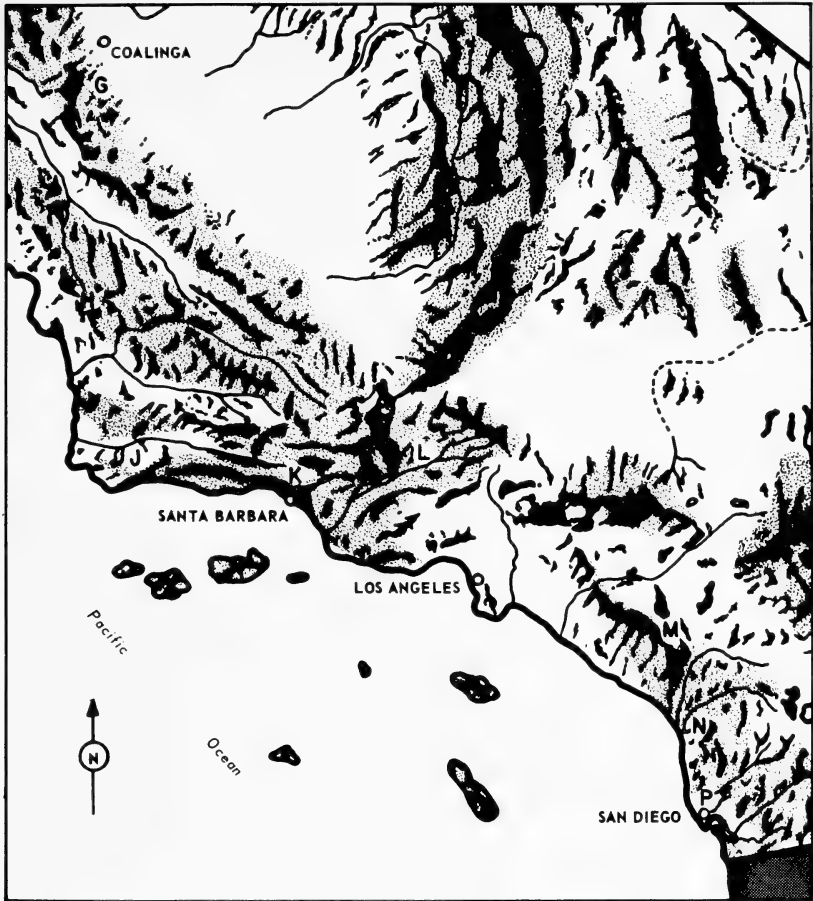
Fig. 2. Southern half of California showing collection areas G through P. Note some overlap with Fig. 1.

to northernmost Baja California, Mexico (Munz, 1959). These populations occur in the foothills of the North Coast, South Coast, Transverse, and Peninsular Ranges and on the off shore islands of San Clemente (Raven, 1963), Santa Catalina (Thorne, 1967), Anacapa, San Miguel, Santa Cruz and Santa Rosa (Philbrick and Emery, pers. comm.). The interior group occurs in the Pinal and Mazatzal Mountains (Gila and Maricopa counties) of Arizona (Kearney and Peebles, 1951). Since differences are not yet understood, the loose terms coastal taxon and interior taxon will be used to avoid questions regarding possible subspecific epithets.

The present study is based on the coastal group, including populations from the North and South Coast Ranges, the Transverse and Peninsular Ranges, and the Central Valley. Collection areas are given

by the letters A through F in Fig. 1 and by the letters G through P in Fig. 2. Area A includes the north end of the Sacramento Valley. The Red Bluff, Tehema, Corning, and Orland populations are ruderals along Interstate Highway 5 and varied in size from 300 to 1000 plants in 1968. Area B is northwest of Lake Berryessa between Putah Creek and Pope Creek. The upper Putah populations lie between Pope Creek and Pope Canyon Road on highly eroded slopes. Population size ranged from 300 to more than 30,000 plants in 1967. Area C includes Putah Canyon from Monticello Dam to the valley floor and the foothills between Putah Canyon and Cache Canyon. The Lower Putah populations are situated serially along Highway 128 and are ruderal with varying degrees of disturbance. They vary in size from 200 to approximately 1,500 plants in most years studied. The Mace populations are located near Cottonwood Creek and appear to be relatively undisturbed, except for natural erosion. Mace-30 was approximately 1000 plants in 1967 and Mace-11 became extinct after a population size of 100 was observed in 1963. The valley floor in the vicinity of Davis is designated Area D. Most populations on the valley floor are small, ephemeral colonies. The El Macero populations, which were located along the Southern Pacific railway between Davis and Sacramento, are now extinct. The Davis-1 population is located on a road cut along Interstate Highway 80 on the west edge of Davis and was composed of 328 plants in 1968. Area E includes the foothills in the vicinity of Vacaville and Vallejo. The Vacaville populations are large and occur along the north side of Interstate Highway 80 between Vacaville and Fairfield with varying degrees of disturbance.

In the South Coast Ranges Area F includes the coastal fog-belt along the Pacific Ocean between San Francisco and Santa Cruz. The San Gregorio population is located in the San Gregorio Beach State Park on a steep slope immediately adjoining the beach within reach of the spray and included approximately 80 plants in 1967. The dry foothills of the South Coast Ranges from Coalinga to Taft are designated Area G. The Tar Canyon population is large and is located southwest of Avenal with relatively little signs of disturbance. The Reef City-1 population is ruderal along State Highway 41 between Reef City and Cholame. It included 50 to 60 plants in 1968. Area H includes the coastal area from Atascadero to Santa Maria. The San Luis Obispo-1 population is a roadside colony along U. S. Highway 101, approximately six miles south of San Luis Obispo and was composed of approximately 500 plants in 1968.

In the Transverse Ranges, Area J includes the north-western half of the Santa Ynez Mountains and River Valley. The Lompoc populations are ruderal aong State Highway 1 between Lompoc and Las Cruces. They varied in size from approximately 50 to 300 individuals in 1968. The Solvang-1 population was a very small colony of approximately

TABLE 1. FREQUENCIES AND BINOMIAL STANDARD ERRORS FOR DOMINANTS AT THE
S/s *and* D/d LOCI FROM 1962, 1963, 1966 AND 1967 COLLECTIONS.
THESE POPULATIONS WERE MONOMORPHIC BBPP.

				FREQUENCY	
POPULATION			YEAR	S–	D–
AREA B					
Upper Putah	—	1	1967	.26 ± .036	Mono DD
	—	2	1967	.10 ± .025	Mono DD
	—	3	1967	.41 ± .042	Mono DD
	—	4	1967	.70 ± .019	Mono DD
AREA D					
El Macero	—	1	1962	.05 ± .026	Mono DD
	—	3	1962	.02 ± .016	Mono DD
AREA E					
Vacaville	—	1	1963	.33 ± .023	Mono DD
	—	2	1963	.03 ± .016	Mono DD
AREA F					
San Gregorio	—	1	1967	Mono ss	Mono DD
AREA G					
Tar Canyon	—	2	1967	.81 ± .038	Mono DD
AREA C					
Lower Putah	—	1	1962	.38 ± .069	Poly D/d
	—	2	1962	.46 ± .094	Poly D/d
	—	1	1963	.76 ± .051	.03 ± .025
	—	2	1963	.36 ± .063	.40 ± .036
	—	2	1966	.42 ± .047	.49 ± .058
	—	3	1966	.14 ± .035	.95 ± .022
	—	4	1966	.14 ± .031	.87 ± .030
	—	5	1966	.10 ± .028	.95 ± .021
	—	2	1967	.42 ± .046	.30 ± .040
	—	3	1967	.18 ± .039	.95 ± .026
	—	4	1967	14. ± .034	.91 ± .025
	—	5	1967	.14 ± .026	.94 ± .013
Mace	— 11		1962	Mono ss	Mono DD
	— 30		1967	.01 ± .008	Mono DD

40 plants in 1968, occurring near State Highway 246 on a highly dis-
turbed site. Area K is the south-eastern half of the Santa Ynez Range
and includes the Santa Barbara populations which ranged in size from
approximately 100 to 150 plants in 1968. These roadside colonies occur
along State Highway 154 between Santa Barbara and San Marcos Pass.
Area L includes the interior Ranges between Newhall and the Tejon
Pass. The Castaic populations are large ruderals varying in size from
approximately 300 to 2000 individuals in 1968, and are situated along
Interstate Highway 5 approximately three miles north of Castaic.

In the Peninsular Ranges, Area M includes the area from Lake Elsi-
nore to Fallbrook. The Murrieta population, approximately 200 plants
in 1968, occurs along State Highway 71 just east of Murrieta. Area N
includes the coastal strip between Del Mar and San Clemente. The
Vista-1 population, with approximately 500 plants in 1968, occurs on a
recent road fill along State Highway 78 south of Vista. The southern-

TABLE 2. FREQUENCIES AND BINOMINAL STANDARD ERRORS FOR
S/s LOCUS FROM 1968 COLLECTIONS.

Population	Frequency S–	Population	Frequency S–
AREA A		AREA D	
Red Bluff — 1	.47 ± .043	Davis — 1	.03 ± .019
Tehema — 1	.79 ± .035	AREA K	
Corning — 1	.13 ± .031	Santa Barbara — 1	.62 ± .056
Orland — 1	.77 ± .037	— 2	.70 ± .069
— 2	.77 ± .062	AREA L	
AREA G		Castaic — 1	.36 ± .055
Reef City — 1	.17 ± .059	— 2	.70 ± .044
AREA H		AREA M	
San Luis Obispo — 1	.27 ± .036	Murrieta — 1	.52 ± .096
AREA J		AREA N	
Lompoc — 1	.85 ± .068	Vista — 1	.32 ± .039
— 2	.46 ± .040	AREA P	
Solvang — 1	.71 ± .099	Mission Bay — 1	Mono ss

most populations, including the San Diego and Tijuana areas are designated Area P. This includes the highly disturbed Mission Bay population which had approximately 100 plants in 1968.

The results indicate that all populations sampled are monomorphic BBPP. There were three questionable exceptions: the B/b locus in a small colony in Cowell Valley (Area C), the occurrence of three bb in Davis-1 (Area D), and the P/p locus in a small colony near Winters (Area D). The D/d locus is monomorphic DD in all populations sampled except the Lower Putah Populations (table 1) which have varying frequencies of dd. The relatively infrequent occurrence of polymorphisms for loci affecting flower color may result from natural selection favoring the dark blue color through pollinator preference. In contrast, the S/s locus is polymorphic in nearly all populations sampled (tables 1 and 2). The only exceptions are Mace-11, San Gregorio-1 (based on only 34 individuals, i.e. 68 s alleles) and Mission Bay-1. Populations, therefore, are generally homozygous BBPPDD and polymorphic for the alleles S and s. The Lower Putah Populations are notable exceptions, being polymorphic for D and d. The Lower Putah popoulations were sampled because they were polymorphic for D/d but seed coat variation for S/s was not observed until after the selection of populations to be sampled was made. Consequently, the populations studied are a random sample of *L. succulentus* populations with respect to the S/s locus and the observed ubiquity of this polymorphism is not biased by the choice of populations.

CLINAL AND SEASONAL VARIATION

When the Lower Putah populations were first observed in 1960, it appeared that the frequency of dd was low at the base of the canyon
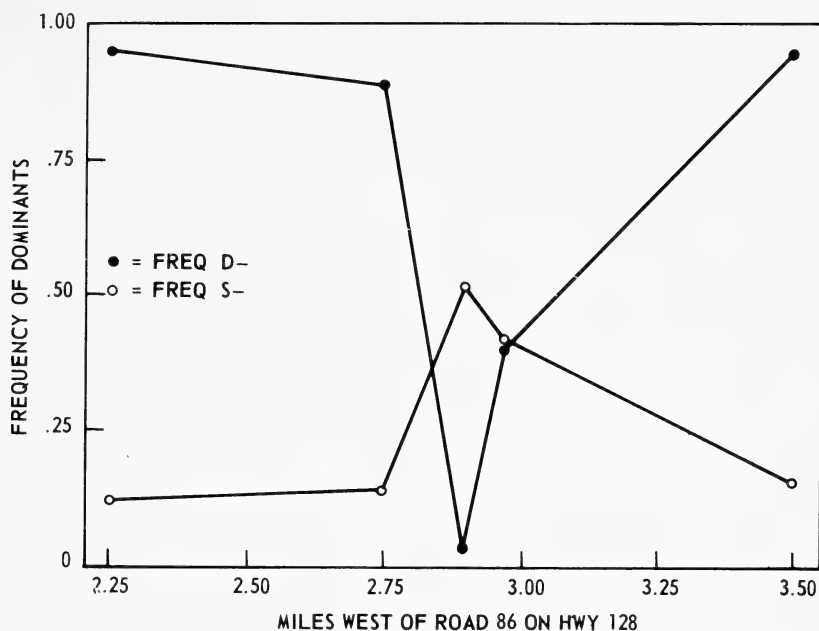
Fig. 3. Frequency of D- and S- in Lower Putah Canyon populations, plotted against distance in miles from an arbitrary point near the mouth of the canyon.

and increased in frequency as the canyon was ascended. After reaching a frequency of more than 50 per cent, the frequency of dd was quickly reduced in subsequent populations near the head of the canyon. The five Lower Putah populations were selected at more or less equally spaced intervals. The frequencies, plotted in Fig. 3, represent means for each population taken over the years sampled (table 1). The miles are measured from a purely arbitrary intersection of roads. Figure 3 shows the predominance of D-ss at both ends of the area with sharp increases of dd and S- in a segment less than one-half mile in length. This represents a sharp increase in genetic variability for D/d and S/s over a very short distance. These distances are well within the radius of activity of the predominant pollinating agent *Apis mellifera* L. The inter-relationship between the linked D/d and S/s loci will be the subject of another paper in this series.

Over the period of 8 years the frequencies in Putah Canyon populations appeared fairly stable. Those populations which have been sampled in more than one year are summarized in Fig. 4. The populations could not be sampled in 1964 and 1968 because there were very few plants presumably due to very low rainfall in those years. Their immediate return to large numbers in 1965 suggests that many seeds remain hard and overwinter during years of low winter rainfall.
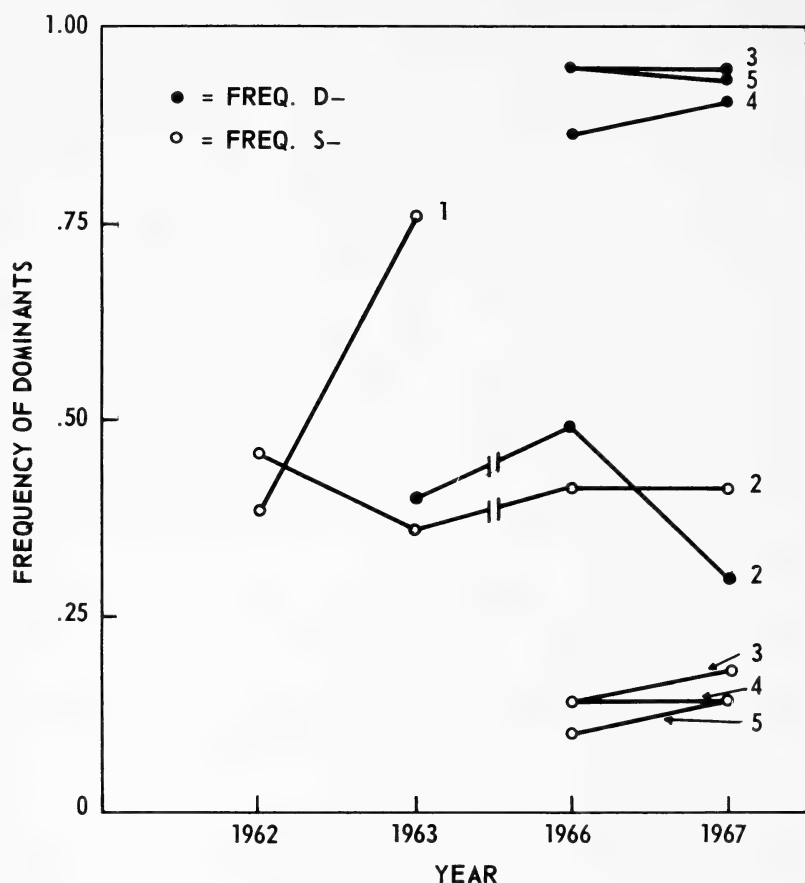
Fig. 4. Frequency of D- and S- in Lower Putah Canyon populations for the years sampled 1964, 1965 and 1968 were not sampled (see text).

Considering the seasonal fluctuations in gene frequency which may be expected in plant populations (e.g. Allard and Workman, 1963) the fluctuations are not great with the exception of S/s in Lower Putah-1 in 1962 and 1963. This population occurred on such a highly disturbed slope that it was abandoned after 1963. Although the remaining four populations are not likely in gene frequency equilibrium, they show a fair degree of stability considering their ruderal nature.

Intra-Population Differentiation

The Vacaville-1 population occupied a very large road-cut, 116 feet across, with population size more than 3,000 individuals in 1963. For convenience of collection the population was arbitrarily subdivided into four sub-populations according to the schematic representation in
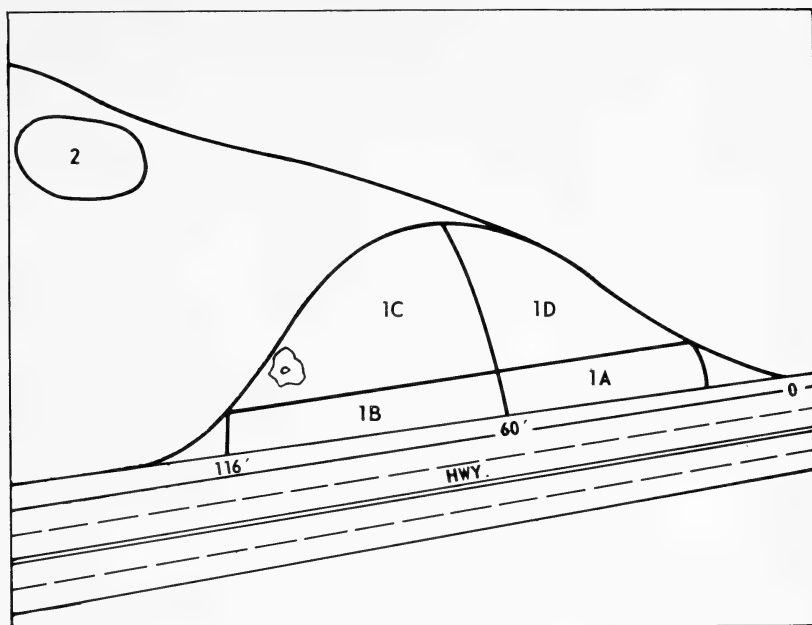
Fɪɢ. 5. Schematic representation of the sub-division of Vacaville -1 and -2 in 1963. The highway was U. S. Highway 40, now Interstate 80.

Fig. 5. Although the frequency of S- in the population as a whole was .33, the frequencies in the sub-populations were: 1C-: .47 ± .047; 1D-: .18 ± .039; 1B-: .50 ± .050; and 1A-: .17 ± .036. The frequencies and standard errors clearly indicate that 1A and 1D can be taken as one group and 1B and 1C as another group. Topographically, the difference is between the two sides of the population. However, further vertical subdivision might have revealed a continuous gradation across the population, i.e., an intrapopulational cline or microcline. This possibility could not be investigated because the population was subsequently destroyed by highway construction.

Another large population, Upper Putah-4, was chosen for further studies on intra-population differentiation. This population occupies a large highly disturbed hillside of approximately two acres with considerable variation in topography and population density. Population size was approximated at more than 30,000 and is probably nearer 50,000. It was subdivided and, although the subdivisions were based on gulleys and density gradients, they are considered fairly arbitrary because the population paproaches one large continuum. The frequency of S- in the population was .70 and the frequencies in the sub-populations were: 4A-: .79 ± .033; 4B-: .75 ± .034; 4C-: .74 ± .035; and 4D-: .53 ± .040. The three sub-populations, 4A, 4B and 4C, are not significantly different, but sub-population 4D differs significantly from the rest. The
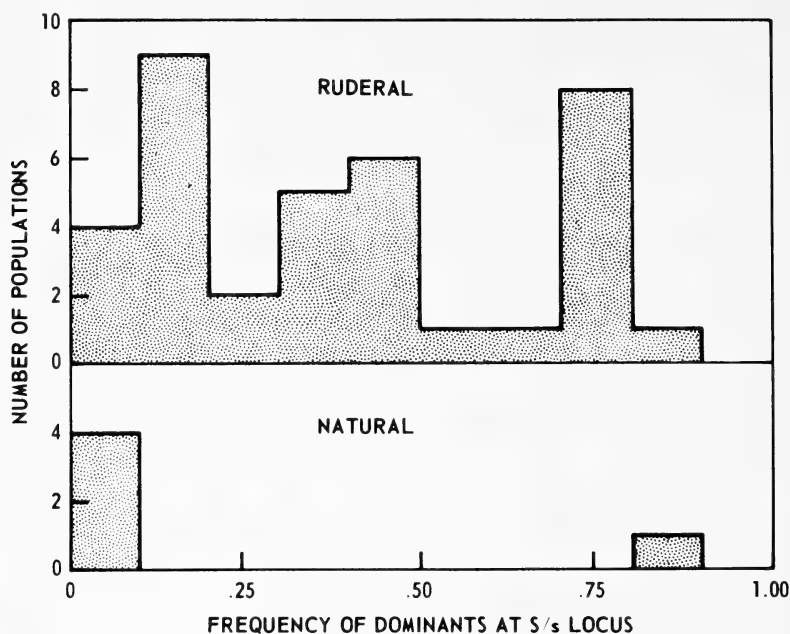
Fig. 6. Frequency of S- in all populations sampled, divided into those appearing natural and those ruderals appearing to be recently colonized.

frequency of S– is high in all sub-populations compared to the frequencies from other populations within Geographic Area-B, viz. .26, .10 and .41 (see table 1).

Population differentiation was not observed in all cases. Three subdivisions of Lower Putah-5 gave frequency estimates of .10, .13, and .16 for S–. The four subdivisions of Mace-30 gave estimates of 0, 0, .02 and .04. Two subdivisions of Castaic-2 gave estimates of .72 and .69 for S–. From these samples the extent of population differentiation cannot be determined. However, intrapopulational differences for the S/s locus were found in two of five populations studied.

Colonization

The populations under study all occupy habitats with varying degrees of disturbance. Attempts were made to locate populations in habitats with a minimum of disturbance. The populations with the least apparent disturbance were the Mace populations, Vacaville-2, San Gregorio and Tar Canyon. The remaining populations are ruderals which probably colonized recently. This classification of populations as to relatively disturbed vs. relatively undisturbed is necessarily subjective and based on limited numbers of observations. The differences (fig. 6) suggest, however, that polymorphisms at the S/s locus are more frequent in more disturbed roadside habitats. Furthermore, the D/d poly-

morphisms and the possible B/b and P/p polymorphisms were found only in disturbed sites and these are not included in Fig. 6.

As a new colony is founded by a limited number of immigrants, genetic drift is expected to reduce the genetic variance to an extent inversely proportional to the number of founders and subsequent effective population size. To the contrary, genetic variance appears to have increased with colonization for the cases studied herein. This increased genetic variation in recently colonized populations may result from several causes. First, as new environments are encountered, new selective forces may also be encountered. For alleles at any particular locus this could result in a change in the direction of selection. In addition, the more disturbed habitats may exhibit more environmental variation leading to increased intrapopulation differentiation. Additional factors may include density dependent and frequency dependent selection.

In the case of the Vacaville populations it appears that Vacaville-1, on a highly disturbed cut, was founded by immigrants from Vacaville-2 (fig. 5). The road cut is deep into relatively undecomposed parent material, presumably low in nitrogen. The nitrogen fixing legume, *L. succulentus*, was apparently suited to colonize such an environment relatively free from the competition of grasses, at least in the early stages of colonization. With the colonization of Vacaville-1 the frequency of S– increased. If this were a purely random process, the majority of ruderal populations would be ss with an occasional population predominantly S–. But, as this is not the case, it appears that selection must have been involved. These hypotheses need testing in situ during the early stages of colonizing episodes and such episodes are presently being sought.

Baker (1965) discussed the various attributes which enable an annual to become a successful colonizer and concluded that "Probably no existing plant has them all." This appears to be the case for *L. succulentus*. While it is self-compatible, many pollen collecting insects cannot manipulate the large and specialized papilionaceous flower. This, however, could be compensated by the wide occurance of *Apis mellifera*. *L. succulentus* has a tremendous seed fertility compared to most other species of *Lupinus* and dispenses its seeds by explosive dehiscence of the pods. Apparently, the colonizing characteristics of *L. succulentus*, particularly self-compatability, fertility and dispersal, are sufficient to account for its recent succes in colonization.

Summary

Preliminary surveys indicate that most populations of *Lupinus succulentus* are genetically monomorphic for three flower color loci, viz., BB PP DD. In one small geographic area, a number of populations were polymorphic for the D/d locus. In this case, clinal variation and seasonal variation were found. The S/s locus which affects seed coat pigmenta-

tion was polymorphic in a large majority of populations and some genetic variation at this locus may be present in all but a very few colonies. Gene frequencies tended toward the limits of zero or one in populations from relatively undisturbed sites but tended toward one-half in the more disturbed ruderal populations presumed to be recently colonized. Five large populations were subdivided and genetic differentiation was found within two of these populations. No ecological basis has been found to account for population differentiation or for changes which occur during colonization. Various characteristics of *Lupinus succulentus*, in particular the dispersal of seeds and the high seed fertility, appear to be most important in determining its success in colonization.

ACKNOWLEDGMENTS

LITERATURE CITED

ALLARD, R. W. 1956. Formulas and tables to facilitate the calculation of recombination values in heredity. Hilgardia 24:235–278.
————., and P. W. WORKMAN. 1963. Population studies in predominantly self-pollinated species. IV. Seasonal fluctuations in estimated values of genetic parameters in lima bean populations. Evolution 17:470–480.
BAKER, H. G. 1965 Characteristics and modes of origin of weeds. *In* H. G. BAKER and G. L. STEBBINS (eds.), The genetics of colonizing species. Academic Press, New York.
BRADSHAW, A. D. 1959. Population differentiation in Agrostis tenuis Sibth. I. Morphological differences. New Phytol. 59:92–103.
DADAY, H. 1958. Gene frequencies in wild populations of Trifolium repens. III. World distribution. Heredity 12:169–184.
EPLING, C., and T. DOBZHANSKY. 1942. Genetics of natural populations. VI. Microgeographical races in Linanthus parryae. Genetics 27:317–332.
EPLING, C., H. LEWIS, and F. M. BALL. 1960. The breeding group and seed storage: a study in population dynamics. Evolution 14:238–255.
HARDING, J., and C. B. MANKINEN· 1967. Genetics of Lupinus. I. Variations in flower color from natural populations of Lupinus nanus. Canad. J. Bot. 45: 1831–1836.
HARLAND, S. C. 1947. An alteration in gene frequency in Ricinus communis L. due to climatic conditions. Heredity 1:120–125.
HARPER, J. L. 1965. Establishment, aggression, and cohabitation in weedy species. *In* H. G. BAKER and G. L. STEBBINS (eds.), The genetics of colonizing species. Academic Press, New York.
IMAM, A. G., and R. W. ALLARD. 1965. Population studies in predominantly self-pollinated species. VI. Genetic variability between and within natural populations of wild oats, Avena fatua L. from differing habitats in California. Genetics 51:49–62.
JAIN, S. K., and B. C. JOSHI. 1962. Local differentiation in some natural populations of Justicia simplex. Genetics 47:789–792.
JAIN, S. K., and D. R. MARSHALL. 1967. Population studies in predominantly self-

pollinating species. X. Variation in natural populations of Avena fatua and A. barbata. Amer. Naturalist 101:19–33.

KEARNEY, T. H., and R. H. PEEBLES. 1951. Arizona flora. Univ. California Press, Berkeley.

KNOWLES, P. F. 1943. Improving an annual brome grass, Bromus mollis L. for range purposes. J. Amer. Soc. Agron. 35:584–594.

LEWONTIN, R. C. 1965. Selection for colonizing ability. In H. G. BAKER and G. L. STEBBINS (eds.), The genetics of colonizing species. Academic Press, New York.

MORLEY, F. H. W. 1958. The inheritance and ecological significance of seed dormancy in subterranean clover (Trifolium subterraneum L.). Austral. J. Biol, Sci. 11:261–274.

MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.

RAVEN, P. H. 1963. A flora of San Clemente Island, California. Aliso 5:289–347.

SAGAR, G. R., and J. L. HARPER. 1960. Factors affecting the germination and early establishment of Plantains (Plantago lanceolata, P. media and P. major). In J. L. HARPER (ed.), The biology of weeds. Blackwell, Oxford.

STEBBINS, G. L. 1965. Colonizing species of the native California flora. In H. G. BAKER and G. L. STEBBINS (eds.), The genetics of colonizing species. Academic Press, New York.

THORNE, R. F. 1967. A flora of Santa Catalina Island, California. Aliso 6:1–77.

WEIL, J·, and R. W. ALLARD. 1965. The mating system and genetic variability in natural populations of Collinsia heterophylla. Evolution 18:515–525.

THE POLYPODIUM VULGARE COMPLEX IN THE PACIFIC NORTHWEST

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INTRODUCTION

The *Polypodium vulgare* complex in the Pacific Northwest has been a problem to taxonomists since a number of names have been applied to ill-defined and inadequately understood taxa. In 1961 the author began a critical study of this complex in northwestern North America using modern biosystematic methods in an effort to clarify the taxonomic situation and if possible to elucidate the evolution of the complex (Lang 1965). The basic findings of this paper have recently been briefly summarized by Taylor (1970). A more detailed discussion is presented here to further clarify the taxonomy and evolution of the complex in the Pacific Northwest.

As defined here, northwestern North America comprises the area from Alaska south along the Pacific Coast to central California and east to the Rocky Mountains. Although most of the populations of the complex examined here were from this area, a number of herbarium specimens from elsewhere in western North America were also studied.

The specimens examined in this study were from UBC, UC, US, V, WS, and WTU. A complete list of specimens examined is available from the author on request.

The genus *Polypodium* in this geographical area centers around two princple groups: one is represented by *P.. glycyrrhiza* D. C. Eaton, the other by *P. hesperium* Maxon. At their morphological extremes these two taxa are distinct; but they are so variable that their boundaries are often blurred, and it is often difficult to distinguish them using the classical characteristics of frond size and frond segment shape.

In central California, *P. californicum* Kaulf. and *P. glycyrrhiza* are apparently closely related (Lloyd and Lang, 1964; Lloyd, 1962). *Polypodium scouleri* Hook. & Grev., distinctive in its morphology and geographical distribution, raises no taxonomic problems. The eastern North American *P. virginianum* L. known also from northeastern British Columbia and the Yukon, is considered only as it relates to *P. hesperium.* These three species appear to have played no immediate role in the evolution of the *P. hesperium-glycyrrhiza* complex.

POLYPODIUM HESPERIUM-GLYCYRRHIZA COMPLEX

As far as can be determined, the European species of the *P. vulgare* complex, as delimited by Shivas (1961a; 1961b), *P. vulgare* L. sens. strict., *P. australe* Fée, and *P.. interjectum* Shivas, are not present in my study area.

During the course of the investigation, an interesting problem was discovered concerning those forms centering about *P. hesperium* Maxon. Typically, any *Polypodium* from western North America, with short blunt frond segments has been considered to be *P. hesperium*. As previously reported, there are two cytotypes within *P. hesperium,* a diploid $n = 37$, (Manton, 1950; Evans, 1963) and a tetraploid $n = 74$ (Knobbloch, 1962; Lloyd, 1963). These reports are from geographically widely separated populations, the tetraploids from Arizona, the diploids from Washington and Oregon. Cytological investigations of populations of *Polypodium* from British Columbia have shown that both cytotypes of *P. hesperium* are present and that *P. glycyrrhiza* is uniformly diploid.

Further study of the tetraploid and diploid cytotypes of *P. hesperium* revealed that there were other differences between them in addition to geographical distribution and cytology. These differences are summarized in Table 1 along with the distinguishing features of *P. glycyrrhiza* and *P. virginianum.*

It is felt that the differences between the two cytotypes usually included in *P. hesperium* sens. lat. are such as to warrant their recognition as two distinct species. The name *Polypodium montense* Lang was proposed for the diploid cytotype formerly included in *P. hesperium* sens. lat. (Lang, 1969).

TABLE 1. CHARACTERS DISTINGUISHING POLYPODIUM GLYCYRRHIZA
P. HESPERIUM, P. MONTENSE, AND P. VIRGINIANUM

	P. glycyrrhiza	P. hesperium	P. montense	P. virginianum sens. lat
Chromosome No.	n = 37	n = 74	n = 37	n = 37, n = 74
Frond shape	oblong to ovate	oblong	oblong	oblong-triangular
Segment shape Index (mean)	1.65	2.72	2.99	. . . .
Segment shape	acuminate to acute	acute to obtuse	obtuse	acute
Sorus shape	circular	oval	circular	circular
Sorus location	median	median	submarginal	submarginal
Paraphyses	absent	very rare	common	common
Rhizome taste	licorice	licorice	acrid	acrid
Scale stripe	absent	absent	+ —	present
New fronds	autumn	summer	spring	summer
Geographical distribution	coastal	interior	western mountains	eastern N. America

The examples of Manton (1950) and Shivas (1961a; 1961b) in considering the cytotypes of the *P. vulage* complex as distinct species have been followed here. As in the European ones the northwest North American cytotypes display the fundamental characteristics of distinct natural taxa. They appear to be reproductively isolated, possess distinctive geographical and ecological distributions, and can be distinguished morphologically, although admittedly not always with ease.

Table 2 indicates the synaptic chromosomal association at diakensis in these plants and the source of the material. The tetraploid populations of *P. hesperium* are from the interior of British Columbia while the diploids, *P. montense,* are from the coastal mountains. Figures 3g, 4f, and 5f show diakinesis in both cytotypes of *P. hesperium* and *P. glycyrrhiza.*

When it was discovered that both the tetraploid and diploid cytotypes were present in British Columbia, a search was made for possible triploid hybrids in areas where all three cytotypes, the two of *P. hesperium* and that of *P. glycyrrhiza,* might be sympatric. A search of the Fraser River Canyon and Cheakamus River regions of British Columbia yielded two morphologically distinct triploid hybrids (fig. 6, 7). At metaphase I of meiosis both triploids showed 37 bivalents plus 37 univalents. Mature sporangia contained aborted spores varying in size and degree of malformation. The aborted spores appeared to be similar to those described by Wagner and Chen (1965) in hybrid *Dryopteris*. The significance of these hybrids will be discussed later.

THE DIFFERENCES BETWEEN
P. GLYCYRRHIZA, HESPERIUM, AND MONTENSE

In addition to Table 1, more information concerning the differences between these three species is provided by the species descriptions in the systematic treatment and the illustrations, Figs. 3, 4, and 5. It is neces-

TABLE 2. CHROMOSOME NUMBERS IN POLYPODIUM IN NORTHWEST NORTH AMERICA

Collections (UBC) are from British Columbia unless otherwise noted. Collection numbers are those of Lang, unless otherwise noted. Meiotic association and/or diploid number are given.

P. hesperium. 74ᵢᵢ, Clearwater, *70, 112*; 74ᵢᵢ, **2n = 148**, Clearwater, *71, 111, 114*; 74ᵢᵢ, **2n = 148**, Craigellachie, *73*; 74ᵢᵢ, **2n = 148**, Wigwam, *74;* 74ᵢᵢ, **2n = 148**, Kootenay Bay, *Bosorowich* s.n.; **2n = 148**, Alta Lake, *212*; **2n = 148**, Marblehead, *Taylor & Szczawinski 610*; 74ᵢᵢ, Cambie, *Taylor & Szczawinski 442*; 74ᵢᵢ, Lake Chelan, Washington, *130, 138*.

P. montense. 37ᵢᵢ, Mt. Seymour, *96, 218*; 37ᵢᵢ, near Cheekeye, *117C2*; 37ᵢᵢ, Yale, *120, 118*; **2n =74**, McGuire, *211*; **2n = 74**, Garibaldi, *214*; 37ᵢᵢ, Alexander Bridge, Fraser R., *122–6*.

P. glycyrrhiza. 37ᵢᵢ, Troutdale, Oregon, *188, 189*; 37ᵢᵢ, Crown Pt., Columbia River Gorge, Oregon, *190, 192*; 37ᵢᵢ, Queen Charlotte Islands, *24, 26, 28, 30, 33;* 37ᵢᵢ, Terrace Bridge, *53;* 37ᵢᵢ, *Squamish, 221;* 37ᵢᵢ, Howe Sound, *222, 223;* 37ᵢᵢ, Pitt River, *216, 217*; 37ᵢᵢ, Cheekeye, *106*; **2n = 74**, Garibaldi Station *213*.

P. hesperium × montense. 37ᵢᵢ + 37ᵢ, Alexander Bridge, Fraser River, *122–3*.

P. glycyrrhiza × hesperium. 37ᵢᵢ + 37ᵢ, **2n = 111**, Alexander Bridge, Fraser River, *125–2*; **2n = 111**, Green River, *210C*.

TABLE 3. SUMMARY OF FROND MEASUREMENTS OF POLYPODIUM GLYCYRRHIZA, P. HESPERIUM, AND P. MONTENSE

	Blade length	Blade width	Stipe length	Segment length	Segment width	Ratio seg. l/w	Segment tip index
P. glycyrrhiza							
N	325*	354	375	339	287	349	210
Observed							
range	20–470	14–156	11–340	7–85	3–11	1.8–12.00	1.0–3.0
Mean	172.6	60.30	93.56	33.28	6.65	5.6	1.65
80% obs.**	69–280	35–92	36–143	18–53	5–8	3.3–7.4	....
P. hesperium							
N	199	171	223	218	215	284	206
Observed							
range	30–265	12–83	12–155	9–45	5–11	1.3–3.8	1.5–3.0
Mean	114.09	33.29	56.75	17.64	7.25	2.44	2.72
80% obs.**	63–189	22–48	28–100	11–25	6–9	1.9–3.1	....
P. montense							
N	216	224	213	221	220	315	217
Observed							
range	18–190	11–45	8–142	5–25	3–12	1.2–3.6	2.0–3.0
Mean	80.58	23.58	57.94	12.92	5.60	2.35	2.99
80% obs.**	46–122	17–30	28–100	9–17	4–7	1.8–3.0	....

* All measurements in mm.
** The two extreme values between which 80 per cent of the observations fell.

sary here, however, to comment on some of the more important differences and to discuss some of the salient features that might be indicative of the relationships of the taxa.
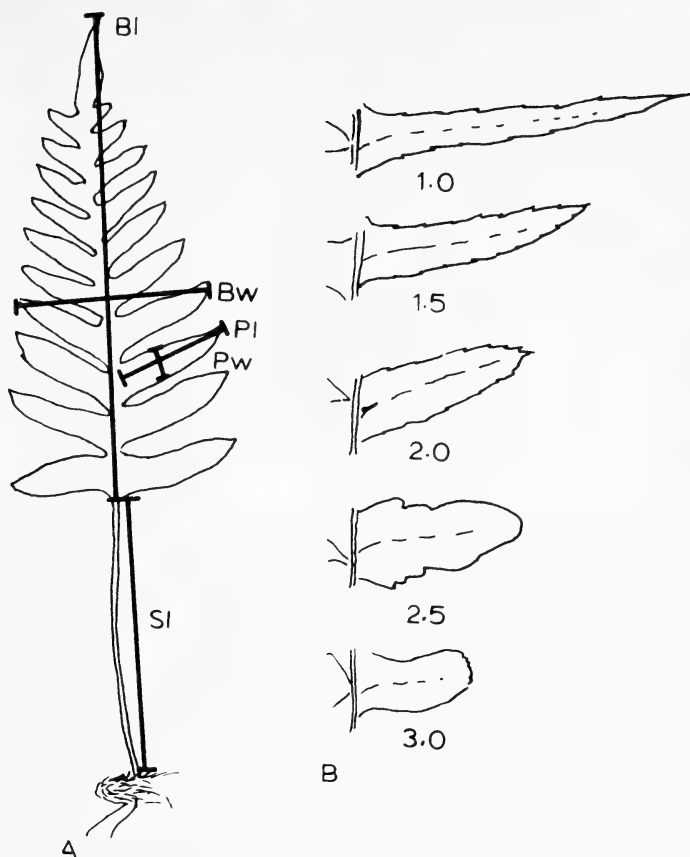
Fig. 1. Quantitative measures made on *Polypodium*: a, linear measurements, Bl—blade length, Bw—blade width, Pl—pinnae length, Pw—pinnae width, and Sl—stipe length; b, numerical index for expressing the shape of the frond segments (see text for explanation).

Figure 1a shows the frond measurements that were taken to circumscribe the variation in the size of the fern. As seen in Table 3, the three species of *Polypodium* from the Pacific Northwest are difficult to separate using the quantitative characters of blade length, blade width and stipe length because of the overlap in size range. The shape of the frond segment has often been used as a diagnostic character to distinguish between *P. glycyrrhiza* and *P. hesperium* sens. lat. To quantify the shape of the frond segments, an arbitrary index was assigned to the range of shapes found in the *P. vulgare* complex in the Northwest. The most attenuated segments were assigned 1.0 with 0.5 steps given to intermediate shapes up to 3.0 for the most obtuse frond segments. Figure 1b shows the shapes and the numbers assigned to them. Specimens of *P. glycyrrhiza, P. hesperium,* and *P. montense* were examined and the shape
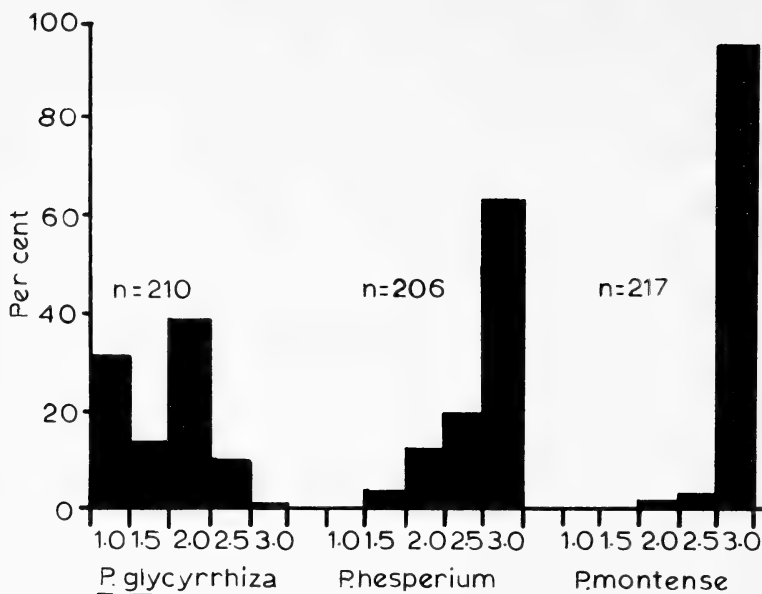
Fig. 2. Distributions of the numerical index of segment shape expressed as per cent of total in *P. glycyrrhiza*, *P. montense*, and *P. hesperium*.

index for each plant determined. The results of this study (fig. 2) show the great overlap between *P. montense* and *P. hesperium*. This overlap in the 3.0 range (obtuse segments) may be one reason why the diploid *P. montense* remained undetected among the plants of tetraploid plants of *P. hesperium*.

The morphology of epidermal cells has recently proved to be valuable in taxonomic and evolutionary studies of the pteridophytes (Blasdell, 1963; Wagner, 1954; Evans and Wagner, 1964). Although epidermal morphology does not provide any clear diagnostic characters for distinguishing members of the *P. vulgare* complex, these cells do exhibit patterns which are useful in assessing relationships among the taxa when other evidence is also considered.

The shape of the epidermal cells differs in the lower and particularly the upper epidermis among the species. The upper epidermal cells in *P. hesperium* (fig. 3c) are more or less intermediate between the two diploids (compare fig. 4c–5c). At the tips of the free vein ends of the fronds, on the upper surface, there are structures that appear to be hydathodes (figs. 3e, 4e, 5e). In *P. montense* these structures are frequently smaller and composed of fewer cells than those of the other two species.

The guard cells of the lower epidermis of *P. hesperium* seem to be larger (usually more than 24 μ long) and fewer in number per square millimeter (average ca. 35 per mm^2) of leaf surface than those of *P.*

montense and *P. glycyrrhiza* (both less than 24 μ long and averaging ca. 50 per mm²). These differences are probably correlated with the tetraploid condition of *P. hesperium.*

Sorus shape, useful in separating the species, is not without some drawbacks. The sorus shape is often obscured in mature specimens by dehisced sporangia. In contrast sorus shape is usually quite clear in specimens with immature sporangia. *Polypodium glycyrrhiza* (fig. 5d) and *P. montense* (fig. 4b) usually have sori that are circular in outline while *P. hesperium* (fig. 3d) has larger oval sori.

The position of the sorus on the frond segment also is a useful character. In *P. glycyrrhiza* and *P. hesperium* the sori are located medially between the segment margin and the costa while in *P. montense* and *P. virginianum* they are located nearer the margin.

Shivas (1961a; 1961b) used the number of annular cells to distinguish the European species with considerable success. Counts of annular cells in Northwest taxa yielded no definite pattern, with sporangia from all species examined having between 12–14 cells per annulus.

One interesting morphological feature is the presence of paraphyses scattered among the sporangia of *P. montense* and *P. hesperium.* The paraphyses are commonly found in *P. montense,* but are very infrequent in *P. hesperium.* They are absent in *P. glycyrrhiza.* The paraphyses seem to be identical to those found in *P. virginianum* (Martens, 1950; Morton and Neidorf, 1954). A paraphysis from *P. montense* is shown in Fig. 4d.

In addition to cytological and morphological differences, the three Northwest taxa differ chemically as well. The rhizomes of *P. glycyrrhiza* and *P. hesperium* taste somewhat like licorice while *P. montense* (and *P. virginianum*) have an acrid taste. Fischer and Lynn (1933) investigated *P. glycyrrhiza* as a possible source of licorice and found that no glycyrrhizin (a compound found in true licorice, *Glycyrrhiza glabra,* that is fifty times sweeter than sugar) was present. They concluded that the licorice-like taste was due to a mixture of a glucoside which they called polypodin, some unidentified substances, and sucrose. The chemical composition of a plant sometimes can be determined by the taste of the rhizome.

Some of the characteristics of the rhizome scales are also helpful in distinguishing between the taxa of *Polypodium* in the Northwest (figs. 3a, 4a, 5a). In addition to differences in size and the degree of toothing on the margin of the scales, when compared to the other species, *P. montense* often has a distinctive dark median stripe down its center. This is invariable the case in *P. virginianum.* The median stripe is absent in *P. glycyrrhiza* and *P. hesperium.* Boborov (1964) used the nature of the rhizome scale as an important diagnostic characteristic in his analysis of the *Polypodium* species of the USSR.

In all three species the old fronds are shed during or shortly after the annual initiation of new fronds. The species produce new fronds at dif-

ferent times of the year and, as a consequence, meiosis occurs and the spores mature at different times.
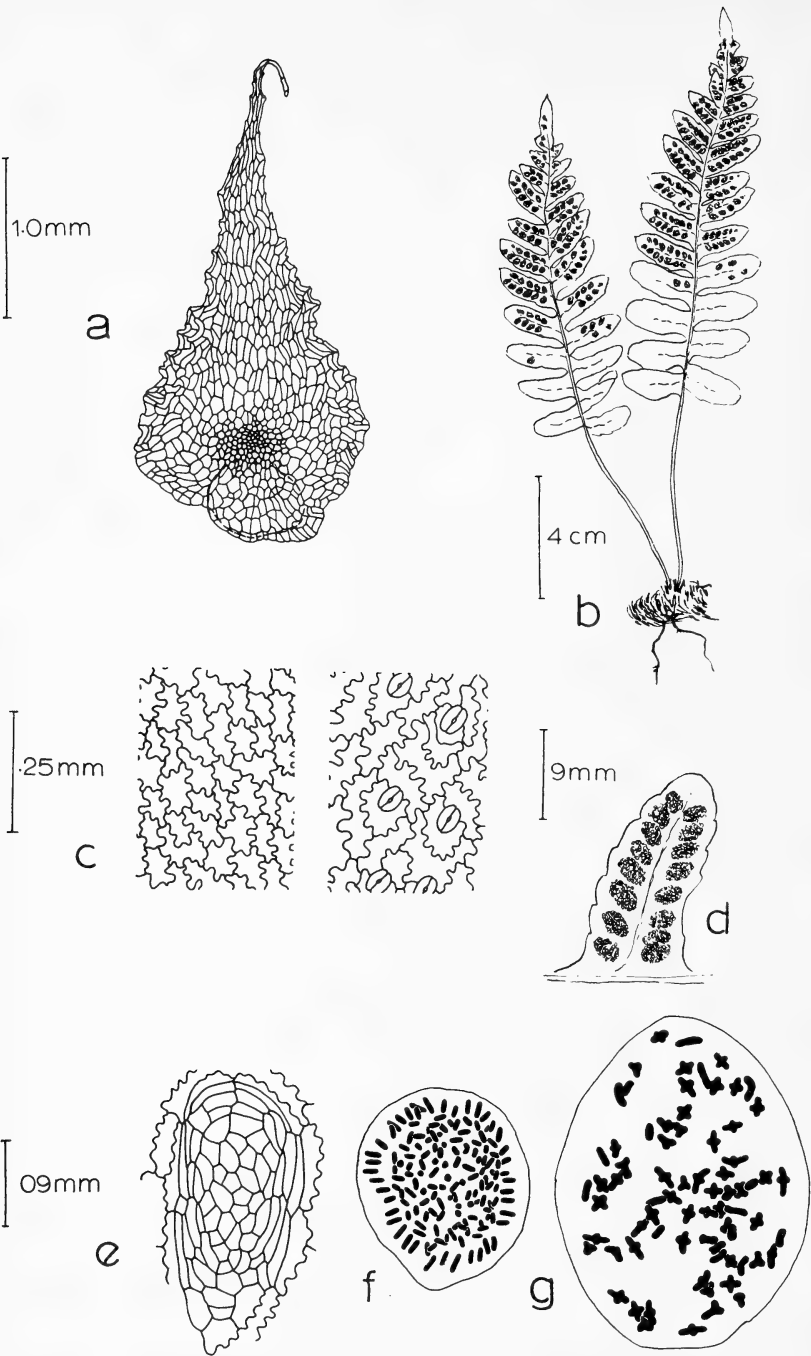
New fronds are produced by *P. glycyrrhiza* from June onward. Most specimens seem to produce new fronds in late summer with meiosis occurring in the fall. Mature spores can be found throughout the fall and winter months. *Polypodium hesperium* produces new fronds throughout the summer with the first being initiated in May. Plants can be found in all stages of development during most of the summer. New fronds are usually produced by *P. montense* in April or May with the spores maturing in June, July, and August.

In any given region the majority of the plants of a particular species produce new fronds at about the same time. In most localities where the species are found together, there is usually a considerable interval between the initiation of fronds in each case. In the Fraser River Canyon of British Columbia, for example, *P. montense* produces new fronds several months before *P. glycyrrhiza* initiates them.

Variations in the time of initiation of new fronds can be related to different climatic conditions in different parts of the species ranges or to annual fluctuations in local climatic conditions. Plants of *P. glycyrrhiza* from the north coast of British Columbia tend to put up their fronds earlier than those on the south coast. This could be accounted for by differences in climatic conditions in the north.

An example of an annual fluctuation of local climate affecting initiation of new fronds was noted in a population of *P. montense* from Mount Seymour, British Columbia. Cytological material was collected late in May 1962. The next spring material in the same condition could not be collected until almost a month later because the growing season was delayed by the late melting of the unusually heavy snowfall the preceding winter.

A map showing the distribution of these species in the Pacific Northwest has already been published (Lang. 1969).

Systematic Treatment

When attempting to identify *Polypodium* species, difficulty is sometimes encountered when the specimen does not clearly show all of the diagnostic characteristics. For this reason a pragmatic key to the species is provided.

Fig. 3. Morphology and cytology of *Polydium hesperium:* a, rhizome scale, *Lang 212-C*; b, type specimen of *P. hesperium, M. W. Gorman 642*; c, upper and lower epidermal patterns, *Lang 74, Lang 111*; d, frond segment, note large oval sori, *Lang 111*; e, hydathode from upper epidermis, *Lang 71*; f, mitosis, $2n = 148$, *Lang 201-A*; g, spore mother cell at diakinesis in *P. hesperium* from type locality, $n = 74$, *Lang 130–4*.
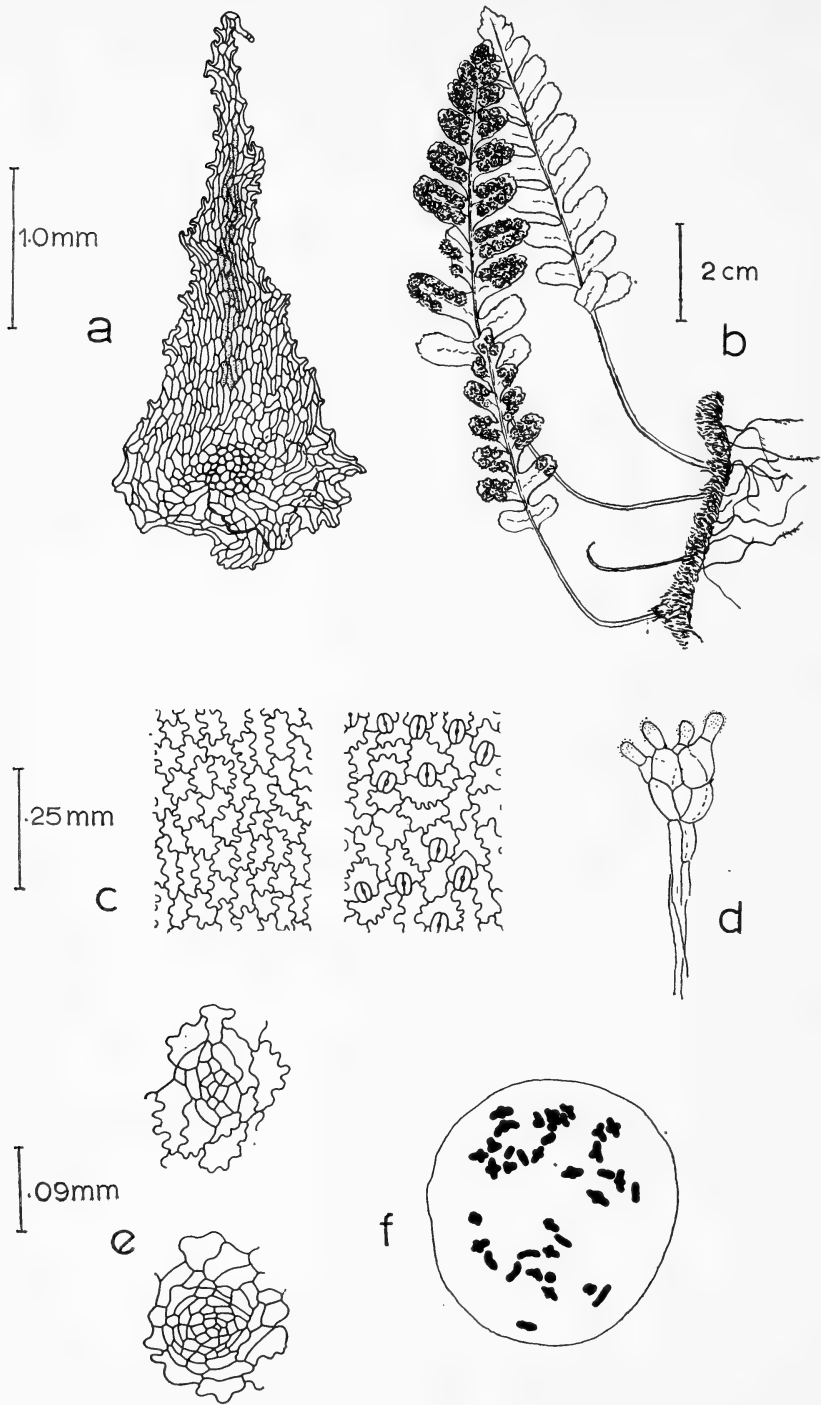
Key to the Species.

Polypodium virginianum and *scouleri* are included for completeness, but are not dealt with directly in this study.

Paraphyses present.
  Sori circular, submarginal; rhizome scales often with a median strike, coarsely toothed; rhizome acrid.
    Frond segments narrowly ovate, mostly acute . . . . . 6. *P. virginianum*
    Frond segments oblong to obovate, mostly obtuse . . . . . 2. *P. montense*
  Sori oval, median; rhizome scales uniformly colored, not coarsely toothed; rhizome sweet.
    Spores normal (not aborted) . . . . 1. *P. hesperium*
    Spores aborted . . . . 5. *P. hesperium* × *montense*
Paraphyses absent.
  Sori circular.
    Sori medial.
      Frond segments usually more than 30 mm long, the ratio of length to width usually more than 3.3 (mean 5.6), acute to attenuate . 3. *P. glycyrrhiza*
      Frond segments usually less than 30 mm long, the ratio of length to width usually less than 3.8 (mean 2.4), obtuse to acute.
        Rhizome scales often with a median stripe, coarsely toothed; rhizome acrid, pruinose . . . . 2. *P. montense*
        Rhizome scales uniformly colored, not coarsely toothed; rhizome sweet, not pruinose . . . . 1. *P. hesperium*
    Sori submarginal . . . . 2. *P. montense*
  Sori oval
    Veins anastomosing . . . . *P. scouleri*
    Veins free
      Spores normal (not aborted).
        Frond segments usually more than 30 mm long, the ratio of length to width usually more than 3.3 (mean 5.6), acute to attenuate. 3. *P. glycyrrhiza*
        Frond segments usually less than 30 mm long, the ratio of length to width usually less than 3.8 (mean 2.4), obtuse to acute . . 1. *P. hesperium*
      Spores aborted.
        Segments entire to crenate, obtuse, the ratio of length to wides less than 2.0 . . . . 5. *P. hesperium* × *montense*
        Segments serrate, acute, the ratio of length to width more than 2.0.
               4. *P. glycyrrhiza* × *hesperium*

1. Polypodium hesperium Maxon, Proc. Biol. Soc. Wash. 13:200. 1900. *P. vulgare* L. var. *columbianum* Gilbert, List N. Amer. Pterid. 19, 38. 1901. *P. vulgare* L. var. *hesperium* (Maxon) Nelson & Macbride, Bot. Gaz. (Crawfordsville) 41:30 1916. *P. prolongilobum* Clute, Fern Bull. 18:97. 1910.

Fig. 4. Morphology and cytology of *Polypodium montense:* a, rhizome scale, *Lang 211-B*; b, habit, *Lang 211-B*; c, upper and lower epidermal patterns, *Lang 211-C*, *Lang 218*; d, paraphyses from sorus; e, hydathode from upper epidermis, *Lang 215*; and f, spore mother cell at diakenesis, n = 37, *Lang 189*.
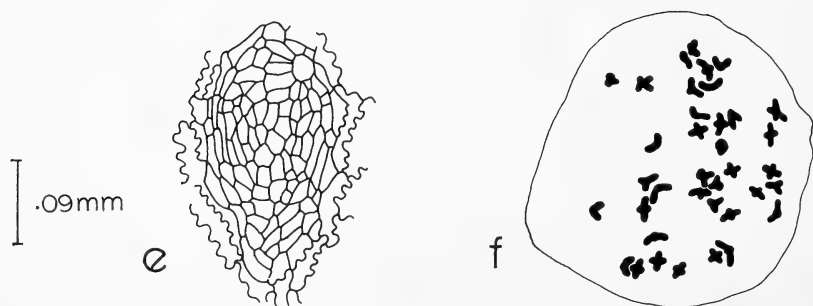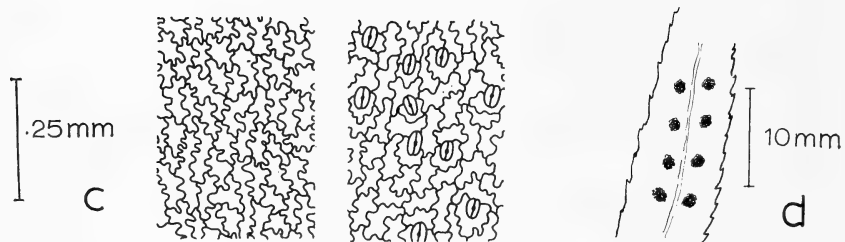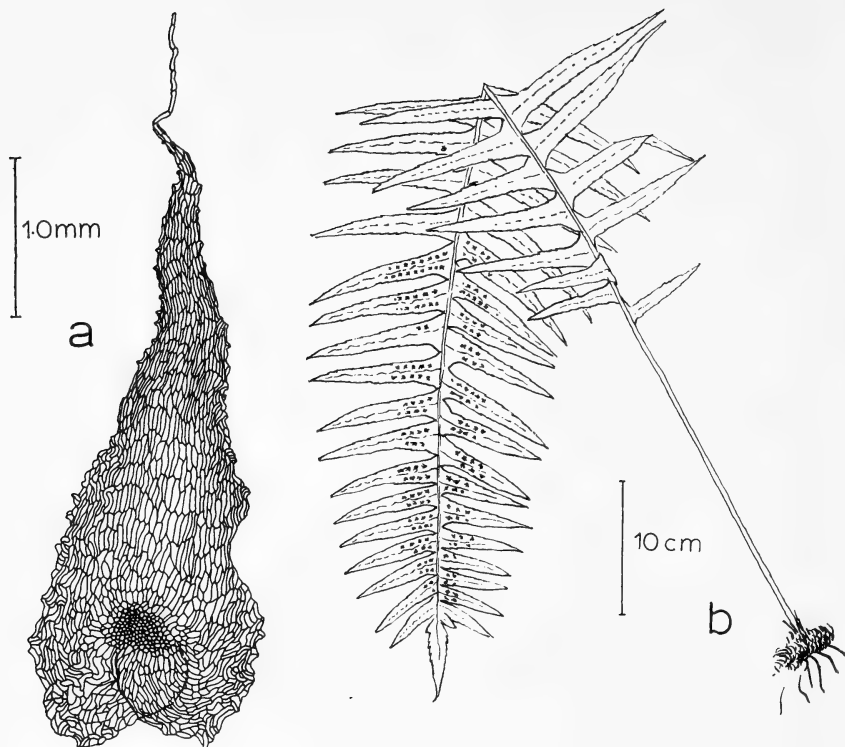
Quantitative measurements are presented in the descriptions—manner to display variability. Using stipe length as an example the shortest stipe measured was (12 mm long) (80% of all stipes measured were from 28 to 100 mm long, the average stipe length being 57 mm long) (the longest stipe was 155 mm long). Quantitative data for *P. hesperium, P. montense* and *P. glycyrrhiza* are shown in Table 3.

Rhizome creeping, with sweet, licorice-like taste, 3–6 mm in diameter, paleaceous; rhizome scales tan to castaneus, ovate, to 5 mm long, somewhat crenate, the cells large, 25–30 in number across scale just above point of attachment; frond averaging 170 mm long, max. ca. 375 mm long; stipe stout, (12) (28–*57*–100) (155) mm long; blades coriaceous or herbaceous to membranous in shade, oblong (30) (163–*114*–189) (265) mm long, (12) (22–*33*–48) (83) mm wide; segments oblong, obtuse to acute, entire to serrate, (9) (11–*18*–26) (45) mm long, (5) (6–*7*–9) (11) mm wide, the ratio of length to width (1.3) (1.9–*2.4*–3.1) (3.8); hydathodes large, oval, many celled; veins free, forking 1–3 times; sori oval, located midway between costa and segment margin; paraphyses very rare; chromosome number $n = 74$, $2n = 148$. Type. Coyote Canyon, Lake Chelan, Washington, *Gorman 642,* US!

New fronds produced from June to September; found growing on rocks and in rock crevices from south central British Columbia south to New Mexico, Arizona, and northern Mexico, east to the Rocky Mountains, west nearly to the coast in Cheakamus and Fraser River valleys of British Columbia, south along the east slope of the Cascade Mountains in Washington to Mount Hood, Oregon, absent from the Columbia Plateau in Washington, central Oregon, and the Great Basin region of Utah and Nevada, western limit of eastern [southerly] extension of range; eastern Washington, northwestern Oregon, Idaho, eastern Utah west of Zion Park in southern part of the state.

The reasons for the restriction of the epithet *hesperium* to the tetraploid cytotype have already been discussed (Lang, 1969).

Since the two cytotypes included in *P. hesperium* are recognized as two distinct species, it thus becomes necessary to establish to which cytotype the epithet *Hesperium* properly belongs, the diploid or the tetraploid. *Polypodium hesperium* Maxon is the oldest available name which must be used for one or the other of the two cytotypes.

The type specimen of *P. hesperium* was compared morphologically with a range of both diploid and tetraploid specimens from throughout the northwest and chromosome determinations were made on topotype material. This comparison makes it clear that the tetraploid cytotype agrees very closely with the type specimen of *P. hesperium* Maxon. Among other

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Fig. 5. Morphology and cytology of *Polypodium glycyrrhiza*: a, rhizome scale, *Lang 213*; b, habit, *Lang 189*; c, upper and lower epidermis, *Lang 33, Lang 217*; d, a portion of the frond segment of the type specimen of *P. glycyrrhiza*; note the round median sori; e, hydathode from upper epidermis, *Lang 24*; and f, spore mother cell at diakensis, $n = 37$, *Lang 189*.
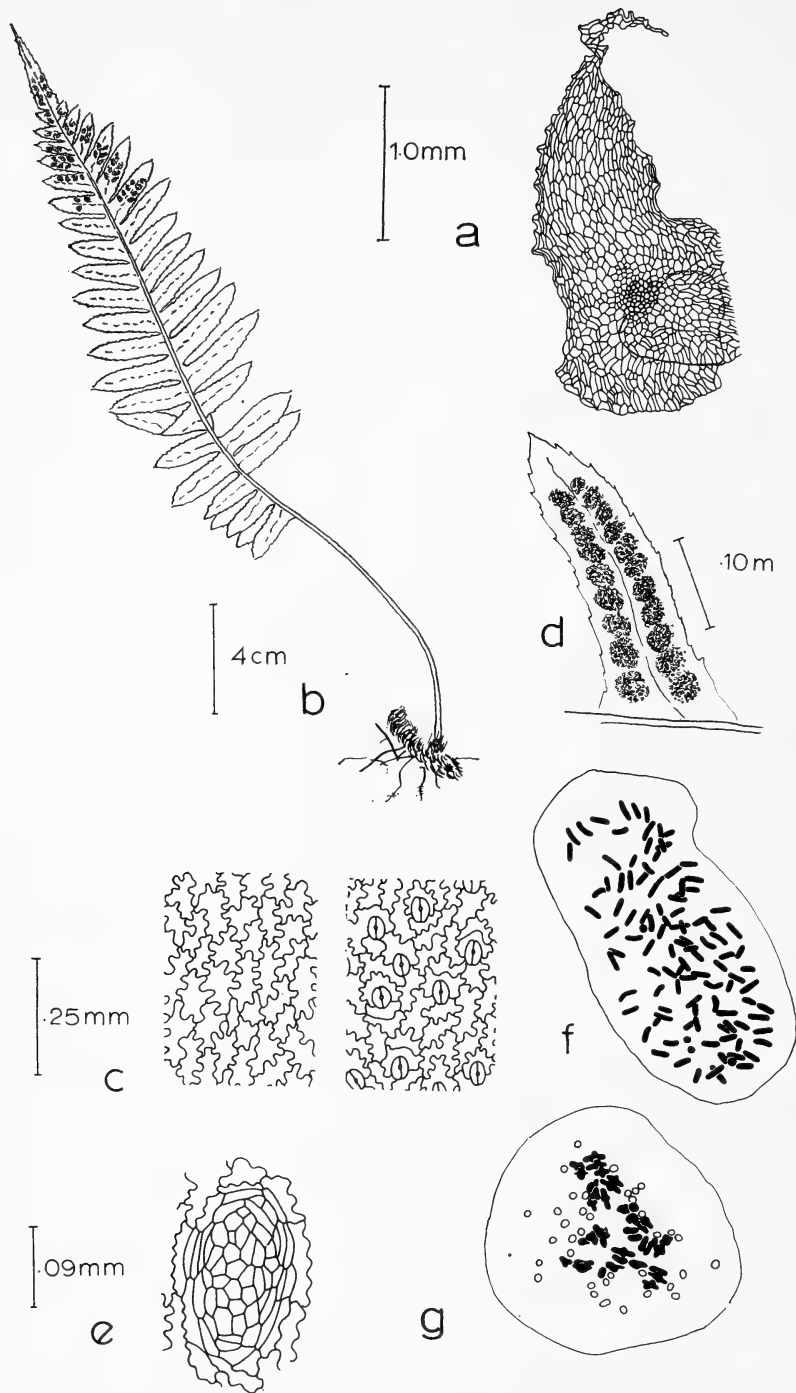
features in common, both have oval sori located midway between the costa and segment margin, and a sweet licorice-like rhizome, as mentioned by Maxon (1900) in his original description. The diploid cytotype, on the other hand, has circular sori near the segment margin and an acrid flavored rhizome. The geographical distributions give further evidence that the holotype of *P. hesperium* is tetraploid since, as far as is known, the diploid cytotype does not occur in the same area as the tetraploid cytotype. A collecting trip to the type locality of *P. hesperium* in Coyote Canyon, Lake Chelan, Washington, yielded several isolated colonies of *Polypodium*. They were essentially similar in morphology, and all plants on which chromosome counts were made proved to be tetraploid. Figure 3g shows a spore mother cell from one of these plants at diakensis with 74 bivalents. On the basis of this evidence there is little doubt that the tetraploid should bear the name *P. hesperium* Maxon.

2. POLYPODIUM MONTENSE F. A. Lang, Madroño 20:57. 1969. *P. amorphum* Suksdorf, Werdenda 1:16, 1927. Holotype: Dog Creek Canyon, near Cooks, Skamania Co., Washington, *Suksdorf 11667*, WS.

Rhizome creeping, acrid, 3–5 mm in diameter, ofter pruinose, paleaceous; rhizome scales dark brown to castaneus, often with a central strip of darkly colored cells, narrowly ovate to obovate, often constricted above point of attachment, to 5 mm long, usually with a capillary tip, margin coarsely toothed, cells large, ca. 25 in number across scale just above point of attachment; frond averaging 130 mm long; max. ca. 300 mm long; stipe slender, (8) (28–*58*–100) (142) mm long; blades coriaceous to membraneous, oblong (18) (46–*81*–122) (190) mm long, (11) (17–*24*–30) (45) mm wide; segments oblong to obovate, tips obtuse to rarely acute, entire to crenulate, (5) (9–*13*–17) (25 mm long, (3) (4–*6*–7) (12) mm wide, ratio of length to width (1.2) (1.8–*2.3*–3.0) (3.6); hydathodes small, round, few-celled; veins free, forking 1–2 times; sori circular, nearer the margin than the costa; paraphyses many; chromosome number **n = 37, 2n = 74.** Holotype. Creakamus River, British Columbia, *Lang 211,* UBC.

New fronds produced from late April to June; found growing in rock crevices in mountains from central Coast Range in British Columbia south through the Cascade Mountains in Washington to Oregon and the Sierra Nevada Range in California, in the Olympic Mountains and Wenatchee Mountains of Washington and the Northern Coast Range of Oregon, usually at high elevations but descending to bottoms of river valleys.

FIG. 6. Morphology and cytology of *Polypodium glycyrrhiza* × *hesperium*: a, rhizome scale, *Lang 210-C*; b, habit, *Lang 210-C*; c, upper and lower epidermal patterns, *Lang 210-C, Lang 125–2*; d, frond segment, note large oval sori, *Lang 210-C*; e, hydathode from upper epidermis, *Lang 210-C*; f, mitosis, **2n = 111,** *Lang 125–2*; and g, spore mother cell at metaphase I, $37_{II} + 37_{I}$, *Lang 125–2*.
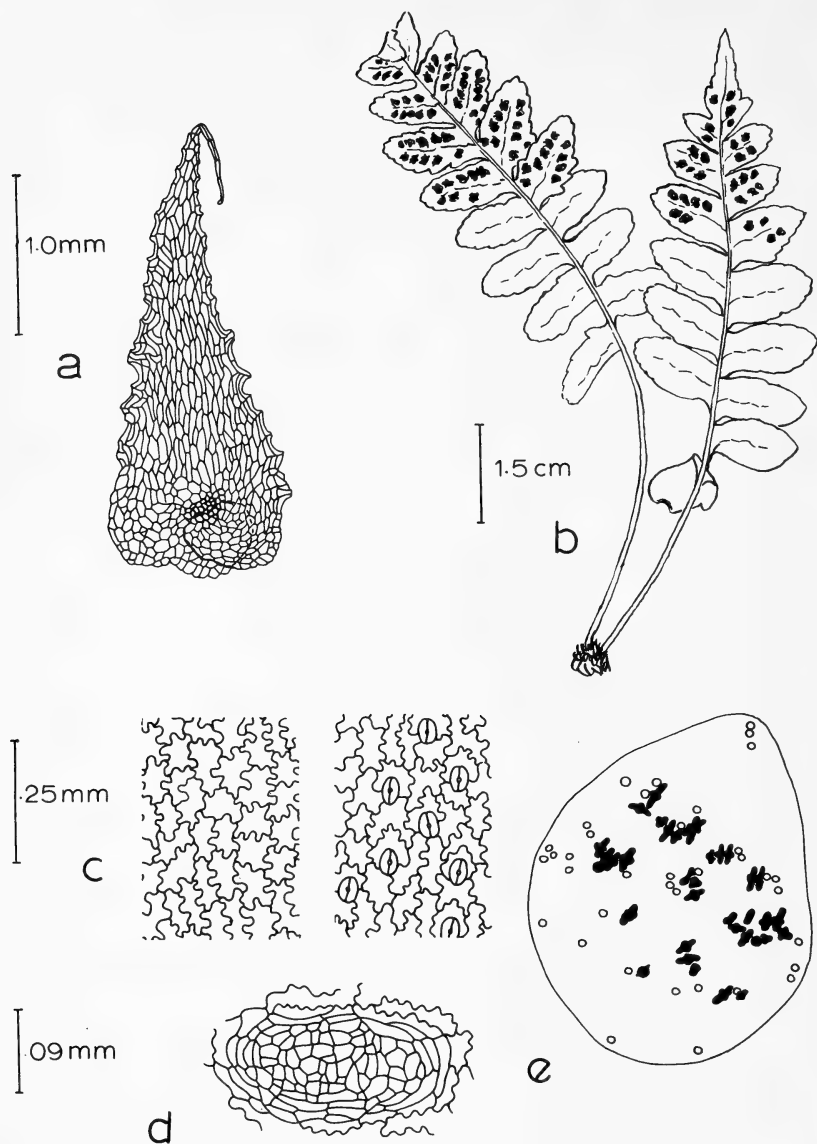
Fig. 7. Morphology and cytology of *Polypodium hesperium* × *montense*: a, rhizome scale, *Lang 122–3*; b, habit, *Lang 122–3*; c, upper and lower epidermal patterns, *Lang 122–3*; d, hydathode from upper epidermis, *Lang 122–3*; and e, spore mother cell at metaphase I, $37_{II} + 37_I$, *Lang 122–3*.

A discussion, treatment, and description of this taxon has already appeared (Lang, 1969).

3. POLYPODIUM GLYCYRRHIZA D. C. Eaton, Amer. J. Sci II. 22:138. 1856. *P. vulgare* L. var. *occidentale* Hook., Fl. Bor. Amer. 2:258. 1840. *P. falcatum* Kellogg, Proc. Calif. Acad. Sci. 1:20. 1854. Non L. fil. Suppl. 446. 1781. *P. vulgare* var. *rotundatum* Milde, Fil. Europ. Atlant. 18. 1867. *P. vulgare* var. *falcatum* (Kellogg) Christ. Beitr. Krypt. Schweiz. 2:51. 1900. *P. occidentale* (Hook.) Maxon, Fern Bull. 12:102. 1904. *P. vulgare* subsp. *occidentale* (Hook.) Hulten, Acta Univ. Lund. 37:44. 1941. *P. aleuticum* A. Bobr. Bot. Zhur. (Moscow & Leningrad) 49:542. 1964.

Rhizome creeping, sweet, with licorice-like taste, 3–6 mm in diameter, pleaceous; rhizome scales narrowly ovate to ovate, up to 10 mm long, tan to castaneus, uniformly colored, more or less entire, sometimes with a prolonged capillary tip, the cells small, about 40 in number across scale just above point of attachment; frond averaging 260 mm long (max. ca. 600 mm) stipes stout, (11) (36–*94*–143) (340) mm long; blades subcoriaceous on exposed rock, herbaceous or membraneous in shade, oblong to ovate, sometimes deltoid, (20) (69–*173*–280) (470) mm long, (14) (35–*60*–92) (156) mm wide; blade segments narrowly oblong-attenuate, more or less falcate, acute to acuminate, (7) (18–*33*–53) (85) mm long, (3) (5–*7*-8) (11) mm wide, the ratio of length to width (1.8) (3.3–*5.6*–7.4) (12.0); hydathodes large, oval, many celled; veins free, forking 2–4 times, sori usually circular, sometimes slightly oval, located midway between costa and margin; paraphyses absent; chromosome number **n = 37, 2n = 74.** Type. Port Orford, Kuntz s.n., YU!

New fronds produced from August to February; found growing at lower elevations on rocks and trees along the Aleutian Islands to Alaska, south through coastal British Columbia, Washington, Oregon and California to Monterey Co.; east to the Cascade Mountains in the southern part of the range and extending up inlets and river valleys in the coastal mountains of British Columbia.

There is no doubt that the correct name of the coastal diploid species is *P. glycyrrhiza* D. C. Eaton since this epithet has priority over the others. Two varieties of *P. glycyrrhiza* might be recognized on the basis of frond segment shape, one with attenuate frond segments, the other with acute to subobtuse segments.

The forms with attenuate frond segments have been recognized as *Polypodium vulgare* var. *occidentale* Hook., and it is possible that *P. vulgare* var. *rotundatum* Milde would include the acute to subobtuse forms. However, new combinations of these parieties in *P. glycyrrhiza* should be delayed until the precise relationship of the two forms has been intensively studied.

4. POLYPODIUM GLYCYRRHIZA × HESPERIUM.

Because of the few plants that were examined, no formal characterization of this and the following triploid hybrid is attempted. The major morphological characteristics are shown in Fig. 6.

Specimens examined. BRITISH COLUMBIA: Kaske Creek, 59 miles E of Prince Rupert, *Lang 99-B*, UBC; Alexandra Bridge, Fraser River, *Lang 125–2*, UBC; Green River, Pemberton, *Lang 210–C*, UBC.

5. POLYPODIUM HESPERIUM $\times$ MONTENSE.

Figure 7 is of the only known triploid of this parentage.

Specimen examined. BRITISH COLUMBIA: Alexandra Bridge, Fraser River, *Lang 122–3*, UCB.

6. POLYPODIUM VIRGINIANUM.

Several specimens of *P. virginianum* from northeastern British Columbia and the Yukon were examined because of their close proximity to the study area.

THE ORIGIN OF POLYPODIUM HESPERIUM

In view of the available evidence a tentative hypothesis may be made concerning the origin of the tetraploid *P. hesperium*. It seems likely that *P. hesperium* is an allotetraploid that arose from the diploids *P. glycyrrhiza* and *P. montense* or their progenitors. Comparison of *P. hesperium* (fig. 3) and the two diploids (figs. 4 and 5) indicate that *P. hesperium* is more or less morphologically intermediate between them. The fact that *P. hesperium* invariably forms 74 bivalent chromosomes (no multivalents) at meiosis is further evidence of its alloploid origin.

Perhaps the most convincing evidence is offered by morphology and the meiotic chromosome behavior of the two triploid hybrids, *P. hesperium* $\times$ *montense* and *P. glycyrrhiza* $\times$ *hesperium*. By comparing the specimens in Figs. 6 and 7, it is clear that there are two morphologically distinct triploid hybrids. Because they have 111 sporophytic chromosomes, they must have been derived from hybridization between a tetraploid with 74 gametic chromosomes and a diploid with 37 gametic chromosomes. The fact that the tetraploid *P. hesperium* and the two diploids, *P. glycyrrhiza* and *P. montense,* are the only species known from the region where the triploids were found is sufficient basis to suspect them as being the parental species. Each triploid probably shared *P. hesperium* as a common parent since it is the only available tetraploid. The two triploids are more or less intermediate between *P. hesperium* and *P. glycyrrhiza* in one case (compare figs. 3, 5, 6), and *P. hesperium* and *P. montense* in the other (figs. 3, 4, 7). It seems that these species are the parents of the hybrids. At meiosis these morphologically distinct triploids both show $37_{II} + 37_I$ chromosomes. This indicates that both the *P. glycyrrhiza* genome and the *P. montense* genome are present in *P. hesperium* if we assume that the pairing is due to genome homology and not some other mechanism. Following the convention of Shivas (1961a), we can assign letters to the genomes of the different species to illustrate what might be occurring at meiosis in the triploid hybrids. *Polypodium glycyrrhiza,* a diploid, possesses sets of homologous chromosomes represented

AA, while *P. montense* has a different set of homologous chromosomes DD (B and C were used by Shivas for other members of the complex). When the gametes from *P. hesperium,* which are diploid, combine with a haploid gamete from one of the diploids, a triploid will result. When meiosis occurs in this triploid, $37_{II} + 37_{I}$ form. If the tetraploid is indeed an allotetraploid derived from *P. glycyrrhiza* and *P. montense,* then one could expect that it would have genomes AA and DD. This assumption is borne out by chromosome pairing in the triploid. In *P. glycyrrhiza* × *hesperium* we find $37_{II} + 37_{I}$, AA + D. The A genome from the *P. glycyrrhiza* gamete is pairing with A genome present in the *P. hesperium* gamete with the *P. montense* genome unpaired. The reverse is true for *P. hesperium* × *montense.* The two DD genomes pair while the single A genome of *P. glycyrrhiza* with 37 chromosomes remains unpaired. From the abortive nature of the spores of the triploid, it seems likely that fertility is greatly reduced in them and that *P. hesperium* is reproductively isolated from the two diploids. It is interesting to note that no hybrids between the diploid cytotypes have been found in nature or have been synthesized in culture. *Polypodium glycyrrhiza* and *P. montense* are occasionally found growing so close together that their rhizomes are intertwined, yet there seems to be no sign of any diploid hybrids.

On the basis of chromosome pairing in these triploids, it appears that both the genomes of *P. glycyrrhiza* and *P. montense* are present in the tetraploid *P. hesperium* .Of course, this is only a tentative conclusion based on the available evidence. Before any definite conclusions are reached concerning the origin of *P. hesperium,* the parentage of the triploids should be confirmed by synthesized hybrids and crosses established between *P. hesperium* and all the diploid members of the complex.

This paper is based on portions of a Ph.D. dissertation submitted to the Department of Botany, The University of British Columbia, Vancouver. Sincere thanks are due T. M. C. Taylor for guidance during the course of this study and to John H. Thomas for his extraordinary help in preparation of the manuscript.

LITERATURE CITED

BLASDELL, R. F. 1963. A monographic study of the fern genus Cystopteris. Mem. Torr. Bot. Club 21(4):1–102.

BOBOROV, A. E. 1964. A comparative morphological and taxonomical study of the species of Polypodium L. of the flora of the U.S.S.R. Bot. Zurn. (Moscow & Leningrad) 49:534–545.

EVANS, A. M. 1963. New chromosome observations in the Polypodiaceae and Grammitidaceae. Carylologia 16:671–677.

————., and W. H. WAGNER, JR. 1964. Dryopteris goldiana × intermedia—a natural woodfern cross of noteworthy morphology. Rhodora 66:255–266.

FISCHER, L., and E. V. LYNN. 1933. Licorice fern and wild licorice as substitutes for licorice. J. Amer. Pharm. Assoc. 22:1225.

KNOBLOCH, I. W. 1962. Tetroploid Polypodium vulgare var. columbianum from Arizona. Amer. Fern J. 52:65–68.

LANG, F. A. 1965. A cytotaxonomic study of the Polypodium vulgare complex in Northwestern North America. Ph.D. thesis, University of British Columbia.
————. 1969. A new name for a species of Polypodium from northwestern North America. Madroño 20:53–60. 1959.
LLOYD, R. M. 1962. Studies in California species of Polypodium (Polypodiaceae) Master's thesis. Claremont Graduate School.
————. 1963. New chromosome numbers in Polypodium. Amer. Fern. J. 53:99–101.
————., and F. A. LANG. 1964. The Polypodium vulgare complex in North America. Brit. Fern Gaz. 9:168–177.
MANTON, I. 1950. Problems of cytology and evolution in the pteridophyta. Cambridge University Press.
MARTENS, P. 1950. Les organes glanduleux de Polypodium virginianum III. Nouvelles donnees géographiques, systematiques et histologiques. La Cuellule. 53:187–212.
MORTON, C. V., and C. NEIDORF. 1954. Polypodium vulgare var. virginianum. Amer. Fern J. 44:111–114.
SHIVAS, M. G. 1961a. Polypodium in Europe and America. I. Cytology. J. Linn. Soc., Bot. 58:27–38.
————. 1961b. Polypodium in Europe and America. II. Taxonomy. J. Linn. Soc., Bot. 58:27–38.
TAYLOR, T.M.C. 1970. Pacific Northwest ferns and their allies. Univ. Toronto Press, Toronto.
WAGNER, W. H. JR. 1954. Reticulate evolution in Appalachian aspleniums. Evolution 8:103–118.
————., and L. L. CHEN. 1965. Abortion of spores and sporangia as a tool in the detection of Drypteris hybrids. Amer. Fern Jr. 55:9–29.

LOCAL PHOTOSYNTHETIC ECOTYPES IN PINUS ATTENUATA AS RELATED TO ALTITUDE

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This paper reports ecotypic varation in *Pinus attenuata* Lemm., as determined by temperature conditioning in greenhouse-grown seedlings from seed collected at the elevational extremes of its range in the San Bernardino Mountains of southern California.

Although most genecological studies are on wide ranging species, a number of instances of localized variability have been published. Culberson and Culberson (1967) found local ecological sorting of a lichen species on a coastal promontory in North Wales. Briggs (1962) demonstrated a mosaic of local ecotypes of a *Ranunculus* species. Squillace and Bingham (1958) showed localized ecotypic variation in western white pine, related to elevation, slope direction and soil moisture. The work of Kruckeberg (1968) has demonstrated many ecotypes related to narrowly restricted edaphic conditions.

Local ecotypes or ecoclines related to altitude have also been found. Papers from the Carnegie group, typified by Clausen, Keck, and Hiesey (1948) involve altitude as a principal habitat gradient. Other geneco-

typic variation related to altitude has been reported by Britten (1960) in *Trifolium repens,* by Grant and Hunter (1962) in *Calluna vulgaris,* by Mark (1965) in *Chionochloa rigida,* by Pisek and Winkler (1959) in *Picea excelsa,* by Myers and Bormann (1963) in *Abies balsamea,* and, originally, Turesson (1925) in numerous species of herbaceous perennials in Scandinavia.

METHODS

Methods of determining genecological variation have involved various morphological and physiological techniques. In this study a physiological approach was used. Turesson (1925) and Heslop-Harrison (1964) have stressed the importance of the physiological response in genecology. Seedlings were grown from seed collected from several trees at 850 m and 1600 m, the elevational limits of knobcone pine in the study area. They were allowed to develop in the greenhouse in pots of native soil until they possessed a mixture of primary and secondary leaves. This corresponds to two year old seedlings in the field. In June, 1968 the plants were placed in a growth chamber on a 15 hour photoperiod with 13°C days and 5° nights. Previous work (Wright, 1970) had shown 7 days in a temperature regime to promote full acclimation to that regime. Light intensity was 2500 ft-c at plant height, from cool white fluorescent lights. After a minimum of 10 days conditioning each plant was withdrawn and its rate temperature curve of net photosynthesis determined with a CO_2 analyser, as described in an earlier paper (Wright, 1970). Following determination the plants were placed in a regime of 15 hour photoperiod, 32° days, 18° nights. After acclimation to these new conditions the rate temperature curve was again determined for the same plants. There was no leaf loss and little apparent growth during the three weeks between runs on a given plant. Temperature regimes were chosen to represent winter and summer conditions as determined by field studies (Wright, 1966). It was felt that, as Heslop-Harrison (1964) states, experimental variety in environment would bring out the capacity of ecotypes to react to peculiarities which would be masked in a uniform environment. This, Heslop-Harrison pointed out, would be especially true with physiological responses.

RESULTS

Table 1 shows the nature of the rate-temperature curve of photosynthesis when plants have been conditioned to a cold regime and subsequently to a warm regime. Plants from high elevation, when cold-conditioned, were advantaged at high temperatures, 30° and 35°. When warm-conditioned, plants from high elevation were advantaged at all temperatures, but the advantage was greatest at low temperatures. Photosynthetic rate was greater after warm-conditioning than after cold-conditioning with plants from both elevations, but the difference was more marked with high elevation plants. Similar trends were found in *Pinus*

Table 1. Net photosynthesis of Knobcone Pine, mg CO_2/gm Leaf Fresh wt./hr.

	15°	20°	25°	30°	35°
Cold conditioned					
1600 m origin	3.57	2.86	1.95	0.96	—0.19
				*	*
850 m origin	3.04	2.38	1.64	0.29	—0.83
Warm conditioned					
1600 m origin	6.12	5.41	4.24	3.00	1.73
	**	*	*	*	*
850 m origin	4.59	3.93	2.86	1.84	0.95

*Significant difference between means
**highly significant difference between means

coulteri D. Don., but sample size was too small to provide conclusive data.

Discussion

The data in Table 1 indicate that in winter when acclimated to cold, the high altitude population would be capable of a higher rate of net photosynthesis during sudden spells of warm weather. In summer when acclimated to heat the high altitude population would have an advantage at all temperatures, but especially during sudden spells of cool weather. The greatest advantage seems to be in conditions that occur infrequently. A lesser but steady advantage obtains for high elevation populations during more normal summer weather. Net photosynthesis in the high altitude population seems to be better buffered against sudden temperature changes. This indicates that response to temperature is critical at upper elevational limits, a thesis supported by most work on upper elevational limits of species (Daubenmire, 1954; Bryson, Irving and Larsen, 1965).

The adaptive value of the genecotypic variation shown by Table 1 is by no means overwhelmingly clear. There may be a case for random genetic drift within small popualtions (Heslop-Harrison, 1964). Although the distance between elevational extremes is only 5 km, and knobcone pine woodland is continuous, gene exchange over this distance may be slow. Colwell (1951) found that very little of coulter pine pollen released at a height of 12 ft travelled as far as 150 ft, even downwind. The populations of knobcone pines within 150 ft of the collection sites comprise only a handful of trees in each case. Therefore, random non-adaptive genetic drift is a distinct possibility. This indicates that ecotypic variation can be on a very local scale, as indicated by the work of Gregor and Watson (1961), even when no sharp habitat discontinuities occur. Heslop-Harrison (1964) has pointed out that ecotypes will evolve even in the face of crossbreeding if there is a range of habitat conditions, especially if the range is extreme. He suggests that phenological differences, such as time of pollen release, may block free gene flow. This may be the case with these knobcone pines. Kruckeberg (1967) has demonstrated many cases of ecotypes persisting in closely

adjacent sites where preadaptedness for the ultramafic habitat outweighs free gene flow. Bradshaw (1960), working with *Agrostis tenuis* in a small area of central Wales, found changes in gentoype to be either gradual or sudden, depending on the smoothness of habitat change. In this study of knobcone pine, apparently selection pressure is high enough to outbalance whatever gene flow occurs, even as judged in seedlings reared artificially where natural selection has not been permitted to operate on the experimental generation. Possibly even more geneco-typic variation would be found if experimental plants could be vegeta-tively propagated from the mature field trees. Future work may employ a grafting technique for rooting fascicle cuttings of pine.

Literature Cited

Bradshaw, A. D. 1960. Population differentiation in Agrostis tenuis. III. Popula-tions in varied environments. New Phytol. 59:92–103.

Briggs, B. G. 1962. Hybridization in Ranunculus. Evolution 16:372–390.

Britten, E. J. 1960. Genetic and environmental control of flowering in Trifolium repens in the tropics. Science 131:100–101.

Bryson, R. A., W. N. Irving and J. A. Larsen. 1965. Radiocarbon and soil evidence of former forest in the southern Canadian tundra. Science 147:46–48.

Clausen, J., D. D. Keck, and W. M. Hiesey. 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of Achillea. Publ. Carnegie Inst. Wash. 581.

Colwell, R. N. 1951. The use of radioactive isotopes in determining spore distri-bution patterns. Amer. J. Bot. 38:511–523.

Culberson, W. L., and C. F. Culberson. 1967. Habitat selection by chemically differentiated races of lichens. Science 158:1195–1197.

Daubenmire, R. F. 1954. Alpine timberlines in the Americas and their interpreta-tion. Butler Univ. Bot. Stud. 11:119–136.

Grant, S. A., and R. F. Hunter. 1962. Ecotypic differentiation of Calluna vulgaris (L.) in relation to altitude. New Phytol. 61:44–55.

Gregor, J. W., and P. J. Watson. 1961. Ecotypic differentiation: observations and reflections. Evolution 15:166–173.

Heslop-Harrison, J. 1964. Forty years of genecology. *In* Advances in ecological research, vol. 2. Academic Press, London.

Kruckeberg, A. R. 1967. Ecotypic response to ultramafic soils by some plants species of northwestern United States. Brittonia 19:133–151.

Mark, A. F. 1965. Ecotypic differentiation in Otago populations of narrow leaved snow tussock, Chionocloa rigida. New Zeal. J. Bot. 3:277–299.

Myers, O., and F. H. Bormann. 1963. Phenotypic variation in Abies balsamea in response to altitudinal and geographic gradients. Ecology 44:429–436.

Pisek, A., and E. Winkler. Licht und temperaturbehangigkeit der CO_2—Assimila-tion von Fichte (Picea excelsa Link), Zirbe (Pinus cembra L.) und Sonnen-blume (Helianthus annuus L.). Planta 53:532–550.

Squillace, A. E., and R. T. Bingham. 1958. Localized ecotypic variation in western white pine. Forest Sci. 4:20–34.

Turesson, G. 1925. The plant species in relation to habitat and climate. Hereditas 6:147–236.

Wright, R. D. 1966. Lower elevational limits of montane trees. I. Vegetational and environmental survey in the San Bernardino Mountains of California. Bot. Gaz. (Crawfordsville) 127:184–193.

———. 1970. CO_2 exchange of conifers in the laboratory in relation to lower elevational limits. Amer. Midl. Nat. 83:291–300.

NOTES AND NEWS

Trifolium hirtum L. (Fabaceae) in California.—Since P. H. Raven (Leafl. W. Bot. 7:151. 1954) first reported *T. hirtum* in California from Butte Co., the number of records as based on herbarium specimens (CAS, DAV, DS, JEPS, UC, US) and plotted as Fig. 1 has increased considerably. *Trifolium hirtum* is an excellent soil-builder (Love, R. M., and D. C. Sumner, Univ. Calif. Coll. Agric. Exp. Sta. Circ.

Fig. 1. Distribution of *Trifolium hirtum* in California.

407. 1955) and as such has been planted on denuded land surfaces adjacent to highways and freeways, on and about dam sites, and in chaparral after fires (Raven, P. H., Leafl. W. Bot. 9:79–80. 1960). *Trifolium hirtum* being a Mediterranean species can be expected in many parts of California in the future, usually associated with man's less gentle dealings with the landscape.—John H. Thomas, Department of Biological Sciences, Stanford University, Stanford, California 94305.

BOTANICAL COLLECTING RAMBLES WITH
PROF. ERIC HULTEN IN THE ALEUTIAN ISLANDS

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As a naturalist and biological collector in many lands, I have worked with several notable biologists of the Swedish Riksmuseum which I visited twice after journeying through the U.S.S.R.

My first great inspiration in tropical collecting was during nearly five months in Haiti as constant companion of Dr. Eric Ekman. He was the unexcelled botanist of West Indian flora and a fine naturalist. Although excentric in many ways, he was one of the greatest naturalistic friends I have ever had, and his untimely death in the jungles of the Dominican Republic in 1930 was a great shock to me, as we had planned to be together again in Venezuela. On two excursions around the world, while stopping in Western Europe, I visited Ekman's two other collaborating colleagues of the West Indian Botanical Triumvirate, as he called them. These were Professor Gunnar Samuelsson, Curator of Botany at the Riksmuseum, and Professor Ignatz Urban of Berlin-Dahlem. Dr. Urban, on both of my visits to him, talked only of Ekman and his marvelous botanical collecting. He idolized him. I remember that Ekman had beeen offered the position as director of the Botanical Museum of Riksmuseum, but he would not give up his carefree life in the jungles of Haiti, to which he had become adapted. He lived and died for his botanical ideal.

In 1925, while engaged as cooper on the schooner *Apollo* for the Siberian Fish and Cold Storage Company, I was impressed by the luxuriant and rich Kamchatka flora. There, on several occasions, I met Dr. Rene Maliase and Mr. Schoblum. They were members of Hulten's notable Swedish Kamchatka Expedition which landed in that far-off northern land, in the midst of the Russian Revolution in progress. Hulten's superb *Flora of Kamtchatka* was richly augmented by the extensive collections made by Malaise who stayed in that country for ten years. A large part of the plants collected by Professor T. V. Komarov of the great Riabouschinski Expedition some years before the outbreak of World War I (it was in 1908 and 1909), were made accessible to Dr. Hulten at the Academy of Sciences. *Flora of Kamtchatka* stimulated Komarov to compile and publish his *Flora Peninsulae Kamtschatka* in Russian. All of the known collections of higher plants in U.S.S.R. from Kamchatka are included. The two floras which supplement each other are the foundation and inspiration of Hulten's far more important works, *Flora of the Aleutian Islands* (of which two editions were published), *Flora of Alaska and Yukon*, and his most recent *Flora of Alaska and Neighboring Territories*. In these comprehensive floras, the plant migrations from Asia to North America and vice versa are clearly desig-

nated. No work of this kind had ever before been attempted.

After recovering from a severe attack of malignant malaria and dengue fever in the hospital at Cape Haitian in 1927, I came home to Seattle, which is my native place of birth. A few months afterwards, I took a shipment of muskrats to Karaginsk Island on the coast of Kamchatka. There I spent the summer climbing volcanoes and botanizing the Avatcha region of Kamchatka. My companion, William F. Coultas, and I stayed a good part of the summer of 1928 with our friend Rene Malaise at Savoika, formerly Stari-Ostrog, founded by the Cossack Hetman Atlasov in the 17th century. About 500 species of plants were collected and sent to the Riksmuseum where Hulten added them to his *Flora of Kamtchatka.*

Some months after leaving Kamchatka, Mr. Coultas and I traveled in Manchuria, Inner Mongolia and East Siberia. Eventually we visited the Riksmuseum and there I met Hulten for the first time. On the second visit to the Herbarium, I helped to unpack a large box of plants which one of the Sven Hedin's expeditions had collected in Djungaria— also spelled Dzungaria in N. Sinkiang. A notable species of pink *Taraxacum* was included. Two years afterward, when I was again at the Riksmuseum, I had left the Whitney South Sea Expedition in Papua and on my way to Saarzrücken to be married, Dr. Hulten, Dr. Elizabeth Ekman and I opened another large case of botanical specims that Sven Hedin's expedition had collected in Outer Mongolia. This time the rare prize was a blue *Taraxacum.* On this occasion, I spent two weeks in Stockholm as guest of my good friend Maurice Dunlap, the United States counsul. I first knew him in Port-au-Prince, Haiti where he introduced me to Dr. Ekman in 1927.

On my second visit to Stockholm, in December 1930, one evening I was the geust of honor of Professor Sixten Bock at the Travellers' Club. The program lasted from 8:00 P.M. until 4:00 A.M. and every minute of the time was enjoyed and appreciated. One of the highlights of the evening was the fine series of pictures on the screen that Dr. Malaise had made in Kamchatka during his ten years in that most interesting country.

While at the Riksmuseum, Hulten made definite plans with me to botanize the Kodiak and Aleutian Islands and the Alaska Peninsula. A comparatively thorough collecting of vascular plants in this difficult region was a positive necessity in order to work out an understandable and workable theory as to the plant migrations across the Bering Sea.

Hulten, as a young graduate student in botany with his bride, undertook the Swedish Kamchatka Expedition, together with the biologists Malaise, Bergman and Schoblum. This was right in the time of the Revolution in 1920–22. As respected neutrals engaged in important scientific explorations, the Swedes were not molested by either warring factions and were usually received with hospitality wherever it was possible to be given. Sometimes they found themselves in the fighting zone of either

side and they saw considerable bloodshed and misery in this hitherto peaceful land. In spite of many privations and lack of contact with the outside world, and in spite of the rigorous climate and numerous hardships, the intrepid Swedes, full of health and vigor, a keen knowledge of the known biota of Kamchatka and of the data compiled by all previous explorers of the region, accomplished more than any other botanical expeditions to N.E. Siberia. Although a good many botanists had collected plants in Kamchatka since the first collections in the seventeen-forties by George W. Steller and S. Krascheninikoff, only Komarov had accomplished extensive plant explorations before Hulten.

Additional incentive toward a more thorough knowledge of the Kamchatka Peninsula and the whole North Pacific region, including the Kurile Islands and the Bering Sea, was evidently inspired by the far-reaching results of the voyage of the Vega in 1878 and 1879 and the remarkably rich collections of crytogamic flora made by Kjellmann in the Bering Sea region.

With the four volumes of *Flora of Kamtchatka* finished and published in 1930, Hulten made definite plans for a comprehensive botanical survey of the Aleutian and Kodiak Islands. This was accomplishred on our excursions to these islands in 1931 and 1932.

In 1930 I had resigned as ornithological member of the Whitney South Sea Expedition after nearly two years in Western Melanesia, so I could be married in Saarbrücken. Arriving in America with my bride, I had not known before that my country was in the throes of the lowest financial depression. Over six thousand banks had been closed in a week's time when the depression struck and industry had come to almost a dead stop. Millions of people were glad to work for subsistance only. In Seattle there was one large floating herring saltery ready to leave for Alaska. It was the converted steamer *Donna Lane*. The owner was an old friend of mine, Jens Jenson. We agreed that I should work two days per week as cooper for my board and transportation. I had plenty of collecting equipment and several good contracts from museums for plants and fishes. Aboard the *Donna Lane* was a new friend, Ingvar Norberg, from Tromsö, Norway. He had accompanied his father on two excursions to Spitzbergen while making his notable fossil plant collections for Professor Nathorst of the Riksmuseum, Stockholm, in the coal measures. I stopped for the summer at Port Hobron on Sitkalidak Island while Norberg went farther on to the whaling station at Akutan in the Aleutians where the *Donna Lane* operated. Norberg was keenly interested in my work with Hulten so he agreed to collect plants for him on Akutan Island. I gave him plenty of driers and other equipment. In subsequent years, during many seasons, he continued to collect plants for Hulten at many stations in Alaska where he was employed as carpenter, and added several new species to the flora. I collected plants in 1931, mostly on Sitkalidak Island and on Kodiak Island in the areas about Three Saints Bay and Old Harbour and Seldovia on Kenai Peninsula. On one

occasion, I had undertaken too much of a journey in one day, and while night overtook me, I became lost in thick alder brush with a pack frame full of plants on my back. I nearly fell headlong over a huge sleeping Kodiak Grissly bear who suddenly rose up before me on his hind legs. He let out a great snarl and a grunt of surprise. Needless to say, I was very frightened, too, especially because only ten minutes before, I had lost my good hunting knife that I had carried on all outings since I was fifteen years old. The rest of the cold, drizzly night, I struggled around through the tangled alder brush.

The next year, in 1932, Hulten came to Seattle to my home where he visited about ten days before we started on the Aleutian Island botanical excursion. He had just spent most of the winter collecting plants on the volcanoes, Nevada del Toluca and Iztaccihuatl and around Mazatlan and other parts of West Mexico.

We went north on the *Tahoe,* the flagship of the Coast Guard, as guests of Commander Boeddecker and Captain Towle. It was still quite wintery when we arrived at Unalaska on May second, where we established our main base, leaving our provisions, extra collecting supplies and surplus baggage and botanical specimens at the cabin which we rented for five months.

During May and June, Hulten and I were very busy collecting the rich cryptogamic flora, including marine algae around Unalaska and Dutch Harbor. Captains' Harbour proved especially rich in mosses and lichens. Unlike some parts of coastal Alaska, notably the Prince William Sound region, the Aleutian Islands are poorly represented in hepatic species. Surprisingly few were noted and collected. A few grasses and early sedges were about all of the flowering plants in bloom before the last week in June. A week or two later nearly all the coastal flowers bloom at one time. In July, the Aleutians are carpeted with beautiful flowers and the botanist must work long hours of overtime if he would accomplish a good season of plant collecting.

While we waited for the flowers to come into bloom, and for the Alaska Commercial Co. trading boat *Eunice* to get ready for the long trip to Attu Island, we did about ten days' of excavating in an Aleut stone-age village of pre-Russian occupation. I did most of the pick and shovel work, while Hulten did the sifting, photographing and recording of specimens. Several hundred artifacts, mostly of stone, were collected and sent to the Riksmuseum. Records of all species of mammals, birds and marine invertebrates used as food were also made. Distinct evidences of cannibalism were also noted as charred human jaw bones and arm and leg bones were not uncommon in the middens.

Several years later Dr. Ales Hrdlicka, chief anthropologist of the Smithsonian Institution, spent a whole summer with an expedition, carrying on the work where we left off. In his fine, large volume, finished after his death, on the Aleutian Islands and their inhabitants, he de-

scribes all of his archaeological work in the islands and records and photographs of all of the best artifacts.

During World War II, after the Japanese bombed Dutch Harbour, our military diligently went to work and made a real naval base at this spot. A great deal of excavating with big bulldozers in the vicinity unearthed an exceedingly rich archaeological site in an area where no digging had been performed before. Unfortunately, most of this treasure was destroyed by using the artifact-laden earth for filling hollows, etc. No trained scientist was at hand to salvage the material.

Dutch Harbour, on the small Amoknak Island, is hardly a mile from Unalaska Village. There is a rather steep mountain near Dutch Harbour called "Ballyhoo." One day, the Coast Guard ship *Chelan* arrived from Honolulu. The guest passenger was Captain Kirschhaus, ex-German enemy captain of the famous ocean raider, the *Sea Adler*, of which Count von Luckner was the commander. He had come on another ship direct from a survey of the Antarctic whaling grounds to Honolulu. At dinner parties on several occasions, he regaled Dr. Hulten and the American officers with accounts of the daring exploits of the *Sea Adler*. While on a climbing ramble to the top of "Balyhoo," Hulten, in quest of plants, and the captain, for exercise, a spirited debate was carried on between the two in discussing the merits of which was more important to society, a learned botanist, or an important military man. Each, of course, could see only his own profession as the more important. Today, at least in the larger countries, nearly all governments relegate all branches of science to the support of militarism.

In the first week of July, Hulten and I left Unalaska on the *Eunice* for the more westerly islands. I stopped on Atka Iisland where I collected plants for two weeks, including Amlia Island. Hulten went on to Attu, but it was still too early for flowering plants. Later in the summer, he went out there again on one of the Coast Guard boats and collected most of the flowering plants. He was thus able to properly compare the plants of this floristically important island with those of the nearby Commandorski Islands and Kamchatka. On his return from the first foray to Attu, Hulten also made short collecting forays on Agattu, Buldir, Kanaga, Amchitka, Adak, Amlia and Umnak, Alaid and Rat Islands. On account of the difficult landings and general bad weather, some of these stops were very brief. A good example of a brief excursion was a stop-off of less than three hours, that we made together onto the fog-drenched, difficult of approach, Carlisle Island in the Four Mountian groups of Islands. We both went in different directions as we nearly always did, to achieve maximum collecting results. In that short time, more than 100 species of plants were collected.

At that time most of the Aleutian Islands were uninhabited and the aggregate population west of Unalaska was probably less than 300 and composed mostly of native hunters and trappers. Not over a dozen white people lived in this area. Usually there were trappers' winter cabins on the larger islands which we sometimes used with the permission

of the natives. On Rat Island, Hulten saw the rats come down to the beaches in great numbers to eat cast up fish and algae.

The Aleutian Islands are well known for their frequent storms, cold fog and general inhospitable weather conditions. Before the war, with very little transportation between islands and with poor living accommodations, results of Hulten's collecting were surprisingly good in the short summer season. Without assistants and working our separate areas, our joint efforts resulted in an aggregate of nearly 20,000 sheets of all kinds of plants, besides collections of bird and mammal skins, marine invertebrate and fishes and archaelogocial and ethnographical specimens, besides the fine large series of photos that Hulten made. Of the 525 or more species and varieties of plants recorded from the Aleutians from the time of the Bering Expedition, we found about 500 of the known vascular plants and over 20 new species and varieties. Many more have been added since 1932.

No botanical expedition had ever entertained such an ambitious program as Hulten had undertaken, first, by studying and knowing all of the flowering plants of Scandinavia and Northern Europe and exploring Kamchatka and the Aleutian Islands with the fulfillment of a life's ambition of the resultant climax of producing *Flora of Alaska and Yukon* in ten volumes. This comprehensive work records the collections of nearly all botanists and collectors that had collected botanical specimens in this vast area since the Bering Expedition. Hulten continued plant exploration in Alaska and the Yukon through 1965.

In the subsequent years of 1939, 1940, 1945, 1946, 1947, 1948, 1950, 1951, 1952, 1953, 1954, 1955, 1956, I worked in various herring reduction plants in Alaska and always made rather extensive collections of plants which were sent to Hulten for recording in the *Flora of Alaska and Yukon*. In 1947 at Port San Juan, Evans Island in Prince William Sound, I found a record-size skunk cabbage leaf, *Lysichiton americanum* Hulten & St. John. The previous record-size found by J. P. Anderson was 4'10". This one stood erect and measured 6'2½" in length. I measured it nearly every day after it had exceeded Anderson's record until it stopped growing.

Since the war, the Aleutians are in many places well inhabited and numerous military bases had been established as well as easy and quick transportation. Many botanists have collected in the islands but not over two dozen species of the higher plants have been added to the flora of the islands. However, much botanical exploration in the more inaccessible interiors of many of the islands should eventually increase the number of species.

As Dr. Eric Ekman is recognized today as the foremost of the West Indian botanists, so it must also be recognized that Professor Eric Hulten is without comparison the foremost of all botanists of the circumboreal flora of the world.

MADROÑO

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PART ONE OF TWO

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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

A NEW GOSSYPIUM FROM GUERRERO, MEXICO

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Gossypium laxum sp. nov. Arbor 4–6 m alta; truncus ca. 1 altus, cortice griseo-maculoso; rami graciles, patuli, pauci-punctati; laminae foliorum 3–5-lobatae, cordatae, 7–12 cm longae, glabratae ad supre, stellato-pubescentes infra; pedunculi 4–7 mm longi, glabri; bracteolae triangules, glabratae, persistentes, 2-3 mm longae; calyx cupulatus, 8-10 mm longus, punctatus; corolla 5–8 cm longa, tubiformis, erubescentes, intra ad basim rubro-purpurea; capsulae 3–5 loculatae, ovatae, 25–35 mm longae; semina turbinata, 5–7 mm longa, fibris 6–8 mm longis obtecta.

Diffusely branched small tree 4-6 m tall with trunk less than 1 m high, 10–20 cm in diameter, bark mottled gray on trunk and older branches, brown on younger branches, these dotted with reddish-brown, circular lenticels ca. 0.5 mm in diameter; branches slender, flexuous, glabrate, the young stems stellate-pubescent; petioles stellate-pubescent, 3–6 cm long, punctuate with reddish-black glands; leaf laminas 3–5 lobed, 7–12 cm long, 8–14 cm broad, glabrate above, sparingly stellate-pubescent below, foliar nectary absent to vestigial; flowers borne on much reduced, 1–2-jointed sympodia in axils of distal 2–3 nodes of branches; pedicels 4–7 mm long, glabrate; bracteoles triangular, glabrate, 2–3 mm long, each subtended by a vestigial nectary; calyx cupulate, glabrate, 8–10 mm long, punctate with reddish-black glands, the lobes reduced to aristate tips 1–2 mm long; corolla 5–8 cm long, tubular; petals imbricate, sparsely punctate with reddish-black glands, stellate-pubescent, pink with deep-red spot covering lower one-half within; androecium 2.5–3.0 cm long, proximal and distal filaments of about equal length, filaments and anthers reddish; capsules 4–5 locular, 25–35 mm long, ovate, acutely beaked, dotted with dark, slightly raised glands, the sutures lacking cilia along inner margins, seeds turbinate, 5–7 mm long, 2.5–3 mm in diameter, covered with fibers 6–8 mm long; seed coat dark-brown, smooth.

Holotype: 0.2 km from Mex. highway 95 on side road from Milpillas to Xochipala, Guerrero, Mexico, alt. 2200 feet, October 17, 1967, *Phillips 945,* (NCSU).

Representative specimens: 2.5–3.0 miles west of highway 95 on road to Cerro Teotepec, *Anderson & Laskowski 4466,* (MICH). Km 234 Carr. Acapulco, Cañon de Zopilote, cerca Venta Vieja, *Miranda 9254,* (MEXU). Cañon de Zopilote, *Miranda 3969,* (MEXU). Milpillas, at Km 236 on Iguala-Acapulco highway, alt. 2200 feet, *Fryxell 614,* (ARIZ, US). Near Xochipala, alt. 3000 feet, *Fryxell 617,* (F, MEXU).
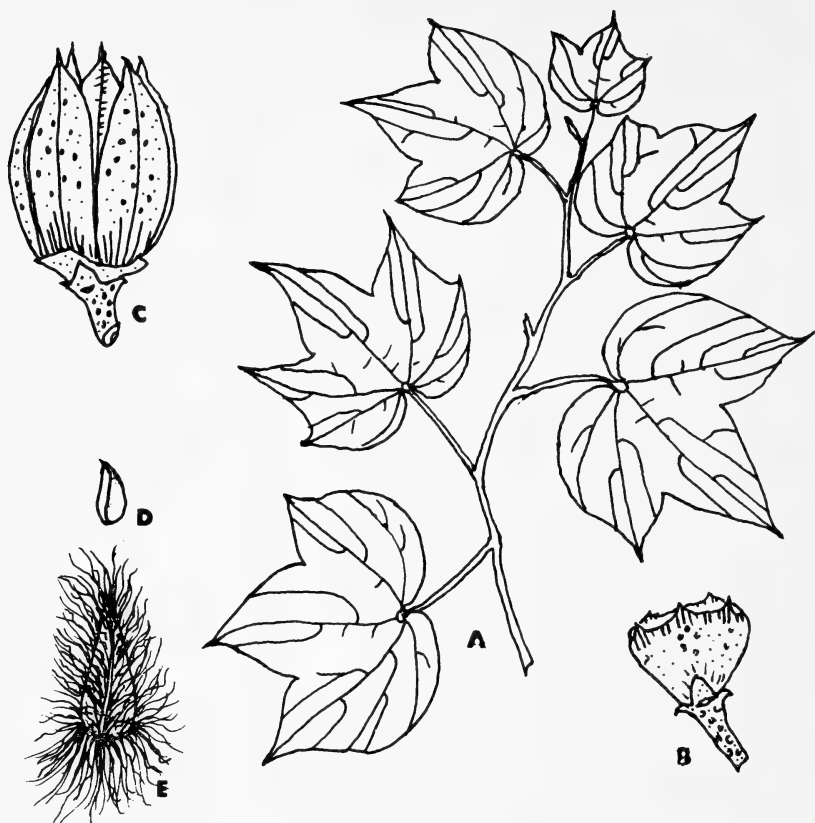
Fig. 1. *Gossypium laxum:* A, vegetative branch, X ⅓. B, calyx, X 1. C, capsule, X 1. D, seed (delinted), X 1. E, seed, X 2.

The type of *Gossypium laxum* was collected from a large population that extends ca. 20 km along Mex. Highway 95 from just north of its crossing of the Rio Balsas, south through Cañon de Zopilote. This distribution ranges from 2200 to 3000 feet in elevation.

Gossypium laxum is apparently more closely related to *G. aridum* (Rose & Standley) Skovsted and *G. lobatum* Gentry than to other taxa of the American diploid cottons, having the pink corolla and large, deep-red petal spot characteristic of these two species. *Gossypium laxum* is a small, open, tree 4–6 m in height, whereas, *G. aridum* (distributed along the Pacific slope from Sinaloa to the Istmo de Tehuantepec and also in Puebla) develops into a columnar tree 10–15 m in height and *G. lobatum* (Michoacan) is a spreading tree 8–12 m high. Other characteristics distinguishing *G. laxum* from *G. aridum* and *G. lobatum* are listed in Table 1.

TABLE 1. PRINCIPAL CHARACTERISTICS DISTINGUISHING GOSSYPIUM LAXUM
FROM G. ARIDUM AND G. LOBATUM.

	G. laxum	G. aridum	G. lobatum
Leaves	3–5 lobed, glabrate above, stellate-pubescent below	entire, glabrate above, puberulent below	3–5 lobed, stellate-pubescent above and below
Foliar nectary	usually absent	usually present	present
Calyx	glabrate, lobes 1–2 mm long	stellate-pubescent, lobes 1–3 mm long	stellate-pubescent, lobes 8–10 mm long
Androecium	apical and proximal filaments subequal in length	apical filaments shorter than proximal	apical filaments shorter than proximal
Capsule	ovate, 3–5 locular, sutures lacking cilia	narrowly ovate, 3 locular, sutures ciliate	narrowly ovate, 3 locular sutures ciliate
Seed	turbinate, 1.5 times longer than broad	elongate, 3–4 times longer than broad	elongate, 4–5 times longer than broad

NOTES AND NEWS

CORALLORHIZA MERTENSIANA BONG. IN MENDOCINO COUNTY.—On 4 May, 1970, a colony of thirteen plants of a *Corallorhiza* species was discovered in a pine woodland at Jughandle Creek at an altitude of 100 feet near Mendocino, Mendocino County, California. The species appears to agree with the description of *C. Mertensiana* Bong. in Munz, P. A., 1959, *A California flora,* pp. 1399–1400, Univ. Calif. Press, Berkeley, and also with the specimens deposited in UC. This locality represents a southward extension of the range of the species, its nearest locality being in Humboldt Co. (Munz, *ibid.*). It is also of interest that the species is growing at a far lowr altitude than is usual. *C. Mertensiana* is usually a plant of montane coniferous forests at an altitude of 4000–5000 feet (Munz, *ibid.*). The occurrence of this species in this locality is problematical. One possible explanation is that the species is a relict one, which is able to maintain itself because of summer fogs in this coastal strip. The fogs would reduce incident radiation and so reduce ambient temperature (Visher, S. S., 1954, *Climatic atlas of the United States,* pp.10–13, p. 177 No. 431, p. 179 No. 438, p. 186 No. 459; Harvard Univ. Press, Cambridge). A further example of a normally montane plant found in this coastal strip is *Menyanthes trifoliata* L., which perhaps gives added support to this possible explanation of the distribution of *C. mertensiana* (H. G. Baker, personal communication). The problem requires further study. A specimen and photograph of the plant have been deposited in JEPS. I am indebted to L. R. Heckard and H. G. Baker for information on this species.—WILLIAM ELFYN HUGHES, Ty-Pella, Siliwen Road, Bangor, N. Wales, U.K.

THE MANZANITAS OF BAJA CALIFORNIA,
INCLUDING A NEW SPECIES OF ARCTOSTAPHYLOS

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As long ago as 1905, an undescribed species of *Arctostaphylos* was thought to occur in northern Baja California (Goldman, 1916, p. 359): "A specimen of an undetermined and perhaps undescribed manzanita bearing ripe fruit was taken at about 1500 meters altitude along the trail on the west slope of the San Pedro Mártir Mountains between Rancho Santo Tomás and San Antonio, July 28. The species is less abundant than *A. glauca*, with which it occurs. In habit of growth it is similar to *glauca*, reaching a height of 1.8 to 3 meters."

During the past decade, Reid Moran of the San Diego Museum of Natural History has made numerous collections of a peculiar glaucous manzanita (possibly Goldman's) from the same area and elsewhere in Baja California—from the Sierra Juárez south to the Sierra San Borja, nearly halfway down the peninsula. It is a new burl-forming species, not belonging to either the *Arctostaphylos glandulosa* or the *A. tomentosa* groups. In the glaucous foliage, there is a resemblance to *A. glauca* Lindley, but it differs from that well-marked species in 20 other characters out of a total of 70 characters that I have examined.

Arctostaphylos peninsularis P. V. Wells, sp. nov. Frutex erectus, 1–3 m altus, 1–5 m latus; caudex tumescens; cortex levis ruber; ramuli glabrati; folia glauca, stomatifera supra et infra, ovata oblongave, apice obtusa acutave, basi acuta obtusave, petiolo 4–6 mm longo; inflorescentia paniculata, congesta, ramulis 1–6, saepe 2–3, glabrati; bracteae subulatae, acuminatae, glabratae; pedicelli glabratis, 4–6 mm longi; corolla globosa, 5–6 mm longa, 5 mm lata; ovarium glabratum; drupa globosa, glabrata, glauca, cinnamomea, 5–9 mm in diametro; endocarpus solidus, nuculis coalescentibus.

Holotype: gravelly hillside 1 mile east of Corral de Sam, elevation 2200 meters (7200 ft.), Sierra San Pedro Mártir, Baja California, near 31°03′ N, 115°33′ W, *Reid Moran 15531*, SD.

Erect shrub, 1 to 3 m high by 1 to 5 m wide, with a basal burl as much as 6 dm in diameter, or in some individuals the burl apparently absent; lower branches sometimes prostrate on ground, sometimes rooting adventitiously. Bark red-brown, smooth, branchlets glabrous; foliage buds smooth, not viscid. Leaves isofacial with about equal numbers of stomata above and below, glabrous and glaucous, oblong-ovate to ovate, apex obtuse or rounded to acute, base acute to obtuse or rounded, 2–4 cm long, on petioles 4–6 mm long. Panicle compact, with 1–6 (mostly 2–3) rachis-branches, the flowers crowded; nascent inflorescence cernuous, with closely appressed, scale-like deltoid-subulate, glabrous bracts; during anthesis lower as well as upper bracts subulate, with acuminate tips, not

becoming foliaceous and not elongating much in fruit. Pedicels glabrous, 4–6 mm long, not recurved in fruit. Corolla globose, 5–6 mm long, 5 mm wide. Ovary glabrous; mature fruit globose, 5–9 mm in diameter, light tan or reddish brown, glabrous, glaucous; exocarp thin, glaucous; mesocarp (pulp) thin; endocarp a solid, apiculate stone, not separating into nutlets.

Arctostaphylos peninsularis is a well-marked species that has been overlooked because of its out-of-the-way distribution in the mountains of Baja California. The glaucous foliage is deceptively similar to that of *A. glauca*. However, *A. peninsularis* differs from *A. glauca* and all other known taxa of *Arctostaphylos* in a wide array of characters. It is a crown-sprouting, shrubby species, tending to develop massive burls and widely-spreading lower branches that sometimes take root. *Arctostaphylos glauca* is an erect, arborescent shrub, lacking the burl. In *A. glauca* the bracts of the nascent inforescence are deltoid or broadly subulate with divaricate tips; at anthesis it has a larger and more diffuse inflorescence with the lower bracts foliaceous, and all of the bracts become enlarged and prominently divaricate in fruit. Moreover, in *A. glauca,* the glandular-hispidulous pedicels are longer (6–8 mm); the urceolate corolla is larger (9 mm long by 7 mm wide); the ovary and fruit are extremely glandular-viscid, never glabrous; and the mature fruit is much larger (10–15 mm) with a thick, leathery pericarp that is never glaucous.

In fact, *Arctostaphylos peninsularis* resembles *A. glauca* chiefly in the glaucous foliage and solid stone-like endocarp, two striking characters that have been weighted in *Arctostaphylos* taxonomy. Even though they differ in at least 20 other characters, I refrain from calling this a superficial resemblance because it seems possible that there may have been a close connection between *A. glauca* and *A. peninsularis*. On the other hand, one of the traits the two species hold in common—the solid, stone-like endocarp—appears as a striking parallelism in most of the manzanitas endemic to Baja California and adjacent southern California from the Transverse Ranges south, but not in the manzanitas of northern California. The prevalent condition in the genus is, of course, an endocarp irregularly divided into several, often 4–6, nutlets. The other species having drupes with a single massive stone are *A. australis* Eastw., *A. parryana* Lemm., *A. pringlei* var. *drupacea* Parry, and *A. refugioensis* Gankin. The other narrow endemic of the extreme south, *A. otayensis* Wiesl. & Schreib., also has solid stones, but shows variation to separable nutlets. Significantly, the allied monotypic genus *Xylococcus*, another endemic of southern California and Baja California, also has massive, undivided endocarps. It is well known that the germination of many chaparral species is triggered by fire (Sampson, 1944; Stone and Juhren, 1951; Sweeney, 1956; Quick, 1959, Wells, 1969), but it is probable that limits of heat tolerance exist. It seems likely that the thick-walled, woody, undivided endocarp has been selected because of its greater resistance to fire,

even though it greatly dimishes the dispersal capacity; the problem invites experiment.

With the aid of the following key, *A. peninsularis* can be distinguished from other members of the genus, and from the closely allied monotypic genera, that occur in Baja California and adjacent southern California.

Key to the Manzanitas of Baja California and Vicinity

a. Leaves opposite or whorled, or, if alternate, then in two ranks, bifacial, strongly revolute, usually tomentose below; inflorescence either diffusely cymose with oppositely arranged rachis-branches and pedicels, or compactly umbelliform; sepals wooly on outer face; ovary tomentose, fruit glabrescent.

    b. Leaves opposite or whorled, linear or linear-lanceolate; inflorescence diffusely cymose with filiform, oppositely-branched rachises; pedicels filiform, in pairs or whorled, much longer than the tiny urceolate flowers; each pedicel bearing a pair of scale-like bracts toward the middle; endocarp divided into nutlets. Narrow endemic, n.w. Baja California. *Ornithostaphylos oppositifolia* (Parry) Small [*Arctostaphylos oppositifolia* Parry]

    bb. Leaves alternate and two-ranked, or opposite, oblong-ovate; inflorescence compactly umbelliform with a short, thick, simple rachis; pedicels stout, shorter than the coarse, saccate, obovoid flowers; each pedicel subtended only at the base by a pair of bracts; endocarp a solid, apiculate stone. Los Angeles Co. south to central Baja California. *Xylococcus bicolor* Nutt. [*Arctostaphylos bicolor* (Nutt.) Gray]

aa. Leaves alternate, in more than two ranks, isofacial or bifacial (ours all isofacial), not strongly revolute; inflorescence paniculate or racemose, with spirally arranged rachis-branches and pedicels; ovary and fruit tomentose, glandular-viscid, or glabrous . . . . *Arctostaphylos*

    c. Bracts of inflorescence at anthesis foliaceous, thick, not membranous or scale-like; rachis of nascent inflorescence thick with densely imbricated bracts.

        d. Burl present at base of stem, crown-sprouting; nascent inflorescence cernuous, with 2–3 branches, the bracts deltoid to short-lanceolate; endocarp divided into nutlets. Wide-ranging, Oregon to n. Baja California . . . . *A. glandulosa* Eastw.

        dd. Burl absent, not crown-sprouting; nascent inflorescence stiffly erect, with 4–5 branches, the bracts elongate-lanceolate and widely overlapping; endocarp a solid stone or irregularly divided into nutlets. Narrow endemic, mountains of southern San Diego Co.
                                                 A. otayensis Wiesl. & Schreib.

    cc. Bracts of inflorescence at anthesis scale-like (or membranous and bright red), deltoid to subulate, or the lowermost 1–2 bracts foliaceous; rachis of nascent inflorescence with minute, scale-like bracts.

        e. Leaves bright green with lustrous cuticle; endocarp divided into several nutlets; burl absent.

            f. Inflorescence racemose or with 1–2 branches, with a prominently clavate rachis, the flowers long-pedicelled, crowded at the thick distal end; rachis and bracts not glandular. Wide-ranging, Monterey Co. to Sierra San Pedro Mártir, n. Baja California; Arizona to Oaxaca . . . . . *A. pungens* H.B.K.

ff. Inflorescence an ample, several-branched panicle; the slender rachises and bracts glandular-puberulent. Wide-ranging, California to Colorado, south at high elevations (above 7,000 ft.) to the Sierra San Pedro Mártir, Baja California.

A. patula subsp. platyphylla (Gray) Wells

ee. Leaves glaucous, pallid, or gray-green, dull; endocarp a solid stone, not separating into nutlets (except in A. pringlei subsp. pringlei).

g. Bracts membranous, bright red or pink at anthesis; sepals linear-oblong, promiently glandular-ciliate; ovary, pedicels, bracts, rachises, and branchlets densely glandular-pubescent; fruit glandular-viscid; leaves scabrous with glandular hairs.

h. Endocarp separating into several discrete nutlets. Sierra Juárez and Sierra San Pedro Mártir, n. Baja California; Arizona . . . . A. pringlei Parry subsp. pringlei

hh. Endocarp a solid, undivided stone; leaves usually grayer, more orbicular and subcordate. Mountains of s. California from San Bernardino and Santa Ana Mtns. south. A. pringlei subsp. drupacea (Parry) P. V. Wells, comb. nov. [A. pringlei var. drupacea Parry, Bull. Cal. Acad. 2:495. 1887].

gg. Bracts mostly scale-like, not membranous or red; sepals ovate, eglandular; leaves glabrous and smooth.

i. Nascent inflorescence with stiffly erect, thread-like rachises and minute, deltoid, scaly bracts; at anthesis panicle diffusely branched; leaves elliptic, pallid or gray-green. Narrow endemic, near coast, n.w. Baja California: Pine Canyon, San Antonio del Mar (31°18′N); Cerro Blanco (32°03′N).

A. australis Eastw.

ii. Nascent inflorescence mostly cernuous, with stout rachises and coarser, subulate bracts; leaves ovate, very glaucous.

j. Basal burl absent; erect, arborescent shrub, lower branches not prostrate and rooting; panicle large and openly branched, the lowest bracts foliaceous, the upper bracts enlarged and divaricate in fruit; pedicels 6–8 mm long, glandular-hispid; corolla urceolate, 8–10 mm long; ovary glandular; fruit very glandular-viscid, 10–15 mm in diameter, with thick leathery pericarp; leaves round-ovate with truncate to subcordate base, on petioles 10 mm or more long. Wide-ranging in Coast, Transverse and Peninsular Ranges from Contra Costa Co. south to Sierra San Pedro Mártir; to Sierra San Borja, c. Baja California.

A. glauca Lindl.

jj. Basal burl usually present; erect or spreading shrub, lower branches sometimes prostrate and rooting; panicle more compact, the bracts not foliaceous, not enlarging much in fruit; pedicels 4–6 mm long, glabrous; corolla globose, 5–6 mm long; ovary glabrous; fruit glabrous and glaucous, 5–9 mm in diameter, with thin pericarp; leaves oblong-ovate with acute to rounded base, on petioles 4–6 mm long. Endemic to mountains of northern half of Baja Califrnia, from Sierra Juárez to Sierra San Borja . . . . A. peninsularis Wells

Reid Moran has collected in coastal northwestern Baja California a number of specimens of *Arctostaphylos* that are not accommodated by the existing taxonomy. They recombine, in limited ways, the characters of *A. glauca, A. glandulosa,* and *A. australis.* Field studies will be required to establish the characteristics of the populations from which these samples were taken.

Arctostaphylos peninsularis has its principal populations in the Sierra San Pedro Mártir from 31°16′ N south to 30°35′ N, with outliers in the Sierra Juárez (to Laguna Hanson, near 32° N), Cerro San Luis (29°19′ N), and the Sierra San Borja (28°47′ N). The latter range is isolated from the San Pedro Mártir populations by about 150 miles of *Idria* desert, and is the southernmost known outpost of *Arctostaphylos* on the peninsula (R. Moran, personal communication). Moran has made several collections of manzanitas in the Sierra San Borja, one of which (*Moran 9926,* SD, UC; Tigre Canyon, 28°51′ N) appears to be the only record of *A. glauca* south of Cerro Matomí and Cerro San Juan de Dios, two isolated peaks just south of the San Pedro Mártir range. Specimens of *A. peninsularis* from Cerro el Sauco at 28°46′ N in the San Borja range differ from the typical San Pedro Mártir populations in having minutely glandular-puberulent rachises, bracts, pedicels, and in some, branchlets and petioles. Disposition of this glandular form is deferred until further examination of the San Borja manzanitas can be made in the field.

In the Sierra San Pedro Mártir, *Arctostaphylos peninsularis* has been collected at elevations of about 4000 to 8000 ft., a zone intermediate between, and partly overlapping, the zones occupied by *A. glauca* and *A. patula* subsp. *platyphylla.* Below 4000 ft., *A. glauca* fills the manzanita niche, and above 8000 ft., *A. patula platyphylla* predominates. The partial coexistence of the burl-forming *A. peninsularis* with two nonsprouting taxa, lacking burls, follows the general rule for sympatry in *Arctostaphylos*: species with dissimilar modes of reproduction in response to fire tend to grow together more often than species with similar strategies (Wells, unpublished data). An analogy can be drawn with a very similar trio of manzanitas segregating along an elevation gradient in the Sierra Nevada: *A. viscida* Parry, *A. mewukka* Merriam, and *A. patula* Greene subsp. *patula.* The species occupying an intermediate zone of elevation, *A. mewukka,* is a burl-forming manzanita superficially resembling *A. peninsularis,* and intermediate in morphology and ecology between *A. viscida* (a lower elevation, nonsprouting species related to *A. glauca*) and *A. patula* subsp. *patula* (a higher elevation, burl-forming version of *A. patula platyphylla*). For the Sierra Nevada trio, we also have cytological information; *A. mewukka* is tetraploid ($n = 26$), and the other two taxa are diploid (Wells, 1968). This, in conjunction with the morphological, ecological, and spatial intermediacy of *A. mewukka,* suggests that it is

an amphidiploid species stemming from the cross *A. viscida* × *A. patula*. If there is predictive value in a comprehensive cytotaxonomic, morphological and ecological survey of the genus, it seems likely that the species *A. peninsularis* may have had an analogous ancestry, involving *A. glauca* and *A. patula*.

LITERATURE CITED

GOLDMAN, E. A. 1916. Plant records of an expedition to Lower California. Contr. U. S. Nat. Herbarium 16:309–371.
QUICK, C. R. 1959. Ceanothus seeds and seedlings on burns. Madroño 15:79–81.
SAMPSON, A. W. 1944. Plant succession on burned chaparral lands in northern California. Univ. Calif. Coll. of Agri. Bull. 685.
STONE, E. C. and G. JUHREN. 1951. The effect of fire on the germination of *Rhus ovata* Wats. Amer. J. Bot. 38:368–372.
SWEENEY, J. R. 1956. Responses of vegetation to fire. Univ. Calif. Publ. Bot. 28:143–250.
WELLS, P. V. 1968. New taxa, combinations, and chromosome numbers in Arctostaphylos (Ericaceae). Madroño 19:193–210.
———. 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. Evolution 23:264–267.

LEGUMES OF THE U.S. VI.
CALLIANDRA, PITHECELLOBIUM, PROSOPIS

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Herein, I complete a generic summary of the mimosoid legumes of the United States, except for cultivated *Acacia*. The objectives and format of these publications are briefly delineated in Isely (1969). The treatments include generic descriptions, keys to species, range and habitat characterization, and taxonomic and nomenclatural commentary.

Accessions of material of the subject genera from the following herbaria were studied in preparation of this paper: NY, ISC, TEX, NMC, LAF, ARIZ, FSU, USF, POM, and RSA. Selected materials and (or) types have been studied by courtesy of: GH, MO, LL, US, LA, and PH. My debt to the institutions and curators is obvious. And my thanks to several botanical friends (Rupert Barneby, Marshall Johnston, R. W. Pohl, Jean Wooten) who reviewed this manuscript or portions of it.

CALLIANDRA BENTH.

Low perennial herbs or shrubs; or (not in U.S.) trees. Leaves twice compound without foliar glands. Pinnae 1—several pairs. Stipules small but usually persistent and evident. Peduncles axillary, clustered or racemose. Flowers capitate, often relatively few in each head, white, pink or red. Calyx campanulate. Corolla tube funnelform, equalling or exceeding lobes. Stamens numerous, fused below, much exserted. Legume compressed, cuneate-oblong, not septate, dehiscent; margins thickened; valves membranous to subwoody, separating from apex and curling individually.

A primarily tropical American genus of possibly 100 or more species (estimates vary widely, e.g.: Britton and Rose, 1928; Hutchinson, 1964; Woodson and Schery, 1950). Ours southern Texas to California; several tropical species slightly introduced.

Chromosome base number x = 8 determined from two species (Atchison 1949, 1951).

In the United States, *Calliandra* is easily defined and recognized on the basis of its distinctive pods (both as to shape and mode of dehiscence), and few-flowered heads. Our native representatives are primarily of two complexes, one woody and the other herbaceous, that center about *C. eriophylla* and *C. humilis* respectively. Both groups require biosystematic investigation throughout their entire ranges.

Perhaps ten species of tropical *Calliandra* have been introduced into the United States in specialized plantings. I have admitted two as constituents of our cultivated flora.

CALLIANDRA Benth., Hook. Jour. Bot. 2:138. 1840! nom. cons. Type species: *Mimosa houstoni* L'Heritier, nom. illeg. [*Calliandra houstoni* (L'Heritier) Benth., nom. illeg.] *Calliandra inermis* (L.) Druce.

ANNESLIA Salisb. Parad. Lond. Pl. 64. 1907! nom. rejinciendum.

Further synonyms are tabulated by Hutchinson (1964); these represent names either based on tropical species that I have not studied or are spelling variants of *Anneslia*.

Key to species

Flower heads 4–6 cm in diameter; cultivated ornamentals of urban California and possibly southern Florida and Texas.
  Pinnae 1 pair; leaflets ca 5 pairs, to 6 cm long; heads pinkish.
                                                                     C. inaequilatera
  Pinnae ca 4 pairs; leaflets 15–20 pairs, less than 1 cm in length; heads red-scarlet. . . . . *C. tweedii*
Flower heads much smaller than above; native species, Texas to Arizona.
  Flowers 2 per head; corolla 4–5 mm high; pinnae 1–3 pairs; local, southern Texas . . . . *C. biflora*

Flowers 4–10 per head; if from southern Texas, pinnae 1 pair and
corolla 3.0–3.5 mm.

Leaflets not imbricate, 4–6(7) pairs; pubescence when present
of tiny hairs 0.1–0.2 mm long; corolla ca 2.5 mm in
length; local woody species of Pima Co., Arizona.

C. schottii

Plants not with above combination of characters; widely dis-
tributed species; if from Pima Co., Arizona, herba-
ceous with corolla 4–5 mm long, or woody with 7–10
pairs imbricate leaflets.

Plants herbaceous; petioles of well developed leaves 1.5–
3(4) cm long; pinnae 1–6 pairs   .   *C. humilis*

Plants woody; petioles less than 1 cm long; pinnae 1–3
pairs.

Pinnae 1 pair; Texas . . . . *C. conferta*

Pinnae 2–3 pairs (some leaves may have 1 pair); Ari-
zona and slightly into New Mexico.

C. eriophylla

Calliandra biflora Tharp

Southern Texas. Adjacent Mexico. Local, sandy or loam soil. May-July.

Calliandra biflora lies at the periphery of the range of *C. eriophylla*
var. *conferta*. But the differences are so numerous, I would hesitate to
postulate a close relationship.

The Texas stations (DeWitt and Goliad Co's. for *C. biflora* are local
and moderately disjunct from the Tamaulipas collection sites. It is to be
sought in the intervening portion of southern Texas.

U.S. material of *C. biflora* appears to be herbaceous-suffrutescent, the
tops dying back to the ground each year. But Mexican specimens are low
shrubs with perennial stems.

Calliandra BIFLORA Tharp, Rhodora 56:132. 1954! Type TEX! Isotype SMU!
Reidel & Tharp 44419.

Calliandra conferta Benth.

Southern to western Texas. Adjacent Mexico. Calcareous, gravelly hills,
canyon slopes, desert scrub. 500–4000 ft. April-July.

Relationships of *Calliandra conferta* to *C. eriophylla* are discussed
under the latter species.

Turner (1959) has noted that western Texas forms differ from those in
central and southern Texas in the possession of "much longer peduncles."
I have plotted on a distributional map two forms: (1) peduncles 1 cm
or more, (2) peduncles less than 1 cm. I agree with Turner. Perhaps this
feature marks a geographic variety.

Calliandra CONFERTA Benth. in Gray, Pl. Wright 1:63. 1852! Isosyntypes U.S.!
    Wright 166 & 167, NY! *Wright 166*.

Calliandra eriophylla Benth.

Southern California to western New Mexico. Adjacent Mexico. Rocky desert slopes and plains, washes, canyons, cliffs, usually with *Franseria, Carnegia, Cercidium, Prosopis*. Common. 400–4500 ft. (Jan.) March-May, Sept.-Nov.

Calliandra eriophylla presents no major problems in the United States. The closest relative is *C. conferta* Benth. The two species are easily distinguished morphologically and are disjunct geographically. However, interpretation of some Mexican material is uncertain, and it may be that *C. eriophylla* and *conferta* constitute geographical phases of one species.

I am treating an equivocal, rare form of western Texas and possibly adjacent New Mexico as a variety of *C. eriophylla* as follows:

Pods 2.5–5.0 (7.0) cm long, oblanceolate; petioles 3–5 mm long; flowers (4)5–10(12); pinnae (1)2–4 pairs . . . . var. *eriophylla*
Pods 7–9 cm long, narrowly oblong; petioles 5–7 mm long; flowers 2–5; pinnae mostly 2 pairs . . . . var. *chamaedrys*

Var. *chamaedrys* Isely

In 1967 I encountered three sheets at NY *(Wright 1367; Wright 1043; Parry Mexican Boundary Survey 317a)* from the 1840's and '50's that represented *C. chamaedrys* sensu Gray 1853 (loc. cit.; non *C. chamaedrys* Engelm. 1849). They seemed probably referable to *C. eriophylla* but differed strikingly in the narrowly oblong pods which tapered only proximally. They came from an area approximately intermediate between the apparent ranges of *C. eriophylla* and *C. conferta*. I looked through ample Mexican material of the *C. eriophylla* complex (NY) but found nothing with pods like the sheets at hand. Lacking any modern collections I deferred taxonomic consideration. Two years later, I encountered a single, recent collection possessing the distinctive pods and other features of var. *chamaedrys*. Information for a decision is all too limited, but this taxon seems too distinctive to ignore. Hopefully, future collectors will encounter it in West Texas, and adjacent New Mexico, and Mexico.

Calliandra eriophylla var. **chamaedrys** Isely, var. nov.

Fruticulus humilis. Petioli 5–8 mm longi; pinnae (1)2-jugae. Flores 2–5. Legumina 7–9 cm longa, 5 mm usque lata, anguste oblonga nunc basin versus sensim attenuata. Holotype: SMU! *Turner 3642*. 15 miles north of Uvalde, Uvalde Co., Texas. June 26, 1954.

Calliandra chamaedrys sensu Gray, Pl. Wright 2: 52. 1853! non *C. chamaedrys* Engelm. 1849.

Gray (loc. cit.), citing both the Wright gatherings that I have seen, recognized this taxon over a century ago and I have taken up the name as he used it. Since, however, his name probably represented a misapplication of the Englemann *chamaedrys,* my epithet is not based on his.

Var. *eriophylla*

Distribution and habitat as species.

Exomorphic variance within this variety relates to number of pinnae, length of pod, and size and showiness of flower heads (length and color of stamen filaments). A single plant may possess leaves with 1–4 pairs pinnae. The leaves of most California material are limited to 1–2 pairs pinnae and I believe there is some correlation with small size of flower heads. Thus, in these attributes, these forms exhibit a reverse cline towards *Calliandra conferta.* Occasional plants possess pods approaching those of var. *chamaedrys* in length yet lack other features of that variety.

Calliandra ERIOPHYLLA Benth., Lond. J. Bot. 3: 105. 1844!*Feuilleea eriophylla* (Benth.) Ktze., Rev. Gen. 1: 187. 1891! *Anneslia eriophylla* (Benth.) Britt., Trans. N.Y. Acad. Sci. 14: 32. 1895!

I follow the application of the binomial *Calliandra eriophylla* that has been consistent since Bentham's time. However, I have not seen the type.

My identification of *Calliandra chamaedrys* Engelm. is primarily from the description. Engelmann based his name upon a Gregg and a Wislizenus specimen. There is a Gregg specimen (probably typical *C. eriophylla* but lacking pods) designated *C. chamaedrys* Engelm. in GH and stamped isotype. But the locality designation does not match that cited by Engelmann.

Calliandra humilis Benth.

Western Texas to northern Arizona. Adjacent Mexico. See varietal treatment.

Conspicuous variation in the *Calliandra humilis* complex relates to three kinds of features:

(1) Pinnae and leaflet number, and leaflet size. One suspects that variance in these features is correlatively controlled by one gene system. The forms with small leaflets have numerous leaflets and pinnae and *vice versa.* All extremes occur in Arizona, but Texas lacks the phenotypes with few, large leaflets.

(2) Flower heads pedunculate or sessile. There is little intermediacy between these conditions except that some specimens (mostly Arizona) have both sessile and stalked heads. Variance in this feature appears largely independent of that pertaining to leaves, but in western Texas, there is some relationship between sessile heads and reduced number of

pinnae. Both sessile and pedunculate heads occur in most parts of the range.

(3) Plants pubescent or glabrate. Plants with large leaflets are glabrate. Those with small leaflets may be either glabrate or pubescent, a few are conspicuously villous.

It is possible to roughly sort material into four groups by leaf and peduncle diversity. Each variant has been the recipient of epithets (in binomial or trinomial form) as follows:

Key to variants
Pinnae 3–6(8) pairs; leaflets 6–14 pairs, 3–5 mm long

Heads pedunculate   .   Variant 1. *Calliandra herbacea* Engelm.; *C. humilis* Benth. non *Acacia humilis* Schlecht.

Heads sessile . . . Variant 2. Primarily *C. humilis* auct.; in part *Calliandra herbacea* auct.

Pinnae 1–2 (3) pairs; leaflets 5–6 (8) pairs, (4) 5–10 (12) mm long

Heads pedunculate   .   Variant 3. *C. reticulata* Gray; *C. reticulata* and *C. humilis* auct.

Heads subsessile . . Variant 4. *Acacia humilis* Schlecht.; *C. reticulata* and *C. humilis* auct.

Recent interpretations of this complex (Britton & Rose, 1928; Benson, 1943; Turner, 1959; and Kearney *et al.*, 1960) assign names (as species or varieties) to various combinations of these variants. My postulate is to recognize two overlapping geographic varieties: variants 1 and 2 are var. *humilis;* variants 3 and 4 are var. *reticulata.* In making this decision, which parallels that of Benson (1943), I am giving leaf characters more weight than peduncle variance because leaf features exhibit geographic orientation and broader correlation with pubescence.

Key to varieties
Pinnae 3–6(8) pairs; leaflets 6–14(20) pairs, 3–5 mm long, pubescent in Arizona portion of range; western Texas to Arizona. var *humilis*
Pinnae 1–2(3) pairs; leaflets 5–6(8) pairs, (4)5–10(12) mm long, glabrate; Arizona and adjacent New Mexico . . var. *reticulata*

Var. *humilis*
Western Texas to northern Arizona. Texas: open rocky, igneous and limestone soils; Arizona: grassy slopes, oak woodland, pinyon-juniper or yellow pine. 3000–8000 ft June-July (Aug.)

This variety seems to occur essentially throughout the U.S. range of the complex and is the only variety in Texas. There is a geographical break between the Texas and the Arizona forms. But there seems to be no morphological differentiation except that both glabrate and pubescent forms occur in Texas.

The Arizona populations of var. *humilis* include both variants 1 and 2 (with and without peduncle) with a preponderance of the latter. Mapped, they seem to display no distributional differences; correlation with other features is abortive. Benson (1943) indicates that his typical var. *humilis* (Arizona) usually occurs at lower elevations, 3000–5000(7000) ft., and that var. *reticulata* is of pinyon-juniper or yellow pine at higher elevations. My field observations suggest that the two forms are rarely geographically or ecologically sympatric, but I have not confirmed a distinct altitudinal zonation.

In western Texas, where populations are exclusively of var. *humilis* as I have delimited it, variants 1 and 2 are treated as *C. herbacea* and *C. humilis* by Turner (1959). Here, pubescence and pinnae number correlate with peduncle length to a reasonable degree, and two forms can be characterized with reasonable clarity. But such differentiation doesn't work in Arizona.

Calliandra HUMILIS Benth., Lond. J. Bot. 5: 103. 1846! Fragment of type GH! Coulter "Azcatecas sp. n." non *Acacia humilis* Schlecht. 1838!

C. HERBACEA Engelm. in Gray, Mem. Amer. Acad. Arts. Sci. series II, 4: 39. 1849! Type GH! Fendler 180. *Anneslia herbacea* (Eng.) Britt. & Rose, N. Am. Fl. 23: 57. 1928!

Calliandra humilis Benth. is the binomial the species must take. *Acacia humilis* Schlecht. is the oldest name referable to this species (var. *reticulata* below), but its transfer to *Calliandra* is blocked by the Bentham name. Benthan was not making a combination; he cites a different type than did Schlechtendal, and does not cite him.

Both *Calliandra humilis* Benth. and *C. herbacea* Engelm. are easily referable, both as to type specimen and description, to var. *humilis* as I have circumscribed it. Reference of these names to the variants tabulated above is less than consistent. Some authors have treated *C. humilis* as a taxon with sessile heads but those of the type are distinctly pedunculate. *Calliandra herbacea* Engelm. has "peduncles one inch" but the Fendler sheet cited has both sessile and pedunculate heads on the same plant. Gray earlier compounded confusion about application of these names through distribution of *Wright 1044* which is an exsiccatae melange of several gatherings that include both forms.

Var. *reticulata* (Gray) Benson

Southwestern New Mexico to central Arizona. Grassland to pine forests and open gravelly slopes near mountain peaks, wooded ravines, swales. 4000–8000 ft. (May) July-August.

This variety apparently does not go as far north in Arizona as var. *humilis* ano material from Coconino and Yavapai Co's. and is said (Benson, 1943) to occur at higher altitudes. As to specimens, vars. *hu-*

milis and *reticulata* intergrade, and determination of some material is arbitrary. However, in the field I have not seen the two in contiguous areas, and their identity has seemed unequivocal.

Calliandra humilis var. *reticulata* (Gray) Benson, Amer. J. Bot. 30: 630. 1943!
    C. RETICULATA Gray, Pl. Wright. 2: 53. 1853! Type GH!, isotype US!
    Wright 1045. Anneslia reticulata (Gray) Britt., Trans. N.Y. Acad. Sci. 14: 32.
    1895! *Feuilleea reticulata* (Gray) Ktze., Rev. Gen. 1: 189. 1891!

Acacia HUMILIS Schlecht., Linnaea 12: 567. 1838! Presumed type (photo) NY!
    Ehrenberg 563, Propre Regla., non *C. humilis* Benth. 1842! *Anneslia humilis*
    (Schlecht.) Britt. & Rose, N. Am. Fl. 23: 57. 1928! *Feuilleea humilis* (Schlecht.)
    Ktze., Rev. Gen. 1: 188. 1891!

Calliandra inaequilatera Rusby

Urban southern California. Cultivated ornamental. Native of South America. Nov.-April.

This species is not uncommon in the Los Angeles area; it is treated by Enari (1962) and enumerated by Mathias and McClintock (1963). It is related to *C. guildingii* and *C. haematocephala* Hassk., and is probably conspecific with the latter. Recent annotations by Elias and Nevling at NY, noted as this paper goes to press, mark limited material (including the type) of *C. inaequilatera* as *C. haematocephala* Hassk. I maintain use of the traditional name for this species in California pending publication by the above-mentioned authors. (See note page 298.—Ed.)

Calliandra INAEQUILATERA Rusby, Mem. Torr. Bot. Club 6: 28. 1896! Holotype
    NY! *Bang 1568.*

Rusby's specimen (Bolivian material) and description are congruent, and seem to be of the species cultivated in the United States.

Calliandra schottii Wats.

Southern Arizona (Pima Co.) and adjacent Mexico. Rocky slopes, canyons, usually in pinyon belt. 3000–4500 ft. Aug.-Sept.

U.S. collections of this species are nearly all from the Santa Catalina and Baboquivari Mts.

Calliandra SCHOTTII Torr. ex Wats., Proc. Amer. Acad. Arts Sci. 20: 364. 1885!
    Lectotype GH! *Schott.,* Arroyo de los Somotos, Sierra Verde, Sonora. Aug. 20,
    1855. *C. portoricensis* Benth. var. Torr., Emory Rep. 2: 61. 1859! Based on
    Schott. loc. cit. *Anneslia schottii* (Wats.) Britt. & Rose, N. Am. Fl. 23: 67. 1928!

Watson (loc. cit.) cites a Pringle gathering and refers to *C. portoricensis* var. Torr. I am basing *C. schottii* on Torrey's unnamed variety, and designating Torrey's cited specimen as lectotype.

Calliandra tweedii Benth.

Southern urban California, probably also Florida and Texas. Native of Brazil. Cultivated ornamental. Dec.-May. Flame bush.

The forms in the United States which I have seen have about 4 pairs of pinnae. Var. *sancti-pauli* has to 8 pairs pinnae; apparently it has not been introduced in the U.S.

This species is treated by Bailey (1949), Doty and Johnson (1954), Enari (1962), and Mathias and McClintock (1963). I have seen specimens primarily from the Los Angeles area.

Calliandra guildingii Hort. is *C. tweedii*—fide California specimens as well as Mattoon (1958) and Mathias and McClintock (1963). *C. guildingii* Benth. is a species with few, large leaflets (as *C. inaequilatera*). I have not seen *C. guildingii* in the United States. Material passing under this name has been commercially available in Florida and southern Texas as well as California.

Calliandra TWEEDII Benth., Hook. Jour. Bot. 2: 140. 1840! Photo of type (Kew) NY! *Tweedie 78,* Rio Jacury, Brazil. *Anneslia tweedii* (Benth.) Lindm., Bih. Svensk. Vet. Akad. Handl. 24(7):51. 1898!

Another photograph (NY!) purports to be of the type of *C. tweedii* Benth. It is *Sello 1178* Brazil from Herb. Reg. Berolinense, the specimen in the Berlin Herbarium. Since Bentham cites "Mountains of Rio Jaqury. Tweedie." I accept the Tweedie specimen.

Rejected Species

Calliandra anomola (Kunth.) Macbride. California. Novelty in cultivation, Santa Barbara. Determination of subject sheets (LA) is tentative.

Calliandra costaricensis (Britt. & Rose) Standl. Although enumerated by Mathias and McClintock (1963), there are no collections of this species at LA.

Calliandra guildingii Benth. Mattoon (1958) states that this South American species is commercially available from six sources in the United States (Florida, Texas, and California). Doty and Johnson (1954) and Mathias and McClintock (1963) assert that *C. guildingii* of horticulture is *C. tweedii.* Confusion between these two species might seem improbable—the foliage is utterly different—but both have in common the large, brilliantly red flower heads. I have not encountered *C. guildingii* in the United States.

Calliandra haematocephala Hassk. This species is enumerated by Mathias and McClintock (1963). Possibly U. S. material treated as *C. inaequilatera* Rusby (which see) should be referred to *C. haematocephala.*

Calliandra houstoniana (Mill.) Standl. A sheet from the Los Angeles area (LA) is of this species. It is not enumerated by Enari (1962) or Mathias and McClintock (1963).

Calliandra parvifolia (Hook. & Arn.) Speg. Collection from Winter Park, Florida said to have been obtained from a nursery (US; determined by Velva Rudd).

Calliandra portoricensis (Jacq.) Benth. California. Novelty in cultivation, Santa Barbara and Los Angeles (LA). Not tabulated by Mathias and McClintock (1963).

Calliandra selloi (Spreng.) Macb. Cultivated. Winter Park, Florida (US; determined by Velva Rudd).

Calliandra schultzei Harms. I have twice collected, in Florida, material which I took for *C. surinamensis:* in a commercial nursery at Bradenton and on the grounds of the Florida Subtropical Experiment Station at Homestead. Tentative association with *C. schultzei* was made by Dr. Howard Irwin who kindly examined my specimens.

PITHECELLOBIUM MART.

Shrubs or trees. Stipules often spiny. Leaves (ours) twice-pinnate, often with but one pair pinnae and leaflets (thus four leaflets); with a stalked or sessile gland on the rachis between the lower or all pinnae. Leaflets mostly asymmetric, usually relatively large. Inflorescences of heads or infrequently spikes, these axillary or supra-axillary, or racemed or panicled. Flowers usually white. Stamens numerous, the filaments basally fused into a tube. Legume various, dehiscent or indehiscent, fleshy, woody or membranous, often circinately coiled and dehiscent. Seeds frequently with an aril.

A heterogeneous assemblage of species, largely of the American tropics or (if one interprets the genus more broadly) bihemispheric; 100–500 species (?).

Basic chromosome number $x = 13$; determinations on about eight species.

Concurrence concerning the generic limits of *Pithecellobium* has been limited. *Pithecellobium* in the broad sense, sensu Bentham (1875), was fragmented by Britton and Rose (1928). Woodson and Schery (1950) and Standley and Steyermark (1946) reverted to the Bentham concept at least as far as New World species were concerned. More recently, the delimitation of *Pithecellobium* is considered by Mohlenbrock (1963a, 1963b), Kostermans (1952), and Hutchinson (1964). Interpretations range from that of Kostermans who distributes Old World *Pithecellobium* among some nine genera (mostly new) to the conservative viewpoint of Hutchinson who segregates only *Samenea* Merrill from *Pithecellobium sensu lato*.

United States *Pithecellobium* falls into three groups as defined by fruit characters: (1) pods dehiscent, circinate (e.g., *P. unguis-cati*), (2) pods woody, slowly dehiscent, septate *(P. flexicaule)*, and (3) pods compressed, membranous, dehiscent *(P. pallens)*. I suspect that the merit of these groups as genera is as great as that of *Enterolobium* which traditionally has been defined by its distinctive fruits. Thus my viewpoin possibly resembles that of Mohlenbrock, loc. cit., who considers American *Pithecellobium* to represent several genera. But proposals for generic reorganization based on knowledge of only a small proportion of the total species exhibit a high level of abortion. Therefore, I presently abstain and use the name *Pithecellobium* in the traditional, convenient, albeit probably artificial, sense.

PITHECELLOBIUM Mart., Flora 20(2) (Beibl. 8): 114. 1837! (as *Pithecollobium*) nom. cons. Type species: *Mimosa unquis-cati* L.

PITHECELLOBIUM Mart., Hort. Monac. 188. 1829! nom. nud.

ZYGIA Browne, Hist. Jamaica 279. 1756! nom. rej.

SPIROLOBA Raf., Sylva Tellur. 119. 1838!

SIDEROCARPUS Small, Bull. N.Y. Bot Gard. 2: 91. 1901! non *Siderocarpus* Pierre 1890.

HARVARDIA Small, Bull. N.Y. Bot. Gard. 2: 91. 1901!
EBENOPSIS Britt. & Rose, N. Am. Fl. 23: 33. 1928!

The name *Pithecellobium* has been subject to several spellings. I have taken up that first employed (Martius, 1829; loc. cit.) and reiterated in the Nomina Generica Conservanda (Lanjouw, 1966).

Total synonymy of *Pithecellobium sensu lato* is voluminous (Hutchinson, 1964; Woodson and Schery 1950; Kostermans, 1952). My enumeration includes only those represented in the United States.

Key to species

Leaflets 4

Rare cultivated or escaped shrub or tree of southernmost Texas and
 Florida; peduncels villosulous; perianth villosulous or
 puberulent . . . . *P. dulce*
Native shrubs of southern Florida; peduncles and perianth glabrous
 to puberulent.
 Leaflets 1.2–1.6(2.0) times as long as wide, scarcely reticulate;
  petioles usually longer than petiolules; racemes most-
  ly exserted beyond leaves; plants usually spiny.
             P. unguis-cati
 Leaflets (1.2)1.5–2.5(3) times as long as wide, coriaceous-re-
  ticulate; petioles usually shorter than petiolules; ra-
  cemes largely included; plant unarmed . *P. keyense*
Leaflets more than 4; species of southern Texas
 Leaflets 3–6 pairs; flowers in a spike; pod woody, essentially
  indehiscent . . . . *P. flexicaule*
 Leaflets 9–15 pairs; flowers capitate; pod thick-membranous,
  dehiscent . . . . *P. pallens*

Pithecellobium dulce (Roxb.) Benth.

Southern Florida and southernmost (Cameron Co.) Texas, occasional in cultivation and as an escape. Native from Mexico to northern South America where widely cultivated. Introduced in Old World. March-April. Chromosome number $2n = 26$ (Sampath and Ramanathan, 1949).

Pithecellobium dulce (Roxb.) Benth., Lond. J. Bot. 3: 199. 1844! *Mimosa DULCIS*
 Roxb., Pl. Corom. 1: 67. 1798! *Inga dulcis* (Roxb.) Willd. Sp. Pl. 4: 1005. 1806!
 Feuilleea dulcis (Roxb.) Ktze., Rev. Gen. 184. 1891!

Inga PUNGENS H. & B. ex Willd., Sp. Pl. 4: 1004. 1806! *fide* Benth. 1875. *Mimosa*
 pungens (Willd.) Poir., Lam. Encycl. Suppl. 1: 36. 1810!

Acacia OBLIQUIFOLIA Mart. & Gal., Bull. Acad. Brux. 10: 317. 1843! *fide* Benth.

Inga JAVANA DC., Prodr. 2: 436. 1825! Microfiche of fragment marked *Inga*
 javana in Herb. DC!

I. LEUCANTHA Presl, Bot. Bemerk. 65. 1844! *fide* Benth. 1875.

P. LITTORALE Britt. & Rose ex Record, Trop. Woods 11: 15. 1927! Type NY!
    Record & Kuylen 107.

Mimosa dulcis Roxburgh is fortunately identifiable by a fairly good plate.

Pithecellobium dulce, presumably native to the New World tropics, was introduced into the Old World at a relatively early date. Thus it entered nomenclature from far-flung localities. Roxburgh's *Mimosa dulcis* was from India; he notes that it was not native but introduced from the Philippines. The Humboldt and Bonpland *Inga pungens* was New World; Willdenow (loc. cit.) comparing it (almost with perplexity, one feels) with his *Inga dulcis* (Roxb.) Willd. notes "valde affinis praecedent." And *Inga javana* DC. was based on a gathering from Java previously characterized by Ventenat as *Mimosa affinis dulci.*

Pithecellobium flexicaule (Benth.) Coult.

Southern Texas. Mexico, south to Yucatan. Rarely Florida (cultivated). Roadside thickets, thorn scrub, with *Prosopis* and Cactaceae; bottomland woodland; sandy silt to clay loams; frequent in towns as cultivated ornamental. May-July. Texas Ebony.

Chromosome number $2n = 26$ (Atchison, 1951; as *Siderocarpus*)

Pithecellobium flexicaule is common in southern Texas as a small to medium-sized yard tree; it grows as brush in disturbed areas along roadsides. But, in a few remaining havens of relatively undisturbed woodland along the lower Rio Grande, ebony arises to the stature of massive trees with trunks exceeding one meter in diameter.

Pithecellobium flexicaule (Benth.) Coult., Contr. U.S. Natl. Herb. 2: 101. 1891!
    Acacia FLEXICAULIS Benth., Lond. J. Bot. 1: 505. 1842! *Zygia flexicaulis*
    (Benth.) Sudw. Bull. U.S. Dept. Agri. Div. For. 14: 248. 1897! *Siderocarpus*
    flexicaulis (Benth.) Small, Bull. N.Y. Bot. Gard. 2: 91. 1901! *Samanea flexicaulis*
    (Benth.) Macbride, Contr. Gray Herb. 59: 2. 1919!

Hoopsia ARBOREA Buckl., Proc. Phil. Acad. 1861: 453. 1862! Type PH! *Buckley,*
    Corpus Christi, Texas, May, 1860. (Exluding a second specimen on sheet, a
    caesalpinioid, probably *Parkinsonia aculeata*).

P. TEXENSE Coult. Contr. U.S. Natl. Herb. 1: 37. 1890! Type US! *Neally 133,*
    near Roma, Starr Co., Texas.

To date, I have not seen the type of *Acacia flexicaulis* Benth. Bentham's *A. flexicaulis* could scarcely be anything other than our species; yet it is puzzling that, after 33 years Benthan (1875), still retained it in the genus *Acacia*. The identity of Bentham's material, however, seems to have been taken for granted by all workers except Coulter (loc. cit.) who subsequently (1891) decided that his *P. texense* was the same as *P. flexicaule.*

Bentham (1875) states that *Acacia geniculata* Wendl. "appears to correspond precisely with *A. flexicaulis."* *Acacia geniculata* Wendl. is not in Kew Index. There were two Wendlands, J. C. and H., both publishing in the early part of the 19th century. I have examined the published works of both authors in the libraries of the New York and Missouri Botanical Gardens. I have not encountered the binomial in question.

Bentham (1875) placed *Hoopsia arborea* Buckl. in synonymy under his *A. flexicaulis*. However, the description of *Hoopsia arborea* suggests the possibility of a mixture: a caesalpinioid species and *P. flexicaule;* this is verified by the specimen as indicated.

Pithecellobium keyense Britt. & Rose

Southern Florida. West Indies. In coral or sandy soils, usually adjacent to beaches; in open areas, or under pines or broad-leaved "scrub." (Oct.) Nov.-March.

Pithecellobium keyense and *unguis-cati* are briefly discussed on a comparative basis under the latter. *P. keyense* is closely related to *P. bahamense* Northrup of the Antilles. The unpublished combination, *P. bahamense* var. *keyense* Morton, appears on numerous specimens in the U.S. National Herbarium. Morton's disposition may be reasonable; but I have not studied West Indian material of the two taxa on a comparative basis, and I am not herein publishing the combination.

Pithecellobium KEYENSE Britt. ex Britt. & Rose., Fl. N. Amer. 23: 22. 1928! Type NY! *W. C. Coker 57,* Bahamas. *P. keyense* Britt. ex Coker, Veg. Bahamas Isl. 255. 1905! nom. nud.

As to concept:

Pithecellobium guadalupense (Pers.) Chap., Fl. So. U.S. 116. 1860! *Zygia guadalupensis* (Pers.) Heller, Cat. N.A. Pl. 105. 1905! neque *Mimosa GUADALUPENSIS* Pers. 1806. neque *Inga guadalupensis* (Pers.) Desv. 1814.

This species was known as *P. guadalupense* until Britton & Rose (loc. cit.), stating "not *Inga guadalupensis* Desv.", pubilshed the specific epithet *keyense*. The name *guadalupense* traces ultimately to Persoon whose description is too brief for identification. His material was "Hab ad Guadalupam (Herb. Juss.)."

A photograph (US!) of types of Delessert Herbarium includes one marked as *"Inga guadalupensis* Desv." The subject specimen is probably *P. unguis-cati;* it is neither *P. keyense* nor *P. guadalupense sensu* Chapman. But the critical material is that of Persoon which, if existent, is at L, and which I have not seen. In maintaining *P. keyense* Britt. & Rose, I necessarily make the assumption that Desvaux correctly took up Persoon's concept, or, at least, that the latter's specimen was not of *P. keyense*.

Pithecellobium pallens (Benth.) Standl.

Southern Texas and adjacent Mexico. Mesquite brushland on sandy to heavy clay; slightly in cultivation. April-August (Sept.)

Chromosome number $2n = 26$ (Turner and Fearing, 1960).

Pithecellobium pallens (Benth.) Standl., Tropical Woods 34: 39. 1933! *Calliandra*
    PALLENS Benth., Lond. J. Bot. 5: 102. 1846! Isotype or fragment of type
    GH! Photo of type (so designated) US! Coulter, Mexico. *Havardia pallens*
    (Benth.) Britt. & Rose, N. Am. Fl. 23: 42. 1928.

P. BREVIFOLIUM Benth. in Gray, Pl. Wright. 1: 67. 1852! *Feuilleea brevifolia*
    (Benth.) Ktze., Rev. Gen. 187. 1891! *Zygia brevifolia* (Benth.) Sudw., Bull. U.S.
    Dept. Agric. For. 14: 248. 1897! *Havardia brevifolia* (Benth.) Small, Bull. N.Y.
    Bot. Gard. 2: 92. 1901!

Acacia NEUCIANA Buckley, Proc. Acad. Phil. 1861. 453. 1862! Type PH! *Buckley*.
    On the Nueces river, Texas. May, 1860.

I have examined a photograph and presumed fragment of type material of *Calliandra pallens*. They look like *Pithecellobium pallens* (Benth.) Standl. But the specimen is fragmentary; my knowledge of the Mexican relatives of *C. pallens* is limited. Thus, I do not consider the determination unequivocal.

Pithecellobium unguis-cati (L.) Mart.

Southern Florida. West Indlies. Coral soil in wooded scrub, sand ridges, hammocks, roadsides. Oct.-Feb. April-Aug.

Pithecellobium unguis-cati and *keyense* are closely related and similar in appearance. They differ in several usually correlated characters (although there is no absolute delimitation on the basis of any single feature), and are usually distinguished without difficulty. A few specimens are troublesome; possibly this is an indication of limited introgression between the species. *P. unguis-cati* is usually prickly, has long petioles in proportion to the petiolules; the leaflets are of a thinner texture, usually smaller, and of broader proportions; the racemes are more elongate and exserted but the peduncles are usually the shorter of the two.

Although I have collected both species in the field several times, the original habitats (in the United States) are largely destroyed. I have the impression that *P. keyense* is usually of the beaches or contiguous thereto, whereas *P. unguis-cati* tends to be of more inland habitats. *P. keyense*, per specimens seen, is only a winter bloomer; *P. unguis-cati* flowers in the winter but also April-August.

Pithecellobium unguis-cati (L.) Mart., Hort. Monac. 188. 1829! *Mimosa UNGUIS-
    CATI* L., Sp. Pl. 517. 1753! *Spiroloba unguis* Raf., Sylva Tell. 119. 1838!
Feuilleea unguis-cati (L.) Ktze., Rev. Gen. 184. 1891! *Zygia unguis-cati* (L.) Sudw.,
    Bull. U.S. Dept. Agric. For. 14: 248. 1897!

Mimosa GUADALUPENSIS Pers., Syn. 2: 262. 1806! *Inga guadalupense* (Pers.)
   Desv., Jour. Bot. 3: 70. 1814! Photo of Desvaux "type" (Delessert Herb.)
   US!

P. FLAVOVIRENS Britt, Bull. N.Y. Bot. Gard. 3: 442. 1905!

Linnaeus' citations apparently support the classic interpretation of his
M. unguis-cati. The specimen in the Linnaean herbarium (microfiche!)
is evidently of this species, but probably was not in Linnaeus' possession
in 1753. My knowledge of the *P. unguis-cati*-group is not, at the present
time, sufficient to render typification critical.

The identity of *Mimosa guadalupensis* Pers. is discussed under *M.
keyense*.

Further synonymy is given by Bentham (1875).

Rejected species

Pithecellobium saman (Jacq.) Benth. The "rain tree," native from Central
America to Brazil, is widely planted in the tropics of both hemispheres. It is prob-
ably present to a slight extent in southernmost, urban Florida, and is treated by
Bailey (1949). However, I have not observed it in the Miami area, Homestead,
or Key West, neither have I seen U.S. specimens in herbaria.

Pithecellobium calostacys Standl. and *lanceolatum* (H. & B.) Benth. I have
seen collections of cultivated material from extreme southern Texas that I tenta-
tively assign to these species. I have not observed any of Pittier's (1922) "spicate-
flowered species . . . of the *unguis-cati* section" in the field, nor seen previous reports
of their occurrence in the United States.

PROSOPIS L.

Shrubs or small trees usually armed with nodal spines (stipules or de-
terminate branches). Leaves bipinnate; pinnae 1–2 pairs, an obscure gland
between the lower pair. Leaflets several or numerous. Inflorescences spi-
cate (and ament-like) or (one local species) capitate, yellowish. Calyx
synsepalous, scarcely lobed. Corolla of nearly separate petals, but loosely
connate above middle until early anthesis. Stamens 10; young anthers
terminally bearing a quickly deciduous, stalked, capitate gland. Legume
elongate, woody, several-seeded, indehiscent, irregularly moniliform, or
coiled spring-like.

Ca. 35 species of warm regions, primarily of New World, but a few
kinds widely introduced in Eastern Hemisphere. Ours of the Southwest,
Texas to California, *P. glandulosa* extending northward to extreme south-
ern Kansas.

Chromsomse base number x = 14(13?); determinations on about 15
species.

Bentham (1842, 1846, 1875) treated *Prosopis* as a polymorphic genus
with several sections and took active issue with Engelmann and Gray
(1845) and Gray (1852) who believed the U.S. species to include two

genera, *Algarobia* and *Strombocarpa*. Less than unanimous viewpoints have continued. Britton & Rose (1928) divided North American *Prosopis* into three genera, and this position has recently been reiterated by Hutchinson (1964). On the other hand, Burkart (1940) has taken up (and expanded) the Bentham delimitation, and this posture is assumed by most U.S. authors. (More recently, however, Burkart, 1964, has segregated two species, South America to Mexico, as *Prosopidastrum*). It is true that the screwbeans (e.g., *P. pubescens*), possessing uniquely coiled pods and stipular spines, seem very different from mesquite (e.g., *P. glandulosa*) with more conventional indehiscent pods, and spines which are possibly determinate branches. But intermediates mar the picture; and I have taken up the Bentham and Burkart delimitations.

Cherubini (1954), making chromosome number determinations for 15 taxa of *Prosopis,* reported a consistent $2n = 56$, except for a few instances of "56 ± 112." The latter figures presumably mean that he found plates of both 56 and approximately 112. These findings reflect somatic polyploidy which has been reported several times in the Mimosoideae. I have discussed this phenomenon elsewhere (Isely, 1970). Chromosome counts have been made on various forms of *P. juliflora sensu lato* by about eight workers. The results include multiples of both bases 13 and 14, interpretation of which are uncertain (see *P. glandulosa* of this treatment). In any event, *Prosopis* appears to be largely a derived aneuploid group as contrasted to the generalized $x = 13$ for the Mimosoideae.

Burkart (1940) has summarized much of *Prosopis* but his attention to North American forms is limited. He apparently regarded the major U.S. species *(P. glandulosa* and *P. velutina)* as relatives of the South American *P. chilensis* (Mol.) Stuntz, but they are neither treated nor cited as synonyms.

Standley (1922) regarded *Prosopis* of Mexico as four species. Britton and Rose submitted the same taxa to their conventionally rigid, but descriptively useful treatment as three genera including 17 species. The mesquites *(P. juliflora* and relatives) have been more recently studied by Benson (1941) for the U.S. only, and by Johnson (1962) for all of North America.

PROSOPIS L., Mant. Pl. 1: 10. 1767! Type species: *P. spicigera* L. = *P. cineraria* (L.) Druce

NELTUMA Raf., Sylva Tell. 119. 1838!

ALGAROBIA (DC.) Benth., Pl. Hartw. 13. 1839!

STROMBOCARPA Eng. & Gray, Bost. Jour. Nat. Hist. 5: 243. 1845!

SOPROPIS Britt. & Rose, N. Am. Fl. 23: 182. 1928!

The type of *Prosopis* is one of two Asiatic species that constitute the section *Adenopsis* DC. (Burkart, 1940). I am not familiar with these species. Employment of the name *Prosopis* is based on the Bentham (1875) circumscription that associates these Old World kinds with this largely American group.

The name *Strombocarpa* originated as a sectional name of Bentham's (1842). As a genus, it is sometimes cited "(Benth.) Engelm. & Gray." Engelmann and Gray, however, provided no citation, direct or indirect. And if there come those who may desire to revive this name at the generic level, I suggest that they review the original "diagnosis," with respect to valid publication.

Key to species

Flowers in globose heads; leaflets less than 4 mm long; low shrubs at
  most a few dm high; southern Texas only . . *P. cinarescens*
Flowers in spikes; leaflets (4)5–30 mm in length; shrubs or trees, 1–10 m.
  Leaflets 5–8 pairs per pinna, mostly less than 10 mm long; pods
    coiled up spring-like; western Texas to southern California.
                                                      P. pubescens
  Leaflets 10–18(30) pairs per pinna, often exceeding 10 mm in length;
    pod not coiled.
    Local, Nueces Co., Texas; leaflets 4–6(9) mm long.
                                                      P. laevigata
    Widely distributed species; leaflets of forms sympatric with *P.
      laevigata,* 25–35 mm long.
      Leaflets glabrous, 5–12 times as long as broad, mostly 1–4
        cm long, spaced so that intervals between leaflets
        are as great or greater than width of leaflets;
        pinnae 1 pair; Texas to California but largely
        absent in southern Arizona deserts (occasional
        pubescent forms in western Texas; some inter-
        mediacy with following species in Arizona).
                                                      P. glandulosa
      Leaflets pubescent, 3–7 times as long as broad, mostly
        0.6–1.3 cm long, usually crowded so that inter-
        vals are less than width of leaflets; pinnae 1–2(3)
        pairs; southern Arizona . . . . *P. velutina*

Prosopis cinerascens (Gray) Benth.
  Southern Texas and adjacent Mexico. Sandy bluffs, ocean beaches and adjacent dunes, grassland. March-April (June).
  Workers have not been in agreement on the specific distinctiveness of *Prosopis cinerascens* and *P. reptans* of Argentina. Turner (1959) without discussion follows Burkart in treating Texas material as *Prosopis reptans* var. *cinerascens* (Gray) Burkart. Burkart (1940), in reducing *P. cinerascens,* cites only three North American specimens; I defer judgment until more material has been studied on a comparative basis.
  Cherubini (1954) reports a *2n* chromosome number of "56 ± 112" for *Prosopis reptans.*

There is ample evidence throughout the Mimosoideae of the plasticity of inflorescence form and of the limited taxonomic significance that can be attributed to it. This is strikingly documented by *P. cinerascens* and *pubescens* both of which have the unique *Strombocarpa* type pod. But the inflorescence of *P. pubescens* is an amentiferous spike similar to that of *P. glandulosa-velutina,* while that of *P. cinerascens* is a globose head.

Prosopis cinerascens (Gray) Gray ex Benth., Trans. Linn. Soc. 30: 381. 1875! *Strombocarpa CINERASCENS* Gray, Pl. Wright. 1: 61. 1852! *Prosopis reptans* var. *cinerascens* (Gray) Burkart, Darwiniana 4: 75. 1940!

Mimosa CALCAREA Buckl., Proc. Acad. Sci. Phil. 1861: 453. 1862! Type PH! *Buckley.* Near Live Oak, Texas. 1860.

Gray (loc. cit.) cited, "Valley near Azufrora, New Leon, Dr. Gregg." In GH, a sheet marked "type" contains three specimens of *Prosopis cinerascens;* they are marked as Schott, Wright, and "Mexican Boundary Survey" gatherings. I have seen no Gregg material.

Prosopis glandulosa Torr.

Western Louisiana to southern California, north to southern Kansas, occasionally introduced elsewhere. Mexico. Valleys and dry uplands, abundant and extensively dominant. April-June. Mesquite.

Chromosome number $n = 14$ (e.g., Baquar et al., 1966), $2n = 56$ (e.g., Atchison, 1951), $n = 13$ (e.g., Bir and Sidhu, 1966), $2n = $ "56 ± 112" (Cherubini, 1954), $2n = 26$ (Ramanathan, 1950), $2n = 52$ (Sampath and Ramanathan, 1949). (Tabulation includes chromosome counts attributed to *Prosopis juliflora, P. juliflora* var. *glandulosa,* and *P. glandulosa;* see discussion in following paragraphs).

The mesquites range through the southwestern United States, Mexico, and portions of coastal Central America and South America, particularly Argentina and Chile. They are introduced into other parts of the world. They include several related taxa resistant to a satisfactory classification.

Botanists have alternated between treating United States mesquites as one polymorphic species, or segregating several of the variants as specific entities. *P. glandulosa* and *P. velutina* were recognized by Britton and Rose (1928). Benson (1941) believed these taxa conspecific with the *P. juliflora* (Sw.) DC. which in its typical form is a coastal inhabitant of Mexico and West Indies. Standley (1926) felt that *P. juliflora* represents the North American phases of the South American *P. chilensis* (Mol.) Stuntz. Johnston (1962), treating the biosystematics of *Prosopis*: *Algarobia* of Mexico and the southern United States has reversed this trend, recognizing six species of North American mesquites.

I have approximately followed Johnston. Under this interpretation, the traditional *P. juliflora* does not occur in the United States. It is a tropical, coastal plant with glabrous, comparatively broad leaflets. *P.*

glandulosa, then, is the principal mesquite in the United States—its range is interrupted only by a zone of *P. velutina* in Arizona and local *P. laevigata* in Nueces Co., Texas.

One might substantiate a viewpoint that these taxa constitute major subspecific units of a broadly defined *P. juliflora.* In particular, I have difficulty regarding *P. velutina* as more than a desert form of *P. glandulosa.* But Johnston's (1962) historical portrait is reasonably convincing and I have accepted his position. I have not studied the relationship of the South American *P. chilensis* and its relatives to our *P. glandulosa.* Both Benson (1941) and Johnston (1962) reject the thesis that the South and North American plants are conspecific.

The chromosomes of mesquite have been counted many times but a haze of uncertainty remains. Determinations that probably largely represent *P. glandulosa* of present delimitation have been reported as *Prosopis juliflora* or *P. glandulosa.* The *P. juliflora* complex apparently includes polyploid series (independent of somatic polyploidy?) on base numbers of both 13 and 14. Determinations identified with *P. glandulosa* also include both number series. However, a preponderance of these chromosome reports represent work done in the Old World on introduced material; uncertainty of critical identification exists. This cytological situation ostensibly supports Johnston's (1962) viewpoint that the classical *P. juliflora* includes several species; but, contrary to his position, suggests a basis of cross-incompatibility. A critical correlation of taxonomic hypotheses and the genome analyses remains to be accomplished.

Cherubini's (1954) report of only the base number 14 ($2n = 56$ or "56 ± 112") for ca. 15 taxa of *Prosopis* invokes other speculation. Inasmuch as 14 is a derived number in the Mimosoideae, does the *Prosopis juliflora* complex, carrying remnants of a basic 13, occupy a progenitor position to most of the genus? Or, alternatively, are base 13 determinations errors occasioned by interpretational difficulties compounded with the expectation of a base 13 in the Mimosoideae?

In the United States, mesquite is usually regarded as a weed and strenuous efforts have been made to find economical methods of eliminating it from range land. Contrariwise, Standley (1922) enumerates its many virtues; and in Hawaii where a South American mesquite (*P. pallida fide* Johnston, 1962) has been introduced, it is considered a valuable introduced tree. Bogusch (1950) has compiled a bibliography and literature review.

I follow Benson (1941) and Johnston (1962) in distinguishing an eastern and western segment of *P. glandulosa.* The two subordinate taxa are characterized by reasonable correlation of geographic and morphological features. There are indeed a few gross exceptions in the geographic consistency of the two types. The most blatant of these, e.g., var. *torreyana* in Missouri, var. *glandulosa* in California are certainly introductions.

Johnston's and Benson's criteria for distinguishing the two varieties

differ in emphasis; mine bears greater similarity to Johnston's.

Key to varieties

Leaflets mostly 2.5–3.5 cm long, the well-developed narrow ones 8–12
        times as long as broad; leaflets 6–12(15) pairs per pinna, most-
        ly 8–10 pairs; thorns usually solitary; primarily Texas and
        Oklahoma west to the Pecos River, occasional in trans-Pecos
        Texas but less common than var. *torreyana,* exceptionally west
        of Texas . . . . var. *glandulosa*
Leaflets mostly 1–2(2.5) cm long, mostly 5–8 times as long as broad;
        leaflets 9–15(20) pairs, mostly 10–12 pairs; thorns frequently
        paired; trans-Pecos Texas and west except for local eastern
        stations . . . . var. *torreyana*

Var. *glandulosa*

Distribution as key above. Slopes, plains, alluvial soil along streams,
desert scrub. Abundant, often dominant and forming "woodlands" over
thousands of acres. April-May (June).

Var. *glandulosa* is, in Texas, one of the more characteristic woody spe-
cies of open rangeland. Presumably it has invaded much grassland the
last hundred and fifty years as a consequence of overgrazing of the peren-
nial grass cover.

Except for a few pockets of var. *torreyana* and the single introduction
of *P. laevigata,* var. *glandulosa* is the only mesquite east of the Pecos
River. It is sporadically present in trans-Pecos Texas, and, there, usually
distinct from var. *torreyana.* However, the mesquites of the Mesilla Val-
ley in southern New Mexico are ambiguous; as to characters they seem
to overlap vars. *glandulosa* and *torreyana.* I have treated them as *glandu-
los*a. I have seen a few collections of var. *glandulosa* from Arizona and
California; I presume they represent introductions.

Prosopis GLANDULOSA Torr., Ann. Lyc. N.Y. 2: 192. 1827! Type NY! (See dis-
    cussion) *Algarobia glandulosa* (Torr.) T. & G., Fl. N. Am. 1: 399. 1840! *P.
    juliflora* var. *glandulosa* (Torr.) Cockerell, Bull. New Mex. Agric. Expt. Sta.
    15: 58. 1895! *P. chilensis* var. *glandulosa* (Torr.) Standl., Contr. U.S. Natl.
    Herb. 23: 1658. 1926! *Neltuma glandulosa* (Torr.) Britt. & Rose, N. Am. Fl.
    23: 186. 1928!

P. juliflora CONSTRICTA Sargent, Tree & Shrubs 2: 249. 1913! *Neltuma constricta*
    (Sargent) Britt. & Rose, N. Am. Fl. 23: 186. 1928!

Neltuma NEOMEXICANA Britt. in Britt. & Rose N. Am. Fl. 186. 1928! Type US!
    Mearns 2325.

Torrey designates the type of *Prosopis glandulosa* as James: "On the
Canadian?" The collection that I have taken as the type (NY) is un-
identified except for the Torrey Herbarium stamp. Attached to it is a
manuscript description in Torrey's handwriting which is a rough draft of
the published description. Benson (1941) noted that this specimen may

be the type; I take it as the holotype. I have no idea when or by whom this manuscript fragment was attached to the specimen. If this uncertainty is given weight, the specimen could, I suppose, be designated as a lectotype. Probabilities suggest that it can reasonably be called the holotype.

P. juliflora constricta Sargent is *P. glandulosa* with strongly and evenly constricted pods. The type of *Neltuma neomexicana* has been examined by Benson (1941).

Var. *torreyana* (Benson) Johnston

Trans-Pecos Texas to California, sporadically further east; largely absent from Arizona except northern portion. River bottoms and canyon floors, washes, rocky slopes and ridges, desert flats with greasewood, sand dunes; disturbed areas, e.g., along roadsides and irrigation ditches. 200–6500 ft. March-June.

Var. *torreyana* includes a considerably greater range of morphological variance than var. *glandulosa* or *P. velutina*. This variance is matched by the greater number of habitats occupied and the probable number of biotypes included.

The replacement of *Prosopis glandulosa* var. *torreyana* by *P. velutina* in the Sonoran desert is discussed by Johnston (1962). I can discern no morphological differentiation between the eastern and western phases of var. *torreyana* except a limited reverse cline towards the var. *glandulosa* leaf form in California and sporadically in Arizona (mixing following introduction of var. *glandulosa?*).

I have designated only a few sheets east of Brewster Co., Texas, as var. *torreyana*: e.g., one specimen, Bexar Co., Texas, two specimens coastal Texas (Nueces and Kleberg Co's.), and Sheffield, Missouri, "introduced along railroad yards and waste places" (letter, Bush to Small, 1927). I now regard the identity of the Nueces Co. material as suspect. See *P. laevigata*.

Material of var. *torreyana* from the Big Bend area, Texas, tends to possess a high number of leaflets and is sometimes pubescent. Relevant hypotheses are presented by Johnston (1962).

Putative intermediates between *Prosopis glandulosa* var. *torreyana* and *P. velutina* are discussed under the latter species. A few specimens of West Texas and New Mexico fall between vars. *torreyana* and *glandulosa;* I refer to them under var. *glandulosa*.

Prosopis glandulosa var. *torreyana* (Benson) Johnst., Britt. 14: 82. 1962! *P. juliflora* var. *TORREYANA* Benson, Amer. J. Bot. 28: 751. 1941! Isotypes NY! US! *Benson 11000,* Needles, California.

P. ODORATA Torr. & Frem., Report 313. pl. 1. 1845! Type NY! Specimen marked by Torrey as *"Prosopis (Strombocarpa) odorata* Torr. in Frem., Rept." excluding fruits.

The typification of *Prosopis odorata* Torr. & Frem. is discussed under *P. pubescens*.

Prosopis laevigata (Willd.) M. C. Johnst.

Local, Nueces County, Texas. Of wide distribution in Mexico.

Chromosome number $2n = 28$. (Fearing voucher specimen (TEX) annotated by M. C. Johnston as *Prosopis laevigata*).

Prosopis laevigata is reported in the United States by Johnston (1962). He refers to several individuals of *P. laevigata* "growing with *P. glandulosa* and with numerous apparent back-cross types in a small, badly disturbed pasture along Nueces Bay."

Recent correspondence with Dr. Marshall Johnston has elicited the following helpful commentary regarding *Prosopis laevigata* (quoted with permission):

"Calvin McMillan has examined the *P. laevigata* population of Nueces Co. more thoroughly than anyone else. There is probably only one individual of 'pure' *P. laevigata* in Nueces Co., and it seemingly represents a chance introduction. It apparently does not self-pollinate, for progeny tests from its seeds yield a variety of 'hybrid' types. It is surrounded by what Calvin agrees is an authentic hybrid swarm with various back-cross types, presumably involving *laevigata* and the disgustingly abundant *P. glandulosa* of that region. Perhaps the most interesting fact here is the apparently obligate out-crossing."

It may be that material from Nueces Co., that I have associated with out-of-range *P. glandulosa* var. *torreyana* represents some of these backcrosses.

Prosopis laevigata belongs to *P. juliflora* complex and is closely allied with *P. glandulosa* and *P. velutina*. Among numerous Mexican sheets examined, I have seen only two which seemed intermediate with *P. juliflora*. The distinction from *P. velutina* seems more tenuous.

Prosopis laevigata (Humb. & Bonpl. ex. Willd.) Johnston, Britt. 14: 78. 1962!
    Acacia LAEVIGATA Humb. & Bonpl. ex. Willd., Sp. Pl. 4: 1059. 1806!

Synonymy is provided by Johnston (1962). Johnston (correspondence) states, "I looked at the type in the Willdenow herbarium. It checks but is a mere fragment—hard to interpret."

Prosopis pubescens Benth.

Western Texas to southern California, north to southern Utah. Usually creek and river bottoms, flood plains, washes, along irrigation ditches, but also open desert. Locally common. −100–4000 ft. April-May (Sept.) Screw-bean.

Chromosome number $2n = 56$ (Cherubini, 1954).

Prosopis PUBESCENS Benth. Lond. J. Bot. 5: 82. 1846! *Strombocarpa pubescens* (Benth.) Gray, Pl. Wright. 1: 60. 1852!

P. EMORYI Torr., Bot. Emory Report. 139. 1848! Presumed type NY! Unmarked Emory specimen (faded label).

Strombocarpa brevifolia Nutt. ex Gray, Pl. Wright. 1: 60. 1852! As synonym; *S. pubescens* fide Gray.

As to concept:

P. ODORATA Torr. & Frem., Frem. Report 313 pl. 1. 1845! As to fruits; non typ-ification Benson (1959). Type NY! Specimen marked by Torrey as *"Prosopis (Strombocarpa) odorata* Torr. in Frem., Rept." *Strombocarpa odorata* Gray, Bot. U. S. Expl. Exped. (Wilkes) 1: 475. 1854. nom nud. *S. odorata* (Gray) Britt & Rose, Fl. N. Am. 23: 183. 1928! as (Torr.) Gray.

Prior to Benson's (1941) study of *Prosopis*, this species was usually designated *P. odorata* Torr. By both description and plate, the Torrey and Fremont *P. odorata* is obviously *P. glandulosa* var. *torreyana* as to foliage and flowers, and *P. odorata* as to fruit. No specimens were cited but there are three sheets at NY which are mixtures of these two species and ostensibly the Fremont material with which Torrey worked. Benson (1959) has designated these three sheets "the fruit excluded . . . as a lec-totype of *Prosopis odorata* Torr. & Frem." I have subsequently marked one of these sheets as the lectotype, the others as isotypes. *P. odorata* then becomes a synonym of *P. glandulosa* var. *torreyana*.

Prosopis pubescens Benth. was published one year after *P. odorata;* the description provides clear identification.

Prosopis velutina Wooton

Southern Arizona and sporadically in California (introduced?), Mexi-co. Sandy soil in washes, river bottoms or dry flats, canyons; creosote bush-cactus desert, dunes; locally common; slightly in cultivation. 500–5500 ft. (April) May-July (Oct.). Mesquite.

Chromosome number $2n = 56$ (Cherubini, 1954; as *P. juliflora* var. *velutina*).

The peripatetic classification of the mesquites is briefly reviewed under *P. glandulosa*. I have followed Johnston (1962) in treating *P. velutina* as a species. *P. velutina* interrupts the distribution of *P. glandulosa* in South-ern Arizona—the latter species lies to both the east and the west. *P. glandulosa* is, however, irregularly continuous across the higher eleva-tions of northern Arizona. The possible historical basis of this partial dis-junction of *P. glandulosa* and replacement by *P. velutina* is discussed by Johnston (1962).

Johnston refers to presumably recent mixing between *P. glandulosa* var. *torreyana* and *P. velutina*. Benson (1941) notes that there are inter-grades "in many localities" in Arizona. I have encountered perhaps two

dozen problematic specimens in various degrees phenotypically interme-
diate between *P. velutina* and *P. glandulosa* var. *torreyana*. Perhaps the
greatest number are from Yuma Co., southwestern Arizona, where *P.
velutina* grades into the California phase of *P. glandulosa* var. *torreyana*;
others are from north-central Arizona (towards the Grand Canyon form
of *torreyana*) and eastern Arizona. I have defined (and designated) in-
termediates approximately as follows:

Prosposis velutina towards *torreyana*: (1) *velutina* leaflet spacing and
size but reduced pubescence. (2) *velutina* leaflet size and moderate pu-
bescence, but *torreyana* spacing.

Prosopis glandulosa var. *torreyana* towards *velutina* : *torreyana* leaflet-
spacing and size but mildly pubescent.

Turner (1959) has referred several collections from western Texas to
P. juliflora var. *velutina,* and Benson (1941) reports *velutina* from Texas
along the Rio Grande. Johnston (1962) agrees that some of the mes-
quites "in the area from the Big Bend of Texas southwest to central Chi-
huahua have smaller, closer, and more numerous leaflets than usual [in
P.. glandulosa]." I concur, and note that the leaflets of some Big Bend
forms of these are pubescent. Johnston attributes this situation, at least
in part, to introgression of *P. glandulosa* from *P. laevigata*; and I con-
sider this the most reasonable hypothesis. In any event, I cannot pres-
ently associate any Texas material that I have seen with *P. velutina*.

Prosopis VELUTINA Wooton, Bull. Torr. Club 25: 456. 1898! Type NY! *Pringle,*
     Arizona Apr. 23, 1881. *P. juliflora* var. *velutina* (Woot.) Sarg., Silva 13: 15.
     1902! *P. chilensis* var. *velutina* (Wooton) Standl., Contr. U.S. Natl. Herb. 23:
     1658. 1926! *Neltuma velutina* (Wooton) Britt. & Rose, N. Am. Fl. 23: 186.
     1928!

Wooton (loc. cit.) cites several collections; I have seen some of them.
From among these, Britton & Rose (1928) designate the above cited
Pringle collection as the lectotype.

Rejected Species

Prosopis strombulifera (Lam.) Benth. is reported from California by Munz
(1959) as follows: "Native of Argentina and grown at Experiment Station at
Bard, Imperial Co., from which it is reported as escaped." I have seen no confirm-
ing specimens in the herbarium of the Rancho Santa Ana Botanic Garden.

There are two specimens in the University of Arizona herbarium marked *P.
chilensis* (Mol.) Stuntz, one "cultivated from South America, Yuma City Park,"
the other "University farm, Tucson." These specimens do not seem to represent
native kinds, but I do not believe they are *P. chilensis;* the leaflets are too small
and closely crowded. The specimens better meet the criteria for *P. alba*.

Literature Cited

Atchison, E. 1949. Studies in the Leguminosae. IV. Chromosome number and
     geographical relationships of miscellaneous Leguminosae. J. Elisha Mitchel
     Soc. 65:118–122.
————. 1951. Studies in the Leguminosae. VI. Chromosome numbers among

tropical woody species. Amer. J. Bot. 38:538–546.

BAILEY, L. H. 1949. Manual of cultivated plants. Rev. ed. Macmillan Co., N.Y.

BAQUAR, S. R., A. HUSAIN, and S. AKHTAR. 1966. Meiotic chromosome numbers in some vascular plants of Indus delta II. Bot. Not. 119:24–32.

BENSON, L. 1941. The mesquites and screw-beans of the United States. Amer. J. Bot. 28:748–754.

————. 1943. Revisions of status of southwestern desert trees and shrubs. II. Amer. J. Bot. 30:630–632.

————. 1959. Typification of *Prosopis odorata* Torr. & Frem. (Leguminosae). Madroño 15:53–54.

BENTHAM, G. 1842. Notes on Mimoseae, with a short synopsis of species. Hooker J. Bot. 4:323–416.

————. 1846. Notes on Mimoseae, with a synopsis of species. Tribe III. Acacieae. Lond. J. Bot. 5:75–108.

————. 1875. Revision of the suborder Mimosaceae. Trans. Linn. Soc. Lond. 30:335–664.

BIR, S. S., and S. SIDHU. 1966. Cytological observations on the North Indian members of family Leguminosae. Nucleus 10:47–63.

BOGUSCH, E. R. 1950. A bibliography on mesquite. Texas J. Sci. 2:528–538.

BRITTON, N. L., and J. N. ROSE. 1928. Mimosaceae. North Amer. Fl. 23:1–194.

BURKART, A. 1940. Materiales para una monografia del género *Prosopis* (Leguminosae). Darwiniana 4:57–129.

————. 1964. Leguminosas nuevas o criticas VI. Darwiniana 13:428–448.

CHERUBINI, C. 1954. Números de cromosomas de algunas especies del género "*Prosopis*" (Leguminosae - Mimosoideae) Darwiniana 10:637–643.

COULTER, J. M. 1891. Leguminosae. *In* Botany of western Texas. Contr. U.S. Natl. Herb. 2:68–101.

DOTY, W. L., and P. C. JOHNSON (eds.) 1954. Western garden book. 384 p. Lane Publ. Co., Menlo Park, Calif.

GRAY, A. 1852. Leguminosae. *In* Plantae Wrightianae 1:43–67.

ENARI, L. 1962. Ornamental shrubs of California. Ward Ritchie Press, Los Angeles.

ENGLEMANN, G., and A. GRAY. 1845. Plantae Lindheimerianae I. Bost. J. Nat. Hist. 5:210–264 (p 2–56 in reprint).

HUTCHINSON, J. 1964. The genera of flowering plants. Vol. 1. Clarendon Press, Oxford.

ISELY, D. 1969. Legumes of the United States I. Native *Acacia*. Sida 3:365–386.

————. 1970. Legumes of the United States v. *Albizia, Lysiloma, Leucaena, Adenanthera;* and rejected genera of Mimosoideae. Castanea 35:244–260.

JOHNSTON, M. C. 1962. The North American mesquites. *Prosopis* sect. *Algarobia* (Leguminosae). Brittonia 14:72–90.

KEARNEY, T. H., R. H. PEEBLES, and collaborators. 1960. Arizona flora. Univ. of Calif. Press, Berkeley.

KOSTERMANS, A. J. G. H. 1952. A monograph of the Asiatic, Malaysian, Australian, and Pacific species of Mimosaceae, formerly included in *Pithecelobium* Mart. Bull. Org. Sci. Res. Indonesia 20(11):1–122.

LANJOUW, J., ed., 1966. International code of botanical nomenclature. Reg. Veg. vol. 46.

MATHIAS, M. E. and E. McCLINTOCK. 1963. A checklist of woody ornamental plants of California. Cal. Agric. Coll. Man. 32.

MATTOON, H. G. 1958. Plant buyer's guide of seed and plant materials in the trade. 6th ed. Massachusetts Horticultural Society, Boston.

MOHLENBROCK, R. 1963a. Reorganization of genera within tribe Ingeae of the mimosoid Leguminosae. Reinwardtia 6(4):429–442.

————. 1963b. Subgeneric categories of *Pithecellobium* Mart. *Reinwardtia* 6:443–447.

MUNZ, P. A. 1959. A California flora. Univ. Calif. Press, Berkeley.

PITTIER, H. 1922. New or noteworthy plants from Columbia and Central America. Contr. U. S. Natl. Herb. 20:453–490.

RAMANATHAN, K. 1950. Addendum to list of chromosome numbers in economic plants. Curr. Sci. 19:155.

SAMPATH, S., and K. RAMANATHAN. 1949. Chromosome numbers in Indian economic plants. III. Curr. Sci. 18:408–409.

STANDLEY, P. C. 1922. Mimosaceae. *In* Trees and shrubs of Mexico. Contr. U. S. Natl. Herb. 23:348–400.

————. 1926. Mimosaceae. *In* Trees and shrubs of Mexico. Additions and corrections. Contr. U. S. Natl. Herb. 23:1657–1659.

————, and J. A. STEYERMARK. 1946. Leguminosae. *In* Flora of Guatemala V. Fieldiana Bot.: 24(5):1–368.

TURNER, B. L. 1959. The legumes of Texas. Univ. Texas Press, Austin.

————, and O. S. FEARING. 1960. Chromosome numbers in the Leguminosae. III. Species of the southwestern United States and Mexico. Amer. J. Bot. 47:603–608.

WOODSON, R. E., and R. W. SCHERY. 1950. Mimosoideae. *In* Flora of Panama. Ann. Mo. Bot. Gard. 37:184–314.

Note added in proof; see page 280: It is *Calliandra haematocephala* Hassk. Nevling and Elias (1971. *Calliandra haematocephala:* history, morphology, and taxonomy. Jour. Arn Arb. 52:69–85.) cite specimens from Florida as well as California (plus several botanic garden and greenhouse gatherings elsewhere).—Author.

NOTES AND NEWS

PINUS PONDEROSA IN MALHEUR COUNTY, OREGON.—A relict stand of *Pinus ponderosa* Laws. was found on the end of a ridge extending north from Mahogany Mountain toward Leslie Gulch, Malheur County, Oregon, lat. 43° 17′ N, long. 117° 14′W. *(Packard 69–1, 69–2, 69–3,* College of Idaho). The stand consists of four old trees on the edge of one ridge with sixteen younger trees of all age classes including apparent seedlings growing among and below them. One young tree could be seen on the ridge to the east but the terrain discouraged close observation. The ridge where the Ponderosa pine was growing was at an elevation of about 5,000 ft. Only the bare, eroded end of the ridge where the rhyolitic tuff had been exposed was occupied by the pine. Lower slopes and unexposed portions of the ridge were covered sparsely by *Juniperus occidentalis* Hook. which also intermingled with the pine to some extent. The four old trees had an abundant cone crop. The largest was 93 inches dbh. Growth rings in a branch six feet above the root level were too small to count accurately but the branch contained over 90 xylem layers, discounting the possibility of introduction of the trees by early settlers. Estimated age of the four old trees was 300 years or more. Erosion had exposed 30 inches of the root system. The nearest stand of *Pinus ponderosa* is on the Boise Front, 65 air miles northeast but the relict stand differs from these trees, the relict population having needles 10 to 20 cm long on old trees and small cones under 10 cm long with recurved prickles. The next closest Ponderosa pine in the vicinity is a small stand on rhyolitic sand in the Sheldon National Antelope Refuge, roughly 100 air miles southwest (Critchfield and Allenbaugh, 1969), Madroño 20:12–26) just south of the Oregon-Nevada border.—PATRICIA L. PACKARD, Department of Biology, College of Idaho, Caldwell, 83605.

THE PHYTOTOXIC POTENTIAL OF BRACKEN, PTERIDIUM AQUILINUM (L.) KUHN

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Bracken, *Pteridium aquilinum* (L.) Kuhn, has an almost worldwide distribution that extends from the edges of the polar regions to the heart of the tropics. It grows under environmental conditions ranging from tropical through Mediterranean to boreal. There are many references in the literature to the dominating influence of bracken over many types of vegetation in these different situations (Isaac, 1940; Das, 1947; Schelpe, 1951; Winne, 1952; Watt, 1955). It is commonly referred to as a very troublesome weed, with much effort and expense put into its eradication (Fenton, 1936; Braid, 1948; Gilkey, 1957). All of the ecological studies of bracken under these varying conditions name forms of competition (for water, light, or nutrients) as the probable mechanisms that this fern brings to bear upon associated plants. But work now in progress on bracken suggests that the release of phytotoxins from the fern fronds often may be the limiting factor rather than competition.

This study involves areas in the Santa Ynez Mountains near Santa Barbara, California. Meadows that occur as large openings in an oak woodland often are dominated by bracken, this occurring almost to the complete exclusion of herbaceous grasses and dicots and even many woody plants. Portions of the meadow not dominated by bracken are vegetated predominantly by weedy annual grasses such as *Bromus rigidus* and *Avena fatua* and an array of annual dicots. All of the various forms of interference of which bracken might be capable are being examined in order to explain the mechanisms of the fern's dominance over associated species. Laboratory evidence thus far accumulated suggests that allelopathy is one of the most important mechanisms.

Detection of phytotoxicity. In a search for the presence of toxins, both dead and live bracken fronds were collected from meadows in the area of San Marcos Pass in the Santa Ynez Mountains. Water extracts were made by soaking 65 grams of intact fronds in 1500 ml of double distilled water for two hours. The extract was filtered and a portion was then concentrated in a Buchler flash-evaporator at 49°C to four times the original concentration. Both concentrations were subjected to a bioassay for toxicity. Seeds of *Bromus rigidus* were soaked for two hours in the solution in which they were to be tested. Ten seeds were placed on 5 × 5 cm cellulose sponges, 3 mm thick, over which had been placed a 5 × 5 cm square of Whatman #3 chromatogram paper. Each sponge had been soaked in the test solution (the controls in double distilled water) and then placed in petri dishes sealed with parafilm. The dishes were placed in a growth chamber and incubated in darkness for 48 hours at 26°C.

TABLE 1. RADICLE GROWTH (MM) OF BROMUS RIGIDUS IN WATER EXTRACTS OF BRACKEN FRONDS. (N = 30 FOR ALL MEANS, NUMBERS IN PARENTHESES ARE PERCENT OF CONTROL.)

Test	Control	X	4X
Green fronds	25.6 (100)	25.3 (98.5)	——
Yellow fronds	22.3 (100)	22.6 (101.0)	18.3 (81.7)*
Dead fronds collected before rains:			
1967	21.8 (100)	18.6 (85.4)*	8.3 (38.1)**
1968	15.4 (100)	13.1 (85.0)*	5.3 (34.4)**
1969	23.1 (100)	17.6 (76.2)*	5.0 (21.6)**
Dead fronds collected after one rainy season	22.1 (100)	18.1 (82.0)*	15.5 (70.0)*
Dead fronds collected after 2–3 rainy seasons	20.1 (100)	19.9 (99.0)	19.9 (99.0)

*Significant at 5% level.
**Significant at 1% level.

Results of several tests are listed in Table 1. Extracts of green fronds proved to be insignificantly toxic, even the extract concentrated 4 times. Yellow fronds beginning to show signs of senescence exhibited moderate toxicity in the concentrated extract (81.7% of control). Completely dead fronds were collected, over a series of several growing seasons, before any leaching by rainfall had occurred. Water extracts of these fronds proved to be highly toxic even when unconcentrated. As the fronds are exposed to the leaching effects of rainfall, toxicity is rapidly removed. After one winter season, toxicity is severely reduced even in the concentrated extract, and after two or three seasons, the toxic principle appears to be completely removed. Thus it is apparent that when the fronds age and die, toxins are readily leachable, even by such a simple method as soaking in water. Exposed to a series of leaching rains, the toxins are released from the fronds into the surrounding environment.

To test the idea that the toxic effect of bracken can be transferred to other plants by way of the soil medium, water extracts of whole fronds were used to water seeds planted in soil. A sandy-loam soil was collected from the grassland adjacent to the bracken stand at the study site. This soil was air dried, passed through a 2 mm screen (U.S. Standard Soil Sieve #10), and 50 grams then placed in each of 24 covered storage dishes (500 ml size). *Bromus rigidus* or *Avena fatua* were planted in the soil, 20 seeds to a dish, watered with 13 ml of extract, sealed with parafilm, and incubated at 26°C in the dark. *Bromus* was incubated for 48 hours and *Avena* for 72 hours. Six dishes were watered with double disstilled water as controls. Upon measurement of radicle lengths, it was found that *Bromus rigidus* was inhibited significantly only by the extract concentrated four times (39.0% of control). *Avena fatua* was inhibited by the unconcentrated extract to 75.1% of control, while the concen-

trated extract inhibited the growth of the radicle to 37.7% of control. Although germination was practically 100% for the tests involving *Bromus rigidus*, the germination of *Avena fatua* was reduced in the concentrated solution to 76% of control. Thus toxicity is evident even in the soil medium, suggesting that one of the important means of transfer of the inhibitors to other plants in the environment is through leachates from bracken fronds washed into the soil by rain, fog, or dew drip.

Since the principal mechanism of transfer of toxins from the fronds to the environment most likely is in some form of precipitation, an artificial means of collecting rain drip was devised in the laboratory. A four-foot square frame was constructed of wood, and light twine was strung between the sides at 2–3 inch intervals to form a grid into which fronds could be inserted at the same density and in the same upright position observed in the field. The complete grid was then suspended over a funnel constructed from a four-foot square sheet of plastic. Distilled water equivalent to a quarter inch of rain was applied to the grid at intervals over a two-hour period in the form of a fine mist. After the drip was collected, it was filtered, concentrated, and bioassayed by the previously described sponge method. The leaching was repeated five times, with the fronds fully dried between leachings, the entire series being completed in five days. The bioassay results are given in Table 2. The initial leaching

TABLE 2. RADICLE GROWTH (MM) OF BROMUS RIGIDUS IN ARTIFICIAL RAIN DRIP FROM BRACKEN FRONDS. (N = 30 FOR ALL MEANS; NUMBERS IN PARENTHESES ARE PERCENT OF CONTROL.)

Test (Wash #)	Control	X	4X
1	19.6 (100)	15.1 (77.0)*	2.7 (13.8)**
2	20.5 (100)	18.4 (89.7)	10.7 (52.1)**
3	21.2 (100)	19.6 (92.0)	15.5 (73.0)*
4	20.7 (100)	15.0 (72.0)*	12.5 (60.0)**
5	20.8 (100)	16.5 (79.3)*	13.4 (64.4)**

*Significant at 5% level.
**Significant at 1% level.

proved to be quite toxic at both concentrations. The subsequent leaching gradually lost toxicity, but as can be seen in the results of the fifth wash, considerable toxicity is still readily leachable. Thus the inhibitory effect of the first rain would be the most significant, but the following rains could act as a reinforcement.

Greenhouse experiment. An experiment was devised to test for the release of toxins from bracken and their subsequent interference with the growth of other plants. Dead frond material was broken by hand into small pieces, while other fronds were ground in a Thomas Company Wiley Mill using a 20-mesh grid. Grassland soil was again used, with 560 grams placed in each of several small plastic pots. Six grams of broken fronds or ground fronds were added to separate pots and mixed well with the soil, there being four pots in each treatment. Six grams of sterile

pumice rock were added to soil in four other pots as a control. Ten *Avena fatua* seeds were planted in each pot and watered daily with distilled water. Growth of the shoots was measured at 2–3 day intervals (fig. 1)
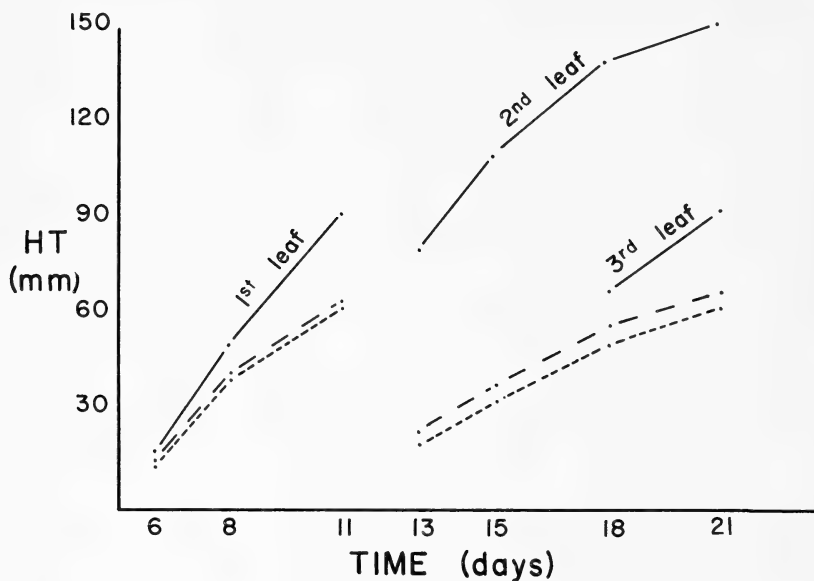

Fig. 1. Height of shoots (mm) of *Avena fatua* grown in pots and measured at intervals. Each point is the mean of 40 plants under a specific treatment: solid line, control; broken line, broken fronds in soil; dotted line, ground fronds in soil. The third leaf was initiated only in the controls.

and after three weeks, roots and shoots were harvested. Dry weights were determined after 24 hours in a drying oven at 70°C. Mean shoot and root weights for the pots containing broken or ground frond material were almost identical, with the roots averaging 0.029 grams per plant and the shoots averaging 0.009 grams per plant. In the controls containing sterile pumice rock the roots averaged 0.036 grams per plant and the shoots averaged 0.019 grams per plant. The reduced yield of both roots and shoots, coupled with the very pronounced inhibition of plant height, demonstrate well the toxic effect of bracken fronds. It is significant that the broken fronds are approximately as toxic as the finely ground fronds, indicating the ease of leaching of the toxic compounds even without so drastic a measure as grinding.

Identification of toxins. Work is still in the initial stages towards the isolation and identification of the toxic compounds involved in the interaction. Because the toxic principle is transported in some form of precipitation, work is being restricted to the water soluble compounds, predominantly the phenolic acids. Cinnamic acid has been tentatively identified.

Reference has been made in the literature to the possible presence of various other cinnamic acid or benzoic acid derivatives in bracken fronds (Bohm and Tryon, 1967), but these have not been isolated thus far.

Discussion. The presence of highly toxic compounds in bracken fern has some very important implications concerning the probably widespread occurrence of allelopathy. It is a common belief that the release of phytotoxins by a plant and their subsequent role as a factor of interference between plants is a geographically restricted phenomenon. Since ecologically effective allelopathy has been worked out in detail in only a few cases (Muller, 1969) under rather localized conditions, many researchers still feel that the other more conventional forms of interference are the only significant interactions determining vegetational composition over most of the world.

Bracken dominates, or even excludes, associated plant species in a broad spectrum of habitats within its wide geographic range. In our numerous field observations, extending over 40° of north latitude and from semi-arid to humid climates, we have been impressed by the similarity of patterns exhibited. Suppression of other species by bracken is not completely density-related. Even open stands of bracken in which ample light reaches the soil surface are characterized by extraordinary reductions in the growth of other species. Thus, in Costa Rica, California, Oregon, Washington, and Montana, in climates ranging from hot to cold and from wet to dry, there occur suppressions of plant growth which cannot be related to light competition, soil moisture, or other forms of physical interference. The toxicity of bracken demonstrated by our laboratory experiments strongly suggests the hypothesis that allelopathy is the mechanism whereby this plant induces the pattern so extensively exhibited. The widely held view that toxic compounds are rapidly removed from the habitat by heavy leaching of the soil is challenged by this proposal. We are currently extending our field experimentation into humid climates with the purpose of testing the hypothesis that phytotoxins of bracken are ecologically effective in areas of high rainfall.

LITERATURE CITED

BOHM, B. A. and R. M. TRYON. 1967. Phenolic compounds in ferns. I. A survey of some ferns for cinnamic acid and benzoic acid derivatives. Canad. J. Bot. 45:585–594.

BRAID, K. W. 1948. Bracken control—artificial and natural. Jour. Brit. Grassland Soc. 3:181–189.

DAS, PRITAM. 1947. Panvin burning in some upper Simla Hill states. Ind. Forester 73:121–122.

FENTON, E. WYLLIE. 1936. The spread of bracken (*Pteris aquilina* L.) in Scotland and its ecological significance. Agric. Prog. London 8:66–72.

GILKEY, HELEN M. 1957. Weeds of the Pacific Northwest. Corvallis, Ore. State College. 441 p. (cf. p. 14–15).

ISAAC, LEO A. 1940. Vegetative succession following logging in the douglas fir region with special reference to fire. J. Forestry 38:716–721.

MULLER, C. H. 1969. Allelopathy as a factor in vegetational process. Vegetatio 18:348–357.

SCHELPE, E. A. C. L. E. 1951. The pteridophyta of Mount Kenya. Amer. Fern J. 41:65–75.

WATT, A. S. 1955. Bracken versus heather, a study in plant sociology. J. Ecol. 43:490–506.

WINNE, W. T. 1952. Pteridophytes from two Liberian counties. Amer. Fern J. 42:7–13.

NOTES AND NEWS

TWO NEW SPECIES OF TRAGOPOGON FOR ARIZONA.—*Tragopogon mirus and Tragopogon miscellus* (Compositae) were first described by Dr. Marion Ownbey from southeastern Washington. Both species are amphidiploids, $n = 12$, resulting from the following hybridizations: *T. mirus (T. dubius* Scop., $n = 6 \times T.$ *porrifolius* L., $n = 6$) and *T. miscellus (T. dubius* Scop., $n = 6 \times$ *T. pratensis* L., $n = 6$) (M. Ownbey, Amer. Journ. Bot. 37:487–499. 1950). The amphidiploid plants are easily distinguished from the diploid parents in the field by their robust nature, expressed particularly in the size of the mature achenes. The tetraploids were previously known only from eastern Washington and areas of Idaho. Recent collections of *T. mirus (442)* and *T. miscellus (479)* were made by Schaack in 1970, near Flagstaff, Coconino County, Arizona (DHA; WS). Examination and counts of chromosomes were made from pollen mother cells using the aceto-carmine squash technique. Specimens of *T. mirus* have been verified by Dr. Marion Ownby, while *T. miscellus* was given tentative identification. *Tragopogon mirus* is well represented in the Flagstaff area; its numbers often exceed those of the parent species in many populations. *Tragopogon miscellus* is known from only two plants in the Flagstaff area. Three species *(T. dubius, T. pratensis,* and *T. porrifolius)* were previously known for Arizona. The addition of two tetraploid species complicates the identification of the Arizona *Tragopogon* using available regional floras. A key contributed by Ownbey (C. L. Hitchcock et al., Vasc. Pl. N.W. 5:327–330. 1955) should be useful in identification of the Arizona specimens. Is is our belief that the occurrence of *T. mirus* and *T. miscellus* in northern Arizona represents an independent origin rather than an extension in range. Thanks are extended to Dr. Marion Ownbey for verification of our specimens and for valuable information.—ROY C. BROWN and CLARK G. SCHAACK, Department of Biological Science, Northern Arizona University, Flagstaff 86001.

LAND-USE HISTORY OF CALIFORNIA AND CHILE AS RELATED TO THE STRUCTURE OF THE SCLEROPHYLL SCRUB VEGETATIONS

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The vegetations of the five Mediterranean climatic areas of the world, California, central Chile, southwest Australia, South Africa, and the Mediterranean, have been long cited as offering classical examples of convergence. All are far separated geographically, all have floras which are uniquely different from one another, and yet, all have vegetation types which resemble one another in their physiognomic aspects. The most distinctive physiognomy of this climatic type is that of a dense, often impenetrable scrubby vegetation composed of diverse, hard-wooded, evergreen species. Although these generalities have been long known, there have been surprisingly few detailed comparisons between the vegetations of two or more of these regions until recently (Naveh, 1967; Specht, 1969a,b; Mooney, et al., 1970).

We are presently making a study of the comparative physiology of sclerophyll shrubs of California and Chile in an attempt to understand the selective basis for the convergence phenomenon. In the process of this study we have gathered information on the characteristics of the dominant plants of these areas. This information forms the basis for an analysis of the degree of convergence between areas. In brief, we are of the opinion that these vegetations are not convergent as has been supposed in certain aspects and that the probable basis for this lack of convergence lies in dissimilar treatments of these vegetations by man through time, and not because of different evolutionary adaptations of these vegetations to essentially identical environmental conditions. This latter possibility, however, is receiving further study.

Degree of Vegetation Convergence

The distribution of the scrubby sclerophyll vegetation of Chile (the "matorral") and of California (the "chaparral") is generally similar (fig. 1) with the centers lying near 35° latitude. The greater extension of the distribution of the chaparral vegetation as compared to that of the matorral is related to the distributions of summer dry climates on these two continents. The Mediterranean-type summer drought extends to much higher latitudes in North America than in South America (Mooney, et al., 1970). At the lowest latitudes (32–34°) the correspondence of climatic types at any given equal position is very close (fig. 2). It is at such latitudes that we make our vegetation comparisons here.
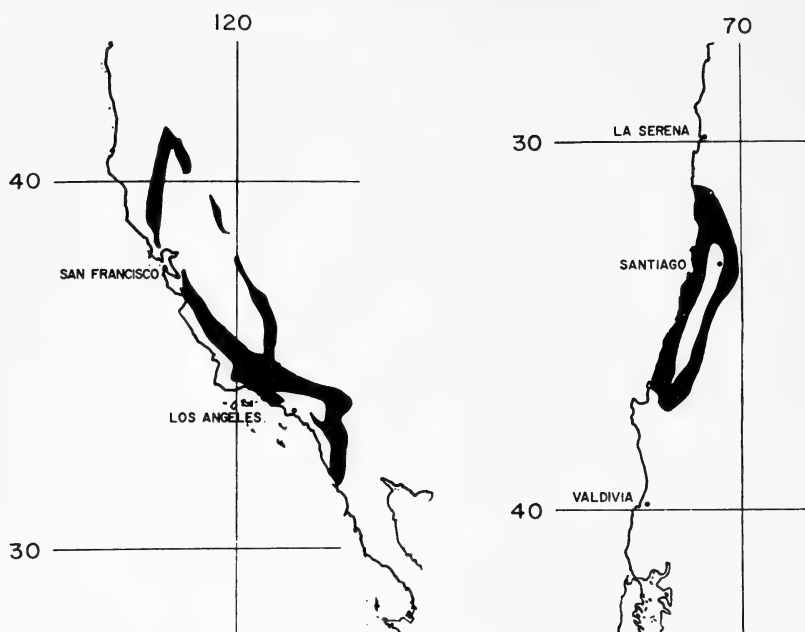
Fig. 1. Extent of the sclerophyll scrub vegetations of California and Chile.

In both of these areas the scrubby sclerophyll vegetations are bordered on the mesic side by a broadleaf, predominately evergeen, sclerophyll forest, and on the dry side by vegetations which are dominated by drought deciduous subshrubs. The details of this entire vegetation sequence and corresponding climatic gradient have been given elsewhere (Mooney, et al., 1970).

A list of the dominant or characteristic chaparral shrubs of southern California and a comparable list for the corresponding northern Chilean sclerophyll area are given in Table 1. The complete lack of taxonomic similarity between these areas is readily apparent.

We have compared the heights, leaf sizes, types, and functions as well as the spininess and flowering periods of these plants (table 2). Both the chaparral and matorral are composed of shrubs which are mostly 2–4 meters high and which have simple leaves of a size mainly between 255 and 2025 mm². Almost 50% of the shrubs from both areas are known fire sprouters. The great similarities in these attributes alone lend a high degree of closeness of general appearance of these vegetations.

These vegetations differ, however, in fine detail in that the chaparral of California is predominately evergreen, whereas the matorral of Chile has a fair number of drought-deciduous types in addition to evergreen species. Further, there is a larger number of spiny shrubs in the matorral and the general flowering activity is earlier. These characteristics of
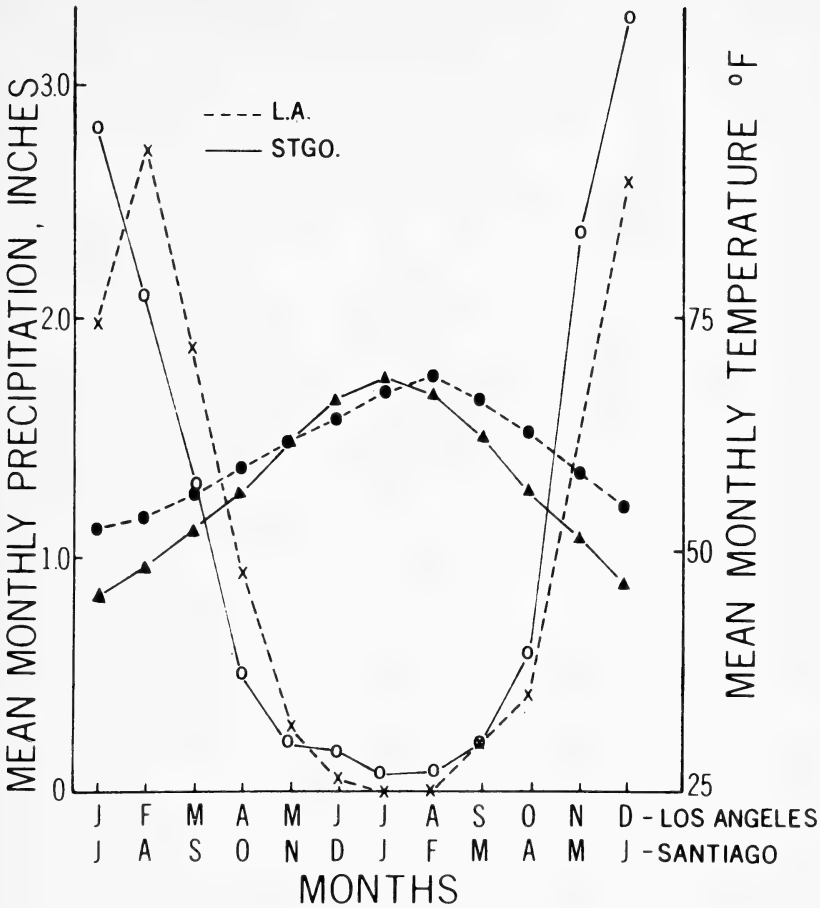
Fig. 2. Mean monthly temperature and precipitation in Los Angeles, California and Santiago, Chile.

earlier flowering, more drought deciduous and spiny types are indicative of more xeric conditions in the matorral. This is probably true, but is not evident from more detailed climatic comparisons than are presented here. Rather, this greater xerophytism of the matorral habitat is probably due to the general degradation of the vegetation by man.

Not all of the species listed for either Chile or California may be found together in any given habitat. In the matorral, the unique palm, *Jubea chilensis,* is restricted to the coastal mountains where it may occur in abundance. *Lithraea caustica, Quillaja saponaria, Kageneckia oblonga, Escallonia pulverulenta* are all evergreen schlerophylls which are generally common everywhere although rarely found in closed stands. In a phytosociological study of the matorral near Santiago, Schlegel (1963)

TABLE 1. CHARACTERISTIC DOMINANT PLANTS OF THE CHAPARRAL AND MATORRAL

The matorral list is derived from personal observations. The list for the Southern California chaparral is from Knapp (1965). The lists do not include elements from the adjacent evergreen forest or semi-arid coastal scrub vegetation types.

Northern Chile Matorral	*Southern California Chaparral*
Acacia caven (Mol.) Hook. & Arn.	*Adenostoma fasciculatum* H. & A.
Adesmia arborea Bert.	*A. sparsifolium* Torr.
Azara dentata R. & Pav.	*Arctostaphylos glauca* Lindl.
Baccharis linearis (R. & Pav.) Pers.	*A. parryana* Lemmon
Baccharis paniculata DC.	*A. pringlei* Parry
Centaurea chilensis Hook. & Arn.	*A. canescens* Eastw.
Colletia spinosa Lam.	*A. gladulosa* Eastw.
Ephedra andina Poepp. ex C. A. Mey.	*A. pungens* HBK
Escallonia pulverulenta (R. & Pav.) Pers.	*Ceanothus crassifolius* Torr.
	C. leucodermis Greene
Eupatorium salvia Colla	*C. oliganthus* Nutt. in T. & G.
Gochnatia fascicularis D. Don	*C. spinosus* Nutt.
Jubea chilensis (Mol.) Baillon	*C. tomentosus* Parry
Kageneckia oblonga R. & Pav.	*C. verrucosus* Nutt. in T. & G.
Lithraea caustica (Mol.) Hook. & Arn.	*C. megacarpus* Nutt.
Lobelia salicifolia Sweet	*Cercocarpus betuloides* Nutt.
Maytenus boaria Mol.	*Fremontia californica* Torr.
Podanthus mitiqui Lindl. in Loud.	*Garrya veatchii* Kell.
Porlieria chilensis Johnst.	*G. flavescens* Wats.
Proustia pungens Poepp. ex Less.	*G. fromontii* Torr.
Quillaja saponaria Mol.	*Heteromeles arbutifolia* M. Roem.
Retanilla ephedra (Vent.) Brongn.	*Mimulus longiflorus* (Nutt.) Grant
Schinus polygamus (Cav.) Cabrera	*M. puniceus* (Nutt.) Steud.
Trevoa trinervis Miers	*Pickeringia montana* Nutt.
Teucrium bicolor Sm. in Rees.	*Prunus ilicifolia* (Nutt.) Walp.
	Quercus dumosa Nutt.
	Rhamnus crocea Nutt. in T. & G.
	Rhus ovata Wats.
	Trichostema lanatum Benth.

found that the total shrub cover in a variety of sites was usually much less than 100% and usually near 50%. These evergreen species are probably the climax types for this climate. *Acacia caven* is a winter deciduous shrub which forms a savanna in certain areas, mainly on the gentle slopes and valley bottoms. *Proustia pungens* and *Trevoa trinervis* are both drought deciduous spiny shrubs which are very common, either occurring in almost pure stands or among the evergreen sclerophylls listed above. *Proustia* and *Trevoa* probably represent disclimax species. It is the widespread mixing of these diverse types which leads to a general vegetation which diverges from its California counterpart.

In contrast to the relatively open vegetation composed of mixed ecological types of the matorral, the chaparral generally forms over 100% cover and is composed essentially only of evergreens. *Adenostoma fasciculatum,* a needleleaf evergreen is the most prevalent species of all those listed for the chaparral. The closely related *A. sparsifolium* is very fre-

quent in the mountains of southernmost California. One or more of the species of *Ceanothus* and *Arctostaphylos* may be locally abundant in any given area. *Cercocarpus, Heteromeles,* and *Quercus,* all evergreen sclero-phylls, are particularly characteristic and abundant everywhere.

There are no areas in California comparable to those in Chile where the vegetation has been repeatedly opened and in which there appears such an admixture of shrub types. The vegetation which borders the arid fringe of the chaparral is composed of partial drought deciduous sub-shrubs such as *Artemisia californica, Salvia mellifera, S. leucophylla, S. apiana,* and *Encelia californica.* Certain of these shrubs may, in certain limited and clearly discernable areas become successional species in the chaparral habitat.

TABLE 2. CHARACTERISTICS OF THE DOMINANTS OF THE SCLEROPHYLL SCRUB[1]

	Percentage occurrence	
	California	Chile
Plant height		
0–1 meters	6.9	4.2
1–2 "	20.7	33.3
2–4 "	55.0	50.0
4+ "	17.2	12.5
Leaf size		
none	0.0	8.3
less than 25 mm²	6.9	16.6
" " 255	17.2	8.3
" " 2025	72.4	50.3
" " 18225	3.4	8.3
Leaf type		
Compound	3.4	13.6
Simple	93.1	81.8
Lobed	3.4	13.6
Leaf function		
Drought deciduous[2]	0.0	22.7
Partial drought-deciduous[3]	10.0	22.7
Evergreen	90.0	50.0
Winter deciduous	0.0	4.6
Spiny branches or leaves	17.2	29.2
Peak flowering months[4]		(Equivalent)[5]
	February 45	57 April
	March 72	61 May
	April 69	43 June
	May 45	39 July

[1] These data derived from field observations and the examination of herbarium specimens and relevant floras.
[2] Abscission layer forms and all leaves drop during drought season.
[3] Leaves dry during drought season. Terminal leaves may remain during peak of drought. If water is availalbe many leaves will remain.
[4] Percentage of species in flower on given month.
[5] Northern hemisphere equivalent months; e.g., the June for Chile is actually December.

LAND USE

The Past

In order to understand the vegetation of the Mediterranean climatic regions of California and Chile it is essential to appreciate the history of land use in these two areas. Knowledge of the treatment of the landscape by the Indians as well as the early European settlers is incomplete. Detailed information of use patterns subsequent to settlement is often lacking; however, enough salient features are known to establish the dissimilarities in usage through time.

Both Chile and California were first penetrated by the Spaniards at virtually the same time; Chile by Diego de Almagro's expedition in the late 1530's and Alta California by Juan Rodriguez Cabrillo in 1542. It is estimated that at that time there were approximately one-half million Indians in the central zone of Chile—in this case, Valparaiso to Puerto Montt (James, 1959; Faron, 1968)—and probably about 200,000–75,000 in southern California (Aschmann, 1959)—in California. These populations were very small compared to the many millions known to have existed in the Aztec and Inca empires. These relatively low Indian densities (although high for their areas since as many as one-quarter of the total U.S. Indian population may have resided in California at the time of contact by the Spanish) were in part responsible for the slow development of at least Chile by the Spaniards, since the early Spanish system of land usage was based on tributes of labor by the native population on trusts granted by the Crown—the *encomienda*. Initially, land without a labor force was of little value. The uncooperativeness and hostility of the native Indians of Chile, the Araucanians, controlled to a large degree the pace of development of this area.

A successful colony was established by Pedro de Valdivia in Santiago, Chile, upon its initial founding in 1541. Santiago lies at the base of the Andes near the northern extremity of the Central Valley (fig. 1). Today the northern valley is virtually treeless. The Andean and Coastal Range slopes are, however, covered with a matorral scrub in various states of disturbance. In the Santiago region, in protected cool canyons, either in the foothills of the Andes or in the Coastal Range, isolated forests of *Cryptocarya alba* (peumo) may be found. Such forests were perhaps more extensive in the Valley proper at the time of the arrival of the Spaniards and formed a mosaic with matorral and grassland (McBride 1936). These scattered trees were evidently quickly harvested in the initial settlement. Fire was used to clear the lowland matorral so that the land could be used for agriculture.

The extent of the Santiago settlement and the intensity of agricultural activity quickly increased. Within a few years European crops were being produced and the settlement extended 90 miles to the south. By 1630 the

land about Santiago was producing crops, stock, and agricultural prod-
ucts in abundance and of high quality. The labor to produce this harvest
was primarily Indian (McBride, 1936).

The first really extensive use of the land in the Central Valley of Chile
was for cattle raising. The initial cattle brought from Peru and Panama
multiplied to such an extent that even in the early days there were com-
plaints of overgrazing on local plots of land.

During the first 200 years following settlement, extensive cattle ranches
characterized the northern Central Valley. These cattle utilized natural
pastures in the Central Valley, the Coast Ranges, and in the summer the
high Andean meadows.

It is important to note that all of this intensive utilization of the land-
scape in Chile was concentrated in the Central Valley in the Santiago
region. The Bio-Bio River remained the southern frontier for a very long
period to come. With the exception of the well-watered Aconcagua Valley
north of Santiago there was little land of agricultural use in the arid
north. Comparatively, it is of importance to note that during this 200-
year-long period of land usage in Chile by the Europeans there was no
attempt to colonize the lands of Alta California. This did not come about
until the founding of the San Diego Mission in 1769.

In Chile, the encomiendas were finally abolished in 1791 and from
them evolved extensive haciendas. Primogeniture, inheritance by the
eldest son, kept properties large. It wasn't until the mid-1800's that this
inheritance system was terminated. Still, by 1880 land was concentrated
into the holdings of fewer people than ever before or since (as recently
as 1955, 4.4% of the Chileans owned 80.9% of the total farm lands).
Stock raising remained very important in the Central Valley. By the early
1900's, however, the number of cattle leveled off and has not increased
greatly even up to the present (Thiesenhusen, 1966).

Labor for these haciendas was provided primarily by Chilean tenant
workers—the *inquilino*. The very low standard of living of these impov-
erished farm workers probably had a long-term detrimental effect on the
landscape of the central region. McBride (1936) describes the intensive
utilization of the matorral-covered slopes surrounding the Valley by
wood gatherers and sheep herders. Present land reform is changing this
system; however, even today one may see anything of potential value
avidly collected from the hillsides—firewood, bark, roots, and herbs.

Apparently, wood gathering for charcoal for heating and cooking was
a major force in the destruction of the local forests and scrublands in the
central Chile region (di Castri, personal communication). The long-term
supply of energy from the native plants to the population of the Santiago
area resulted in the continual degradation of the vegetation. The wood
gathering activity first opened the vegetation, and subsequent intensive
grazing further degraded it.

After 200 years of neglect subsequent to discovery, Alta California was

finally colonized by the Spaniards, starting in 1769 with the establishment of the San Diego Mission. Members of the early land expeditions up the coast noted the grassy coastal plains and valleys, "with places adapted for all kinds of cattle" (Priestley, 1937). Certain valley floors, however, evidently were covered with shrubs of the coastal sage vegetation. The chaparral which presumably, then as now, covered the upper hill slopes was evidently periodically burned by the Indians to aid in hunting and to promote the growth of edible plants (Simpson, 1938; Aschman, 1959).

By 1823 the last of the 21 missions was established at Sonoma north of San Francisco. The functions of the missions were to Christianize the natives and provide islands of civilization prior to the arrival of settlers. Each mission became agriculturally self-sustaining, utilizing Indian labor to operate at least 100,000 acres. In addition to cultivated fields each had its herd of cattle. The cattle quickly multiplied, and by 1800 there were probably 150,000 head in Alta California (Salitore, 1967). As an example, the Mission San Luis Obispo had nearly 20,000 livestock in the early 1800's, half of which were sheep (Engelhardt, 1963).

Settlement for non-religious or non-military purposes was very slow. Thirty years after the founding of San Diego there were only 100 colonist families in the State. Direct grants of land to individuals were at first rare. By 1821, forty years after first settlement, only 20 *ranchos* had been established (Salitore, 1967). Apparently, one reason for this slow development was that the choice land was held by the mission. Over one-sixth of the total land of California was under control of the Franciscan missionaries (Dasmann, 1965).

Independence from Spain in 1821 had little effect on life in California or its pace of development. However, secularization of the missions, starting in 1834, brought a large change in land development pattern. By 1846 about 600 private land grants had been made by the Mexican governors. These ranchos were all extensive, in no case less than 45,000 acres, and the largest over 100,000 acres. During the brief period between 1834 and the Gold Rush starting in 1848, the Rancho and cattle raising were the dominant features of life in California. In 1850 there were about one-quarter of a million head of cattle in the State. Of people, there were but 15,000 non-Indians in 1847. Los Angeles, upon incorporation in 1850, contained only 1,610 persons (Salitore, 1967). At this same time in the history of Chile the population was well over a million (CORFO, 1965).

So, as recently as the middle of the 19th century the population of California was very small and spread throughout most of the length of the State. Cattle herds reached fairly large numbers and presumably had at least local detrimental effects on the ranges during periods of severe drought which occurred with great frequentcy: 1809–10, 1820–21, 1828–30, 1840–41, and 1845–46 (Burcham, 1957).

During the Mission Period (1769–1824) many weeds were introduced

into the native California flora, including black mustard and wild oats
(Robbins, 1940). By the time of Brewer's famous travels in California in
the early 1860's the lower slopes of many ranges were already covered
with wild oats (Farquhar, 1966). The native vegetation in such habitats
was apparently already replaced by such weeds. The valleys, in many
places, particularly in the south, became filled with mustard which often
grew to over eight feet tall and constituted a hindrance to livestock. How-
ever, at that time the cattle were restricted to the valleys and lower slopes
and did not penetrate into the chaparral vegetation. Brewer gives many
vivid accounts of encounters with the chaparral where he had to crawl
to make any headway.

The Gold Rush and statehood completely changed the entirely pastor-
al character of the State, particularly in the north. Between 1847 and
1860 the population of the State increased from 15,000 to almost 400,000
(Hansen, 1967). Tremendous demands were put upon the subsistence-
type agriculture that previously existed. Demands for meat from the
mining communities were great and could not at first be met by local
supplies. Cattle were brought in from Texas and the mid-west. By 1862
there were 3,000,000 head of cattle on California ranges (Burcham,
1957). For a quarter of a century tens of thousands of cattle were driven
from the southern ranges in the early winter up along the coast or through
the Central Valley to the northern markets (Cleland, 1951).

The demand for wheat was equally great. During the early period
wheat was largely imported. Chilean production supplied a portion of
that needed. New land, much of it marginal for crop production, was
brought under cultivation in Chile. Thus, the Gold Rush, in addition to
the profound influence it had on the Californian landscape, had its effect
on Chile. In California, wheat production went from 17,300 bushels in
1850 to almost 6,000,000 bushels by the end of that decade (Salitore,
1967).

The Gold Rush period marked the only significant time of contact be-
tween Chile and California. Ships from the east went by way of the Horn
and made stops in Valparaiso. Alfalfa hay and seed were brought from
Chile and introduced as a crop in California (Hansen, 1967). Chilean
miners also made the voyage. This brief period of exchange was termi-
nated, first by the east-west railroad connections in the United States,
and finally by the opening of the Panama Canal.

The landscape destruction of California during the Gold Rush was in-
tense. Hydraulic mining made scars which are still visible today. Forests
in the vicinity of mining activity were felled. Wildlife was greatly de-
pleted (Dasmann, 1965).

The extensive ranges of California were able to support the large cattle
populations of the late 1850's during the normal and above-normal years
of precipitation. However, the occurrence of a drought in 1863–64 brought
disaster to the cattle industry and to the ranges. These pressures prob-

ably dealt the final blow to the native perennial bunch grasses of the Central Valley and resulted in their replacement by introduced annual gresses. As many as a third of the total cattle may have died during this natural disaster (Burcham, 1957). This catastrophe was of the same magnitude as the 1968 drought in Chile when large numbers of cattle died.

After the 1863 Californian drought the preeminence of the cattle industry was replaced by sheepraising. Sheep production, although of importance since the founding of the Missions, was always secondary to cattle raising. During the Gold Rush, sheep were brought into the State to augment the small numbers already present. By 1860, there were over a million sheep. Following the drought-produced decline of cattle raising, sheep numbers increased to almost 3,000,000 in 1870 and over 4,000,000 in 1880. Summer ranges in the Sierra Nevada were so intensely utilized by the sheep that effects are still evident many decades after their removal (Burcham, 1957). Even the arid slopes of the Desert Mountain Ranges in the eastern part of the State were visited by large numbers of sheep (St. Andre, Mooney, and Wright, 1965). Thus, during this period destruction of the ranges was spread from the valleys to the mountain slopes. Changing patterns of agriculture and fencing laws brought a large decline in the sheep industry by 1890 (Burcham, 1957).

The gold boom appreciably slowed by the 1890's. At this same time there was a reaction against the landscape destruction that was experienced during the Gold Rush period. This reaction was in part responsible for a conservation move which resulted in the formation of three national parks in the Sierra Nevada in 1890. The first of California's national forests was formed in 1892. The land controlled by the Forest Service grew to include one-fifth of the total land area of the entire State (Dasmann, 1965). The extensive parks and forests of California are carefully controlled. Their relatively early formation resulted in the protection of large areas of pristine or nearly pristine vegetation from destructive use. The parks and forests are spread throughout the State and represent most types of vegetation found within California. Large national forests include areas which cover shrub and woodland communities of the Mediterranean climatic type. In Chile, few parks or forests are included within comparable climatic and vegetation types, and these are not so tightly controlled.

In California, first Mexican land grants and later federal grants to the railroads resulted in the concentration of the land into the hands of a relatively few people during the period prior to 1880. The railroads alone held 20 million acres. Ranches existed which approached a half million acres in size (Dunne, 1967). As an example of this concentration of land ownership, almost the whole of Marin County was controlled by but 30 people (Dasmann, 1965). In southern California, in 1862, the ranch of Abel Stearns encompassed over 200,000 acres of the choicest land in the Los Angeles-San Bernardino area (Cleland, 1951).

Thus during the latter part of the 19th century the land ownership pattern was comparable to that which long characterized Chile. However, there was a great difference in the type of labor which worked these lands. In Chile, the tenant *inquilinos* were tied to the land. In return for their labor they were provided for throughout the year and essentially for life by the landowner. Their standard of living was very low. In addition to working the landowner's fields and their own small plots, often they harvested the natural products of the surrounding uncultivated landscape. There was intense and continuous activity within the center and the environs of the haciendas.

The labor to work the vast Californian farms was of a completely different nature. The major source was that of migrant workers, people who were not tied to the land, but who were brought in for the harvests. In Chile the ethnic background of owner and laborer were the same; in California this was not the case. The first large farm labor supply to the Californian farms were Chinese immigrants originally brought in for railroad construction. In the 1870's they constituted three-quarters of the farm labor force of the State. They were subsequently replaced as the prime labor supply by Japanese, and later Mexicans (Dunne, 1967). The labor supply, being of a migratory nature, probably had a limited impact on the native vegetation within or surrounding the farms.

Some of the important differences in early land use between Chile and California may be summarized as follows: although both were discovered at the same time by the Spaniards about 450 years ago, California was not settled until over 200 years later. In Chile the population grew quickly and steadily and was concentrated in the northern Central Valley. In California the population remained very low until only a hundred years ago when it started growing precipitously. The population was concentrated in several areas at places distant within the State.

There probably has been continuous misuse of the natural landscape in Chile throughout its entire history through grazing practices, burning and wood gathering. Destructive land use in California was especially concentrated in the latter half of the 19th century when it reached monumental proportions principally through overstocking in ranges. The formation of large forest reserves and parks at the turn of the century resulted in the preservation of large segments of the natural landscape. There has been no comparable conservation move in Chile.

Large agricultural landholdings have been characteristic of both Chile and California; however, the nature of the labor supply has been very different in both and has resulted in dissimilar land treatment.

The Present

At present the population of Chile is about half that of California, although its areal extent is nearly twice as large. In 1960 there were 7,727,-662 people in Chile (CORFO, 1965) and in California, 15,717,204 (State

of California, 1967). Chile has an area of 286,369 square miles as contrasted to the 158,693 square-mile area of California. Three-quarters of the Chilean population is concentrated in the central zone between La Serena and Concepcion (James, 1959), with one-third centered in the 6,700 square-mile province of Santiago alone. California, on the other hand, has two geographically separated population centers, the southern California coastal region between Los Angeles and San Diego, and the San Francisco Bay area, the former being the denser of the two. In 1960 there were over 6 million people in the 4,000 square miles of Los Angeles County (State of California, 1967).

Although the rural populations of both Chile and California have declined markedly in recent years both are still important agricultural regions. In California only 4.6% of the total labor force is engaged in agriculture, yet it leads the nation in crop value and is second in livestock production (Salitore, 1967). Chile is still much more rural in character with 27% of the Chilean labor force engaged in agriculture at present (CIDA, 1964). The percentage of cropland in both California (Parsons and McCorkle, 1963) and Chile (CIDA, 1966) is approximately 10%. Almost 6½ million acres of California croplands are irrigated as are approximately 3½ million acres of Chilean land.

Range and pasture land accounts for over a third of the total area of Chile (CIDA, 1966) and a quarter of California (Parsons and McCorkle, 1963). The pattern of stock raising in the two areas is quite different. California has nearly 5 million cattle, one and a half million sheep and about 200,000 hogs and pigs (State of California, 1967). Goats are very low in number. The great majority of the cattle are raised on feed lots. Grazing on public lands is now strictly controlled (Salitore, 1967). Chile, on the other hand, has about 3 million cattle, over 6 million sheep, which are concentrated mostly in the south, and nearly a million hogs and pigs. The most significant difference relating to landscape treatment between California and Chile, however, is the fact that Chile has a population of over a mililon goats (CORFO, 1965). The majority of these goats are concentrated in the province of Coquimbo to the north of Santiago (Matthei, 1939). Covarrubias et al. (1934) have vividly described contemporary mismanagement of land in this depauperate region by overgrazing, principally by goats, cutting of trees and shrubs for firewood and charcoal and the marginal dry land cultivation of wheat. This area includes the transition between the matorral and desert vegetation types.

The amount of forested land in Chile is rather small, less than 15%, 1½% of which is in plantations (CIDA, 1966). In contrast, nearly 43% of the California landscape is forested (Salitore, 1967). Many aspects of the management of these lands differ greatly between California and Chile. One of the more important differences is that of fire control. An extensive and elaborate network of fire-control stations exists throughout the forest and woodland regions of California, as well as in urban areas.

In contrast, in Chile fire-fighting activities are more or less limited to the vicinity of urban centers (FAO, 1967).

Vast areas of California are owned by the government. Of the total area of the State of 100,207,000 acres, 44% is controlled by federal agencies. The Department of Agriculture alone manages 20% in National Forests and the Department of Interior somewhat more in National Parks and in the holdings of the Bureau of Land Management. These lands include considerable tracts of woodlands and scrublands in addition to forests (State of California, 1967). In Chile, only about 6% of the land is in forest reserves and 3% in national parks; virtually none of these lands are holdings which include Mediterranean-climate scrub vegetation (CIDA, 1966).

Summarizing the important differences in contemporary land use between Chile and California which relate to the comparative conditions of the natural vegetation of the Mediterranean-climate ones: California has a great amount of land, including much scrubland, which is closely administered by various governmental agencies; grazing activities on natural pastures are now minimal and fire protection great. The population of California is primarily urban and concentrated in two geographic centers. In contrast, very little of Chile's land is under governmental stewardship. Poor grazing practices still exist. There is little fire control. A large portion of the population is still engaged in agriculture. The most intensive use of the landscape is centered in the Santiago region.

Future changes in the natural vegetations of these regions will occur at increasingly greater rates as the populations grow. The populations of both California (Salitore, 1967) and Chile (CIDA, 1964) are increasing at an annual rate of about 2.5%. Massive urbanization in California is pushing agriculture out of the productive valleys and on to the slopes and into the deserts. Atmospheric pollution is affecting not only the crops near the urban areas but the natural vegetation at increasingly higher elevations in the mountains. Bulldozers are reshaping the entire landscape with new dams, new roads and sites for new homes. The assault on the Chilean landscape will be as great but the weapons of destruction will be not as forceful because of the lower degree of industrialization and mechanization of the Chilean society.

CONCLUSION

The northern sclerophyll region of Chile which centers in the Santiago area has had a very long history of intensive mistreatment which includes overgrazing, woodgathering, and frequent burning. This could explain why the extant vegetation in this region has a more xerophytic character than does the homologous chaparral vegetation type which occurs in California under essentially identical climatic conditions.

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LITERATURE CITED

ASCHMANN, H. 1959. The evolution of a wild landscape and its persistence in
    Southern California. Ann. Assoc. Amer. Geogr. 49:34–57.
BURCHAM, L. T. 1957. California range land. An historico-ecological study of the
    range resource of California. State of California, Division of Forestry, Depart-
    ment of Natural Resources, Sacramento.
CLELAND, R. G. 1951. The cattle on a thousand hills. The Huntington Library. San
    Marino, Calif.
CORPORATION DE FOMENTO DE LA PRODUCCION (CORFO). 1965. Geografia economica
    de Chile. Santiago.
COMITE INTERAMERICANO DE DESARROLLO AGRICOLA (CIDA). 1964. Inventory of
    information basic to the planning of agricultural development in Latin America.
    Chile. Pan American Union. Washington, D. C.
————. 1966. Chile: Tenencia de la tierra y desarrollo socio-economico del sector
    agricola. Santiago.
COVARRUBIAS, RENE, INES RUBIO, and F. DI CASTRI. 1964. Observaciones ecologico-
    cuantitativas sobre la fauna edafica de zonas semiaridas del norte de Chile
    Provincias de Coquimbo y Aconcagua. Boletin de Produccion Animal. Serie A:
    Monografias Sobre Ecologia y Biogeografia de Chile No. 2. Univ. de Chile.
DASMANN, R. F. 1965. The destruction of California. Macmillan Co., New York.
DUNNE, J. G. 1967. Delano. Farrar, Strauss and Giroux, New York.
ENGELHARDT, Z. 1963. Mission San Luis Obispo. W. T. Genns, Santa Barbara.
F. A. O. 1967. Institute for the Development of Forest Resources. Chile. General
    Report.
FARON, LOUIS C. 1968. The Mapuche Indians of Chile. Holt, Rinehart and Winston,
    Inc. New York.
FARQUHAR, F. D. 1966. Up and down California in 1860–1964. The Journal of Wil-
    liam H. Brewer. Univ. of Calif. Press, Berkeley and Los Angeles.
HANSEN, H. 1967. California. A guide to the Golden State. Revised Edition. Hastings
    House, New York.
JAMES, P. E. 1959. Latin America. 3rd Edition. Odyssey Press, New York.
KNAPP, R. 1965. Die Vegetation von Nord- und Mittelamerika und der Hawaii-
    Inselin. Gustav Fischer Verlag, Stuttgart.
MATTHEI, A. 1939. Agricultura en Chile y la politica agraria chilena. Nascimento.
    Santiago, Chile.
MCBRIDE, G. M. 1936. Chile: land and society. American Geographical Society,
    New York.
MOONEY, H. A., E. L. DUNN, F. SHROPSHIRE, and LEO SONG, JR. 1970. Vegetation
    comparisons between the mediterranean climatic areas of California and Chile.
    Flora. 159:480–496.
NAVEH, Z. 1967. Mediterranean ecosystems and vegetation types in California and
    Israel. Ecology 48:445–459.
PARSONS, P. S., and C. O. MCCORKLE, JR. 1963. A Statistical Picture of California's
    Agriculture. Univ. Calif. Agric. Exp. Sta., Extension Service Circular 459.
PRIESTLEY, H. I. 1937. (Translator and Editor) A historical, political, and natural
    description of California by Pedro Fages, soldier of Spain. Univ. of Calif. Press,
    Berkeley.
ROBBINS, W. W. 1940. Alien plants growing without cultivation in California. Univ.
    Calif. Agric. Exp. Sta. Bull. 637.

SALITORE, E. V., and E. D. SALITORE. 1967. California. Information Almanac. Double-
    day Co., Garden City, New York.
SCHLEGEL, F. 1963. Estudio floristico y fitosociologico de la Quebrada de la Plata,
    Hacienda Rinconada, de Lo Cerda, Maipu. Thesis, Facultad de Agronomia.
    Universidad de Chile.
SIMPSON, L. B. 1938. California in 1792. The expedition of Jose Longinos Martinez.
    Huntington Library, San Marino.
SPECHT, R. L. 1969a. A comparison of the sclerophyllous vegetation characteristics
    of mediterranean type climates in France, California, and Southern Australia.
    I. Structure, morphology, and succession. Austral. J. Bot. 17:277–292.
———— 1969b. Ibid. II. Dry matter, energy, and nutrient accumulation. Austral.
    J. Bot. 17:293–308.
ST. ANDRE, G., H. A. MOONEY, and R. D. WRIGHT. 1965. The pinyon woodland in
    the White Mountains of California. Amer. Midl. Nat. 73:225–239.
STATE OF CALIFORNIA. 1967. California statistical abstract. Sacramento, Calif.
THIESENHUSEN, W. C. 1966. Chile's experiments in agrarian reform. Univ. of Wis-
    consin Press, Madison, Wisconsin.

AN ANNOTATED CHECK LIST OF THE GROVES OF
SEQUOIADENDRON GIGANTEUM
IN THE SIERRA NEVADA, CALIFORNIA

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One of the outstanding characteristics of *Sequoiadendron giganteum*
(Lind.) Buchh. (Taxodiaceae) is its disjunct distribution, restricted to
a series of relatively distinct groves extending along the west slope of
the Sierra Nevada of California. *Sequoiadendron,* whether known as
giant sequoia, big tree, or Sierra redwood, is clearly one of the most prom-
inent species of plants in the world and this fact has led to the present
preservation of more than 95% of the area of existing groves in publicly

owned preserves. Despite the available access to almost all of the groves today and the voluminous popular literature on the species, no accurate description of grove localities has been published and available check lists for the groves are extremely inconsistent in terms of number of groves recognized and grove nomenclature.

A major problem in grove nomenclature is the lack of an operational definition for delimiting the boundaries of an individual grove. Fry and White (1938) considered that a distinct grove must be clearly separated by a belt of forest at least half a mile wide in which no individuals of *Sequoiadendron* occur, or separated by some natural division, such as a rocky ridge, that clearly delimits a forest area. Such a definition is obviously somewhat arbitrary, and from their check list of the groves, it can be seen that Fry and White did not always follow their own rule.

It is unlikely that any satisfactory operational grove definition can ever be made. The present disjunct distribution of the groves represents the remnants of what was once a relatively continuous *Sequoiadendron* forest along the west slope of the Sierra Nevada, which was dissected by conditions associated with the Wisconsin glaciation. Altithermal conditions of heat and drought, following the Wisconsin, restricted the remaining elements of the *Sequoiadendron* forest to montaine sites characterized by mesic soil moisture conditions throughout the summer periods of drought. Because of this habitat restriction for individual trees, the concept of the "grove" has little biological reality.

Grove nomenclature used in the literature has been applied in a haphazard manner, and for this reason a tremendous proliferation of synonymous grove names has appeared; approximately 200 individual grove names have been applied in the literature. In many cases, tradition or historical accidents have led to separate names for portions of single continuous groves. The descriptions of the Mountain Home, Rancheria, and Crystal Springs "groves," for example, undoubtedly resulted from three parties viewing the same grove from three different directions (Floyd L. Otter, personal communication). In reality, only a single continuous grove exists in this area, and thus only the name "Mountain Home Grove" has been retained in this list.

Early annotated check lists of the *Sequoiadendron* groves were published by Sudworth (1908) and Jepson (1910), but these accounts were based on incomplete knowledge of the distribution of the groves, and not surprisingly contain much misinformation. The annotated check list of the groves by Fry and White (1938) remains the most complete published listing. Although relatively complete in its coverage (information was included for each grove on general location, number of trees over ten feet in diameter at six feet above ground, and miscellaneous comments), numerous inaccuracies within their work reduce its value. At least two nonexistent groves are listed, and certain integral parts of single groves appear under separate names. In the 1946 printing of their book, grove

names in their checklist and on the map inside the cover are inconsistent. In addition, data on the numbers of large trees are unreliable.

The most recent check list of the groves appeared in a report to the California State Legislature (California State Park Commission, 1952). Data were included on grove name, ownership, and acreage.

In the present list geographic distinction has been maintained as the primary criterion for the distinction of individual groves, but historical tradition in names has not been ignored. A blending of these two criteria has been used. Outliers of a small number of trees are considered to be colonizers rather than relic groves, and for this reason, they are described under the supposed "parent" grove rather than given individual names. Several groups of contiguous "groves" have been lumped under single names.

Groves have been listed in alphabetical order. Data on the location of each grove is included based on maps and descriptions in the listed references, as well as: U.S. Geological Survey quadrangle maps; U.S. Forest Service maps on file at Sequoia National Forest Headquarters, Porterville, California (Snider, 1938a, b; Evans, 1937, n.d.); personal communications from Floyd L. Otter, Forest Manager, Mountain Home State Forest; Calaveras Big Trees State Park maps (Evans, 1924); and U.S. National Park Service maps on file at Sequoia and Kings Canyon National Park (Been, 1938; Hammon, Jensen, and Wallen, 1964; Western Timber Service, 1970).

THE GROVES OF SEQUIADENDRON GIGANTEUM

Abbott Creek Grove—T13S, R28E, Sec. 30; one small grove along and south of Abbott Creek shown on the Tehipite Dome 15 min quadrangle; one unit described by Hartesveld, et al. (1967); Sequoia National Forest; Fresno Co.

Agnew Grove—T13S, R29E, Sec. 13; Rattlesnake Creek, Sequoia National Forest; Fresno Co.

Alder Creek Grove—T20S, R31E, Sec. 9, 15, 16, 17, 21; Alder Creek, 2 miles east of Camp Wishon; Sequoia National Forest; Tulare Co.

Atwell Grove—T17S, R30E, Sec. 1, 2, 10, 11, 12, 14; Sequoia National Park; Tulare Co; single outlier 150 yards above grove is highest known giant sequoia at 8800 ft.

Bearskin Grove—T13S, R28E, Sec. 34; Bearskin Creek, Sequoia National Forest; Fresno Co.

Belknap Grove—T20S, R31E, Sec. 34 and T21S, R31E, Sec. 2; 1 mile southwest of the McIntyre Grove, Sequoia National Forest; Tulare Co.

Big Stump Grove—T14S, R28E, Sec. 7, 8; along Hwy 180; Sequoia National Forest and Kings Canyon National Park; Tulare Co.

Black Mountain Grove—T21S, R31E, Sec. 6, 7, 8, 9, 16, 17, 18, 20, and unsurveyed; T21S, R30E, Sec. 1, 12 and unsurveyed northeast margin of the Tule River Indian Reservation; primarily Sequoia National Forest; Tulare Co.

Boulder Creek Grove—T13S, R29E, Sec. 26, 35; along and southwest of Boulder Creek; Norris (1963) incorrectly describes it as south of the Little Boulder Grove; Sequoia National Forest; Fresno Co.

Burro Creek—T19S, R31E, Sec. 32, 33; T20S, R31E, Sec. 4, 5; Burro Creek, 2 miles east of Balch Park (Philip F. Corson, personal communication); Sequoia National Forest; Tulare Co.

Burton Grove—T13S, R29E, Sec. 28; between Kennedy Grove and Little Boulder Creek, Sequoia National Park, Fresno Co.

Cahoon Creek—T17S, R30E, Sec. 27; 1½ miles east of Eden Creek Grove on Cahoon Creek, Sequoia National Park; Tulare Co.

Case Mountain Groves—T17S, R29E, Sec. 26, 35, 36 and possibly T18S, R29E, Sec. 1; two units fall under this name, the larger portion occupies the large basin east of Case Mountain; Been (1938) terms this portion the Salt Creek Ridge Grove; Tulare Co.

Castle Creek Groves—T16S, R30E, Sec. 14, 22, 23, 26, 27, complex of four groves along Castle Creek termed Castle Creek North, South, East and West by Aley (1963); the North and South Castle Creek Groves are extremely small; Sequoia National Park; Tulare Co.

Cherry Gap Grove—T13S, R28E, Sec. 19, 20; just west of Highway 180 at Cherry Gap; Sequoia National Forest; Fresno Co.

Coffeepot Canyon Grove—T17S, R30E, Sec. 31, 32; Coffeepot Canyon 1 mile east of Case Mountain Grove, Sequoia National Park; Tulare Co.

Converse Basin Grove—T13S, R28E, Sec. 4, 5, 7, 8, 17, 18; T13S, R27E, Sec. 12, 13; considered to include the Boole Tree and Cabin Creek Groves, which are continuous with the Converse Basin Grove, Sequoia National Forest; Fresno Co.

Cunningham Grove—T22S, R32E, Sec. 30, 31; on ridge south of Long Meadow Creek, 1 mile east of Long Meadow, Sequoia National Forest; Tulare Co. Norris (1963) lists this as the Long Meadow Grove.

Deer Creek Grove—T23S, R31E, Sec. 2, 3; 2 miles east of Pine Flat, Sequoia National Forest; Tulare Co.

Deer Meadow Grove—T13S, R29E, Sec. 24; immediately south of the Agnew Grove, Sequoia National Forest; barely separated from Agnew Grove by ridge crest; Sequoia National Forest; Fresno Co.

Dennison Grove—T18S, R30E, and/or T19S, R30E (?); exact location not established; variously reported as within Sequoia National Park, straddling the park boundary, and just outside of the park; Tulare Co.

Devil's Canyon Grove—T18S, R30E, Sec. 31 (?); exact location not established; variously reported to be within or just outside of Sequoia National Park; Tulare Co.

Dillonwood Grove—T18S, R30E, unsurveyed; T19S, R30E, Sec. 2, 3, 4, 9, 10, 11 (?); really an extension of Garfield Grove across Dennison Ridge; if the ridge is considered the dividing point between the groves then part of the grove is included in Sequoia National Park; the groves traditionally, however, are divided at the park boundary, Sequoia National Forest; Tulare Co.

East Fork Grove—T17S, R30E, Sec. 12, 13, 14, 23, 24; T17S, R31E, Sec. 7, 18; Sequoia National Park and Sequoia National Forest; Tulare Co; eastern portion has been separated as the Silver City Grove (Fry & White, 1938).

Eden Creek Grove—T17S, R30E, Sec. 28, 29, 32, 33; Eden Creek; Sequoia National Park; Tulare Co.

Evans Grove—T13S, R29E, Sec. 15, 16, 17, 20, 21, 22; includes Horseshoe Bend and Windy Gulch Groves; Norris (1963) divides grove into two portions, an eastern Evans Grove and a western Horseshoe Bend Grove; Tehipite Dome 15 min quadrangle of the U.S.G.S. shows it as three groves with the Windy Gulch dominating most of the area; lack of topographic breaks in the combined grove areas indicates that they can best be treated under a single name. California State Park Commission (1952) shows a Horse Bend grove northeast of the Lockwood Grove but this position is considered in error; Sequoia National Forest; Fresno Co.

Freeman Creek Grove—T20S, R32E, Sec. 27, 28, 29, 32, 33, 34, 35; T21S, R32E, Sec. 2, 3; Freeman Creek; Sequoia National Forest; Tulare Co.

Garfield Grove—T18S, R30E, Sec. 20, 21, 22, 23, 26, 27, 28, 33, 34, 35; Sequoia National Park; Tulare Co. Several outliers occur along the South Fork of the

Kaweah River below the South Fork and Garfield Groves; the Cedar Flat Grove mapped by Been (1938) seems to represent an outlier near the junction of Garfield Creek and the South Fork of the Kaweah, although there is some question as to the actual location; definite outliers occur ¼ mile below the South Fork Ranger Station in Sequoia National Park and at several points further down the river to 2700 ft. (Hartesveldt, 1965).

Giant Forest—T15S, R29E, Sec. 36; T15S, R30E, Sec. 31, 32, 33; T16S, R29E, Sec. 1, 12; T16S, R30E, Sec. 4, 5, 6, 7, 8; Sequoia National Park; Tulare Co. Two small groups of outliers occur: 1) ½ mile northwest of Kaweah Camp (T16S, R29E, Sec. 1); and 2) five trees ¼ mile south of Marble Fork bridge on Crystal Cave Road (T15S, R29E, Sec. 36).

Grant Grove—T13S, R27E, Sec. 36; T13S, R28E, Sec. 31; Kings Canyon National Park and Sequoia National Forest, Fresno Co.

Homers Nose Grove—T18S, R30E, Sec. 9; incorrectly labeled on Mineral King quadrangle; located on what is plotted as Cedar Creek on the quadrangle map; Sequoia National Park; Tulare Co.

Horse Creek Grove—T17S, R30E, Sec. 26, 27; ¼ mile east of Cahoon Creek Grove on Horse Creek, Sequoia National Park; Tulare Co.

Indian Basin Grove—T13S, R28E, Sec. 4, 8, 9, 16, 17; two miles northwest of Hume Lake; Sequoia National Park; Fresno Co.

Kennedy Grove—T13S, R29E, Sec. 27, 28, 21 (?), 22 (?); two miles on Tehipite Dome 15 min quadrangle, 1 mile southwest of Kennedy Meadow, with the smaller portion, including small parts of Sec. 21 and 22; Evans (1937, n.d.) does not describe this portion, Sequoia National Forest; Fresno Co.

Landslide Grove—T13S, R29E, Sec. 30, 31; along Landslide Creek; Tehipite Dome quadrangle shows two small units; Sequoia National Forest; Fresno Co.

Little Boulder Creek—T13S, R29E, Sec. 27, 34; south margin of Little Boulder Creek, Sequoia National Forest; Fresno Co.

Lockwood Grove—T13S, R29E, Sec. 7, 8, 17; head of Lockwood Creek, Sequoia National Forest; Fresno Co.

Long Meadow Grove—T22S, R31E, Sec. 26, 27, 34, 35, 36, west of Long Meadow, Sequoia National Forest; Tulare Co., Norris (1963) applies this name to the Cunningham Grove.

Lost Grove—T15S, R29E, Sec. 3, 4; west entrance of Sequoia National Park along the Generals Highway; Tulare Co.

McIntyre Grove—T20S, R31E, Sec. 34, 35, 36; South Fork of the Middle Fork of the Tule River, 1 mile east of Camp Nelson; Sequoia National Forest; Tulare Co. Norris (1963) includes the Belknap & Wheel Meadow Groves under this name.

McKinley Grove—T10S, R26E, Sec. 35; 2 miles southeast of Dinkey Creek Ranger Station, Sierra National Forest; Fresno Co.

Maggie Mountain Grove—T19S, R30E, Sec. 20 (NW ¼): 1.5 miles west of Maggie Mountain in Galena Creek drainage; Sequoia National Forest; Tulare Co.

Mariposa Grove—T5S, R22E, Sec. 6, 7, 8, 18; 1.5 miles east of South Entrance Station in Yosemite National Park; Mariposa Co.

Merced Grove—T2S, R19E, Sec. 23, 24; Old Coulterville Road, 2 miles southwest of the Tuolumne Grove, Yosemite National Park; Mariposa Co.

Middle Tule Grove—T19S, R31E, Sec. 18, 19, 30; a few trees in T19S, R30E, Sec. 13; North Fork of the Middle Fork of Tule River, southeast of Moses Mountain; Sequoia National Forest and Mountain Home State Forest; Tulare Co.

Mountain Home Grove—T19S, R30E, Sec. 25, 26, 27, 35, 36; T19S, R31E, Sec. 30, 31; T20S, R30E, Sec. 1, 2, 12; T20S, R31E, Sec. 6; Mountain Home State Forest and Sequoia National Forest; Tulare Co. Outliers includes: 2 large trees in T19S, R30E, Sec. 34; a small group in T20S, R30E, Sec. 2 (SE ¼); and a larger group in T20S, R30E, Sec. 3 at 4200 ft. elevation (Floyd L. Otter, personal communication).

Muir Grove—T15S, R29E, Sec. 8, 9, 16, 17; 1.5 miles west of Dorst Campground, Sequoia National Park; Tulare Co.

Nelder Grove—T6S, R22E, Sec. 5, 6, 8, *et al.;* 4 miles south of Mariposa Grove, Sierra National Forest; Madera Co.

New Oriole Grove—T17S, R30E, Sec. 16, 17; tiny grove ¾ mile south of the Oriole Grove, Sequoia National Park; Tulare Co. Been (1938) lists this as the Oriole Grove.

North Calaveras Grove—T5N, R15E, Sec. 14, 15, 22; Calaveras Big Trees State Park; Calaveras Co.

North Cold Spring Grove—T22S, R30E, unsurveyed; north of North Cold Spring Peak, Tule River Indian Reservatin; Tulare Co.; often considered to be a part of the Parker Peak Grove.

Oriole Grove—T17S, R30E, Sec. 4, 5, 8, 9; along upper Squirrel Creek in Sequoia National Park; Tulare Co. Fry and White (1938) include this under Squirrel Creek Grove, although they show it as distinct on their map.

Packsaddle Grove—T23S, R31E, Sec. 12, 13, 14, 24, Packsaddle Creek, Sequoia National Forest; Tulare Co.

Parker Peak Grove—T22S, R31E, unsurveyed; between Redwood Creek and Eagle Creek, Tule River Indian Reservation; Tulare Co.

Peyrone Grove—T21S, R31E, Sec. 34, 35; T22S, R31E, Sec. 2, 3, unsurveyed; Windy Gap Creek 1 mile suth of the Red Hill Grove, Sequoia National Forest, Tulare Co.

Pine Ridge Grove—T15S, R29E, Sec. 17, 18, 20; two units ½ mile west of Skagway Grove, Sequoia National Park; Tulare Co. Been (1938) mistakenly calls this grove the Skagway.

Placer County Grove—T14N, R13E, Sec. 18, 19; Middle Fork of the American River, Tahoe National Forest; Placer Co.

Powderhorn Grove—T23S, R31E, Sec. 10, 14, 15, 1 mile southwest of Powderhorn Meadow, Sequoia National Forest; Tulare Co.

Putnam-Francis Grove—T18S, R30E, Sec. 10. ½ mile east of Homers Nose Grove, Sequoia National Park; Tulare Co.

Red Hill Grove—T21S, R31E, Sec. 22, 23, 26, 27, and unsurveyed; 1 miles east of Red Hill summit, Sequoia National Forest; Tulare Co.

Redwood Creek Grove—T17S, R30E, Sec. 9, 10, 15; Redwood Creek, Sequoia National Park; Tulare Co.

Redwood Meadow Groves—T16S, R30E, Sec. 13; T16S, R31E, Sec. 16, 17, 18, 19, 20, 21, 29; 6 separate "groves" were included in this complex by Aley (1963); separate names exist for four of these groves but the complex is best represented under the single name: 1) Redwood Meadow Grove is the main grove, including the ranger station; an outlier consisting of a single tree occurs along the creek ¼ mile to the north; 2) Granite Creek Grove is a small grove along Granite Creek 1½ miles northeast of the ranger station; 3) Little Redwood Meadow Grove, as used by Fry and White (1938), apparently applies to a small grove 1½ miles east of the main grove, at a much higher elevation, 4) Cliff Creek Grove includes two small groups of outliers along Cliff Creek, south of the main grove. Norris (1963) uses the name Redwood Meadow for the Long Meadow Grove; Sequoia National Park; Tulare Co.

Redwood Mountain Grove—T14S, R28E, Sec. 10, 13, 14, 15, 16, 21, 22, 23, 24, 25, 26, 27, 28. Primarily in Kings Canyon National Park; Whitaker's Forest (Sec. 15, 16) and the Buena Vista Grove (Sec. 13, 24) represent integral portions of this grove; isolated tiny groups of trees south of this grove include Big Baldy Grove near border of 25 and 26), an unnamed group along Redwood Creek in the NW ¼, Sec. 35, and Big Springs Grove (three sequoias along Redwood Creek near Big Springs in T15S, R28E, Sec. 2); Tulare Co.

Sequoia Creek Grove—T14S, R28E, Sec. 6; Sequoia Creek, Kings Canyon National Park; Tulare Co.

Silver Creek Grove—T19S, R31E, Sec. 29; Silver Creek, 1.5 miles east of Shake
    Camp Pack Station; Mountain Home State Forest, Tulare Co. A small group
    of outliers lie in the SW ¼ of Sec. 29, near the junction of Silver Creek and
    the North Fork of the Middle Fork of the Tule River; Sequoia National Forest;
    Tulare Co. (Floyd L. Otter, personal communication).
Skagway Grove—T15S, R29E, Sec. 16, 17, 20; ½ mile southeast of Muir Grove,
    Sequoia National Park; Tulare Co. Been (1938) uses this name in mistake
    for the Pine Ridge Grove.
South Calaveras Grove—T5N, R16E, Sec. 28, 29, 30, 31, 32, 33; two groups of
    outliers occur just outside of the grove basin; Calaveras Big Trees State Park;
    Tuolumne Co.
South Fork Grove—T18S, R30E, Sec. 14, 15, 16, 22, 23. South Fork of Kaweah
    River, Sequoia National Park; Tulare Co.
Squirrel Creek Grove—T17S, R30E, Sec. 7; Squirrel Creek, 1 mile west of Oriole
    Grove, Sequoia National Park; Tulare Co. Three trees, probably representing
    a dispersal of seed down Squirrel Creek from the Oriole Grove; equated with
    the Oriole Grove in Fry & White (1938).
Starvation Creek Grove—T23S, R31E, Sec. 9, 10, 15, 16; Starvation Creek, 1 mile
    west of the Powderhorn Grove, Sequoia National Forest; Tulare Co.
Surprise Grove—T18S, R30E, Sec. 5, 6, 7, 8; Bennett Creek near Palmer Cave,
    Sequoia National Park, Tulare Co.
Suwanee Grove—T15S, R29E, Sec. 26, 35; 1.5 miles east of Crystal Cave; Sequoia
    National Park; Tulare Co. The Giant Forest quadrangle shows this grove
    ½ mile north of its actual location.
Tenmile Grove—T13S, R28E, Sec. 35, 36; Tenmile Creek Sequoia National Forest;
    Fresno Co.
Tuolumne Grove—T2S, R20E, Sec. 7, 18; Big Oak Flat Road, 1 mile north of
    Crane Flat Ranger Station; Yosemite National Park, Tuolumne Co.
Wheel Meadow Grove—T21S, R32E, Sec. 6, 7, 18; T20S, R31E, Sec. 1; South
    Fork of the Middle Fork of the Tule River, 1 mile southeast of the McIntyre
    Grove, Sequoia National Forest; Tulare Co.

ALPHABETICAL LISTING OF EXCLUDED GROVE NAMES
(Including synonyms, names referring to portions
of groves, and names of grove subunits)

Alder Creek Forest = Alder Creek
American River = Placer County
Atwell Forest = Atwell
Atwell Mill = Atwell
Balch Park = Mountain Home
Belknap Camp = Belknap
Big Baldy = outlying trees south of the Redwood Mountain Grove
Big Baldy North = see Big Baldy
Big Baldy South = pair of outlying trees south of Big Badly reported by Aley
    (1963); no verification of their existence.
Big Springs = three outlying trees south of Redwood Mountain
Black Oak Forest = Muir, Skagway, and Pine Ridge
Boole Tree = considered here to be portion of Converse Basin
Boulder Creek Forest = all of the Sequoia National Forest groves north of Kings
    Canyon and Sequoia, except Converse Basin; 14 groves in all.
Buena Vista = portion of the Redwood Mountain Grove near the Generals Highway
Burton Meadows = Burton
Cabin Creek = considered here to be northern portion of Converse Basin
Calaveras = North Calaveras
Camp #7 = Evans
Carr Wilson = see Wilson

Castle Creek East ⎫
       North ⎪
       South ⎬ units of Castle Creek Groves
       West ⎭

Cedar Flat = possibly an outlier below South Fork or Garfield Grove; shown by Been (1938) at roughly junction of Garfield Creek with the South Fork of the Kaweah River

Cherry Flat = outlying tree 3 miles south of Redwood Mountain Grove reported by Aley (1963); no verification or exact locality given

Cliff Creek = units of Redwood Meadow Groves

Clough Cave = outlying trees below Garfield and South Fork Groves

Coffeepot Creek = Coffeepot Canyon

Conifer = portion of Atwell

Converse = Converse Basin

Converse Basin Forest = Converse Basin

Converse Mountain = see Boole Tree

Crane Flat = Tuolumne

Crystal Springs = southern portion of Mountain Home

Dead = probably portion of Nelder Grove; described by Fry & White (1938)

Deer Creek Mill = Deer Creek

Dillon = Dillonwood

Dillon Forest = Dillonwood

Dillon Mill = Dillonwood

Dinkey = McKinley

Dinkey Creek = McKinley

Dinky = McKinley

Dorst = Skagway

Dorst Creek = Skagway

Dorst Creek Groves = Muir, Skagway, and Pine Ridge (described as two groves by Sudworth, 1908).

Dry Meadow = Long Meadow

East Fork Forest = Redwood Creek, Atwell, and East Fork

East Tule Forest = probably Belknap, McIntyre, and Wheel Meadow; description by Sudworth (1908) fits the area but he describes much larger groves

Eden = Eden Creek

Fleitz Forest = McIntyre, Belknap, and Wheel Meadow

Freeman Creek Forest = Freeman Creek

Freeman Valley Forest = Freeman Creek

Fresno = Nelder

Galena Creek = Maggie Mountain

General Grant = Grant

Granite Creek = unit of Redwood Meadow Groves

Grouse Creek = Dennison

Halstead = Suwanee

Harmon Meadow = Redwood Meadow

Homer Peak Forest = Case Mountain, Coffeepot Canyon, Surprise, Eden Creek, Cahoon Creek, Horse Creek, Homers Nose, and Putnam-Francis Groves

Horse Bend = appears NE of Lockwood Grove on map in California State Park Commission (1952), but not described in text; no known grove at this position

Horseshoe Bend = considered here as portion of Evans

Hossack = Alder Creek

Hossack Creek = Alder Creek

Indian Reservation Forest = Parker Peak (and probably Long Meadow, Starvation Creek, Powderhorn, and Packsaddle Groves)

Jesse Brown = artificial grove; planted in 1912 by USFS Ranger Jesse Brown, 0.5 mile southeast of Capinero Road Bridge over White River, Sequoia National Forest (T24S, R31E, Sec. 15), Tulare Co.

John Evans = Evans
Kennedy Creek = Kennedy
Kennedy Meadow = Kennedy
Kern River Groves = shown by Jepson (1910) as two groves in the area of Peppermint Creek (SW¼, T21S, R32E); no presently known groves in this area
Kessing Groves = Red Hill and Peyrone
Lake Canyon =Oriole
Little Baldy = probably erroneously described grove; Fry & White (1938) describe it as southeast of the Muir Grove, and area where no grove exists
Little Redwood Meadow = unit of Redwood Meadow Groves
Lloyd Meadow = Freeman Creek
Lockwood Creek = Lockwood
Middle Tule River Forest = Middle Tule, Mountain Home, Maggie Mountain, Silver Creek, and Burro Creek Groves
Moses Mountain = Middle Tule
Muir Grove South = Skagway
Mule Gulch = Squirrel Creek
New Oriole Lake = New Oriole
North Grove = used for several groves including the Placer County Grove (Cook, 1961), the North Calaveras Grove, a portion of the Grant Grove (Aley, 1963), and a unit of the Redwood Meadow Groves (Aley, 1963).
North Kaweah = Muir, Skagway and Pine Ridge
North Tule River Forest = Dillonwood
Oriole Lake = Oriole
Packsaddle Creek = Packsaddle
Paradise = Oriole
Paradise Ridge = Oriole
Pixley = Alder Creek
Putnam Mill Forest = Black Mountain
Rancheria = Portion of Mountain Home
Redwood Canyon = Redwood Mountain (many authors); Aley (1963) places it in synonomy with Redwood Creek
Redwood Canyon Forest = Redwood Mountain
Redwood Crossing = Middle Tule
Redwood Meadow (as used in Norris, 1963) = Long Meadow
Redwood Meadow #1 = Redwood Meadow
Redwood Meadow #2 = Long Meadow
Redwood Mountain Forest = Redwood Mountain
Rogers Camp = probably Black Mountain, as used by Fry & White (1938); Cook (1961), however, places it in synonomy with the Peyrone Grove, probably in error
Salt Creek = larger unit of Case Mountain Grove
Salt Creek Forest = Case Mountain, Coffeepot Canyon, Surprise, Eden Creek, Cahoon Creek, Horse Creek, Homers Nose and Putnam-Francis Groves.
Salt Creek Ridge = Larger unit of Case Mountain Grove
Silver City = eastern portion of East Fork
South Big Baldy = see Big Baldy South
South Fork Forest = South Fork
South Fork North = see Cedar Flat
South Fork South — Putnam-Francis (origin of name obscure since it is north of both the South Fork Grove and the South Fork of the Kaweah River)
South Kaweah Forest = Garfield and South Fork Groves
South Tule Forest = Black Mountain
Stanislaus = South Calaveras
Suwanee-Halstead = Suwanee
Suwanee River = Suwanee
Tehipite View = see Cabin Creek

Tule River Forest = Middle Tule, Mountain Home, Maggie Mountain, Silver Creek, and Burro Creek Groves
Wawona = Mariposa
Whitaker = U. C. Berkeley portion of Redwood Mountain
Whitaker's Forest = U. C. Berkeley portion of Redwood Mountain
Wilson = from the description in Fry & White (1938) this might possibly represent a portion of the Black Mountain Grove (the locality is given as Wilson Creek); Norris (1963) described a Carr Wilson Grove on Bear Creek, possibly referring to the Belknap Grove; the separate existence of a Wilson Grove must be considered doubtful
Windy Gulch = considered here as a portion of the Evans Grove
Wishers Mill = East Fork

LITERATURE CITED

ALEY, T. J. 1963. Final report on the type mapping and regeneration studies in the Sequoia groves of Kings Canyon and Sequoia National Parks. Research report. Sequoia and Kings Canyon National Park files. 63 p.

BEEN, F. 1938 (?). Big Tree *(Sequoia gigantea)* Census Survey Report. Sequoia and Kings Canyon National Park files. 10 p. + maps.

CALIFORNIA STATE PARK COMMISSION. 1952. The status of Sequoia gigantea in the Sierra Nevada. Report to the Calif. Legislature. 77 p.

COOK, L. F. 1942. (reprinted 1961). The Giant Sequoias of California. U. S. Govt. Printing Office. 28 p.

EVANS, O. M. 1924. Big Tree Measurements, Calaveras Groves of Big Trees. U.S.D.A., Forest Service. Mimeo. (with maps). Calaveras Big Trees State Park files, Arnold, Calif.

————. 1937. Timber Survey Report, Pinehurst Project. Report in files of Sequoia National Forest, Porterville, Calif.

————. n.d. (193?). Sequoia Forest Map #105 (Dwyer-Rucker lands). Sequoia National Forest files. Porterville, Calif.

FRY, W. and J. R. WHITE. 1938. Big Trees. Stanford Univ. Press. 126 p.

HAMMON, JENSEN and WALLEN, Mapping and Forestry Services. 1964. Sequoia Tree Inventry: Giant Forest, Sequoia National Park. Report and atlas. Sequoia and Kings Canyon National Park files.

HARTESVELDT, R. J. 1965. An investigation of the effect of direct human impact and of advanced plant succession on *Sequoia gigantea* in Sequoia and Kings Canyon National Parks, Calif. Sequoia and Kings Canyon National Park files. 81 p.

————, H. T. HARVEY and H. S. SHELLHAMMER. 1967. Giant Sequoia Ecology: Final Contract Report on Sequoia-Fire Relationships. Sequoia and Kings Canyon National Park files. 55 p.

JEPSON, W. L. 1910. The Silva of California. Memoirs of the University of California 2: 1–480.

NORRIS, N. L. 1963. *Sequoia gigantea* (Sierra Redwood) groves within the boundaries Sequoia National Forest. Mimeographed report on file at Sequoia National Forest, Porterville, Calif.

SNIDER, W. W. 1938a. Sequoia National Forest Big Tree Atlas. Sequoia National Forest files. Porterville, California.

————. 1938b. Sequoia National Forest Big Tree Grove Map. Sequoia National Forest files. Porterville, Calif.

SUDWORTH, G. B. 1908. Forest Trees of the Pacific Slope. U. S. Government Printing Office.

WESTERN TIMBER SERVICE. 1970. Sequoia Tree Inventory: Report and atlas, Sequoia and Kings Canyan National Park files.

MADROÑO

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Contents

THE PLANTS OF SANTA BARBARA ISLAND, CALIFORNIA[1]

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Santa Barbara Island is one of the smallest of the California off-shore islands. It has an area of only 2.6 square kilometers or one square statute mile. Located southwest of Los Angeles, it is 61 kilometers (38 miles) from the nearest point on the California mainland, and 39 kilometers (24 miles) from the nearest island, Santa Catalina (fig. 1). Contrary to several local maps, Santa Barbara Island is in Santa Barbara County (California Government Code, section 23142).

The island is roughly triangular in outline (figs. 2–3). Most of its shoreline is extremely precipitous. There are no sandy beaches, and the few narrow rocky beaches are mostly submerged at high tide. The major portion of the island is composed of gradually undulating slopes flanking a low north-south oriented ridge that connects Signal Peak and North Peak, two small rounded hills with elevations of 193 and 171 meters respectively. Both to the east and west of the ridge are broad sea-formed terraces that extend nearly to the shore. The lower part of the eastern slope is cut by several small gullies. A short distance off the southwest shore is the islet of Sutil, which rises abruptly to a narrow irregular ridge with a maximum elevation of 91 meters. Shag Rock, off the northerly shore, and an unnamed rock just west of Webster Point are both high enough out of the water to support a few plant species; however, neither of these latter two is known to have been botanically collected.

The soil of Santa Barbara Island is thin and coarse at the most windy locations, while on the terraces it is deep, fine, friable, and fertile. Extreme temperatures of 34.5° C (94° F) and 4° C (39° F) have been reported; but the average temperature varies only slightly throughout the year, and the overall climate is remarkably equitable (Dunkle, 1950, pp. 273, 348, 355). Both temperature and soil are strongly influenced by wind which averages more than 27 kilometers per hour (16.8 mph) at exposed sites and about 12.6 kilometers per hour (7.8 mph) at sheltered sites (Dunkle, 1950, pp. 273–274, 349). The prevailing wind is from the west-northwest.

An annual rainfall of roughly 30.5 cm (12 inches) is supplemented by high relative humidity (Dunkle, 1950, pp. 255, 274–275, 353, 355). Nearly all of the rain comes between October and April, but wet fogs
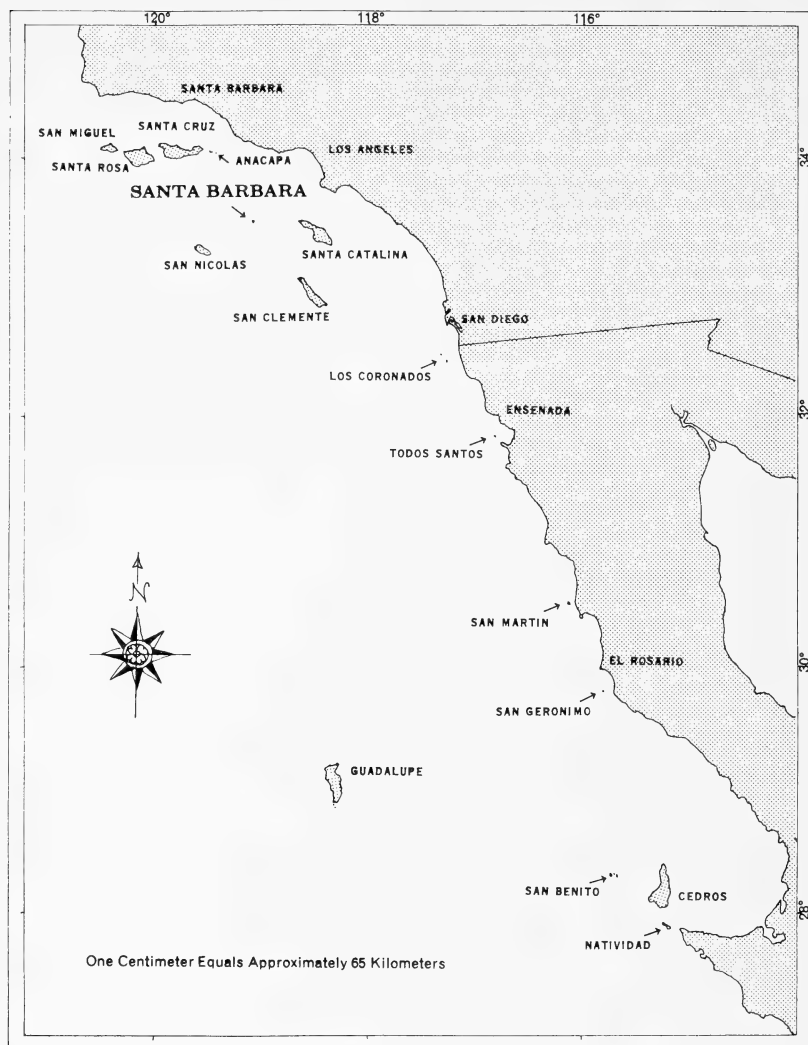
Fig. 1. California off-shore islands.

are frequent during the non-rainy months. Although very small tem-
porary seeps have been reported at various times (Britton, 1897, p. 193;
Dunkle, 1950, p. 270; Sumner, 1958, p. 3), there is no permanent fresh
water on the island.

In the late winter and early spring most of Santa Barbara Island is
covered with a luxuriant growth of suffrutescent and herbaceous plants.
During the dry season the island looks bare and grayish brown. Grass-
land, iceplant, maritime-shrub, and sea-bluff plant communities are the
most conspicuous components of the vegetation while woodland, chap-

arral, riparian, and beach communities are totally lacking. Introduced grasses and introduced iceplant occupy major portions of the slopes and terraces, thus suggesting the effects of man's activities on this island. At present most of the taxonomically important plants are relatively restricted. There are no trees on the island, and the shrubby vegetation is confined to scattered patches.

The native land animals include an insular endemic night-lizard that also occurs on San Nicolas and San Clemente islands, a small bat, and an endemic deer mouse found only on Santa Barbara Island (Savage, 1967; von Bloeker, 1967). California sea lions and a few northern elephant seals frequent the shore wherever it is low enough to provide them access (Bartholomew, 1967). Harbor seals are seen occasionally.

At least 70 different birds have been reported for Santa Barbara Island (Howell, 1917; Sumner & Bond, 1939; Grinnell & Miller, 1944; J. M. Diamond, personal communication, 1970). These include such interesting species and subspecies as the California brown pelican, Baird's pelagic cormorant, peregrine falcon, North American sparrow hawk, black oystercatcher, American pigeon guillemot, northern Xantus' murrelet, northern Cassin's auklet, North American barn owl, western burrowing owl, Costa's hummingbird, Allen's hummingbird, island horned lark, northern rock wren, dusky orange-crowned warbler, western meadowlark, San Clemente house finch, and the endemic Santa Barbara Island song sparrow. (Evaluations of available ornithological lists were provided by Alice I. Richardson and M. R. Benedict, personal communications, 1970).

Within the total of 70 birds reported, no more than 42 were listed in a single paper (Howell, 1917); and even this lower figure is a compilation based on observations over several years. Ten of the land bird species listed in 1917 were actually breeding on the island. By 1968 this number was reduced to six, not only the lowest figure for any of the islands from San Miguel to Los Coronados, but also the only one to show a net decline since 1917 (Diamond, 1969). In addition, the rate of turnover for breeding land bird species was higher than for any other of the above mentioned islands; and unfortunately the endemic song sparrow is now apparently extinct (J. M. Diamond, personal communication, 1970).

A preliminary study of the geology was made by Kemnitzer (1933). He described the island as being composed of two types of volcanic rock separated by a thin whitish foraminiferous zone. The present island was probably the north slope of a Miocene volcano (Emery, 1960, p. 66).

Valentine and Lipps (1967, pp. 30–31) suggested that Santa Barbara Island appeared sometime between 2 and 11 million years ago. They indicated that submarine ridges, possibly including islands near the present-day sites of San Clemente, Santa Catalina, and San Nicolas, were less than 15 kilometers from a similar submarine ridge including Santa Barbara Island, which in turn was connected to the northern
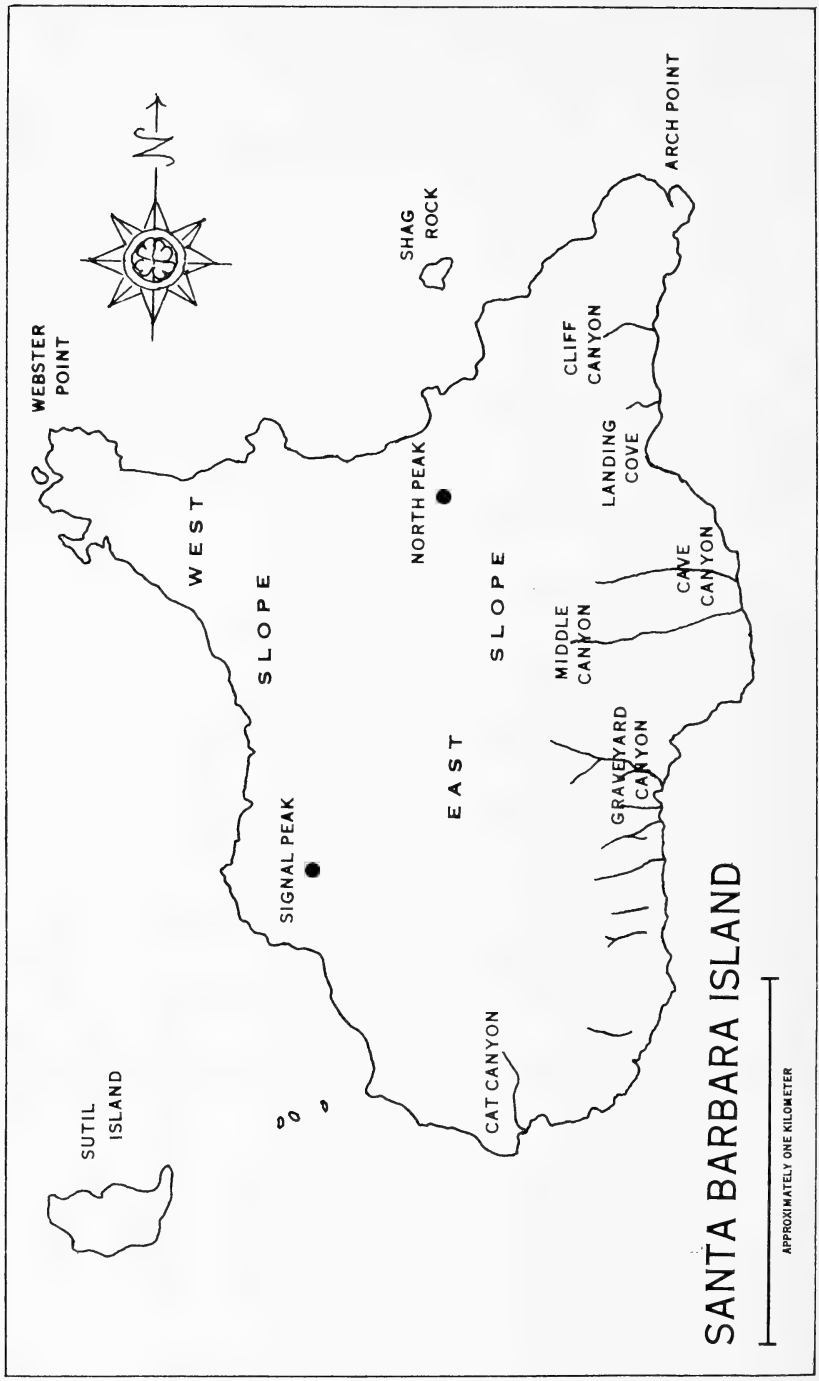
Fig. 2. Principal landmarks on Santa Barbara Island.

U.S. Department of Agriculture Photograph

Fig. 3. Aerial photograph of Santa Barbara Island.

islands. Corey (1954, p. 81), on the other hand, emphasized the possibility that Santa Barbara and Santa Catalina islands actually may have been connected during the Pliocene and that this combined land mass was quite close to San Clemente, San Nicolas, and the northern islands.

In any event, Santa Barbara Island was submerged during the late Pliocene or early Pleistocene (Valentine & Lipps, 1967, p. 30; J. H. Lipps, personal communication, 1970); thus the pertinent floristic history of this island probably begins only a few hundred thousand years ago. The terraces documented by Lipps, Valentine, and Mitchell (1968, pp. 292–294) indicate that subsequent repeated fluctuations of relative sea level restricted and expanded the size of the island during middle and late Pleistocene.

THE FLORA

In spite of its small size, isolation, uniform topography, and recent submergence, this island has a vascular flora of approximately 96 taxa in 75 genera. The best represented of the 32 families involved are Gramineae and Compositae with 18 species known for each. None of the genera are represented by a large number of species; the most for any one genus is five for *Bromus*. Many of the plants of Santa Barbara Island are widely distributed throughout much of California. On the other hand, *Lupinus, Rhus,* and *Haplopappus,* ubiquitous genera with wide-ranging species, are conspicuously absent from the island. The largest shrubby plants are *Eriogonum giganteum* var. *compactum,* three species of *Opuntia, Artemisia californica* var. *insularis, Baccharis pilularis* subsp. *consanguinea,* and *Coreopsis gigantea.*

The current knowledge of the plants of this island is based, in large part, on the herbarium specimens and other records of the following collectors:

James G. Cooper[1]—May 1863
William G. W. Harford and/or Albert Kellogg[2]—about 1871
Blanche Trask—May 1901, May 1902
Robert E. Snodgrass—August 1901
Henry Hemphill[1]—date uncertain
Barton W. Evermann—March 1918
LeRoy Abrams and Ira L. Wiggins—July 1931
Norman E. Bilderback—April 1938
Francis H. Elmore—August 1938
Richard M. Bond—April 1939, May 1940

[1] J. G. Cooper collected only a single known specimen, which is discussed in the plant list under *Galvezia.* The only known Hemphill specimen from Santa Barbara Island is of *Camissonia;* this was collected before September 1927, probably about

Meryl B. Dunkle—May 1939, March 1940, September 1941
George P. Kanakoff[1]—August 1940
Reid Moran—April-May 1941, February 1949
E. R. Blakley—October 1961, May 1963
Martin A. Piehl—May 1963
Ralph N. Philbrick—June 1964, March 1968, April 1969,
    February 1970
Ralph N. Philbrick and Michael R. Benedict—May 1966,
    March 1970
Ralph N. Philbrick, James K. McPherson, and Robert F.
    Thorne—April 1968
Ralph N. Philbrick and Donald W. Ricker—March 1969

The dates of these collections span the years from 1863 through the present; most of the earlier collections were made during the late 1930's and early 1940's at the time of the Channel Islands Biological Survey, organized by the Los Angeles County Museum. The extensive collections of M. B. Dunkle provide the major basis for comparison with today's flora of Santa Barbara Island.

INTRODUCED PLANTS

Twenty-eight species, or approximately 29 percent of the Santa Barbara Island flora, are presumed to have been introduced to California during historic time (modified from Munz, 1959 & 1968); this includes a total of 10 grasses. Nearly all of these same introduced species are shared with each of the other California islands for which comparable data are available, i.e., 22 species shared with San Miguel, 23 with San Nicolas, 27 with Santa Catalina, and 25 with San Clemente.

The overall percentages of introduced plants for these four islands range from about 35 percent for San Nicolas (modified from Foreman, 1967) to about 22 percent for San Clemente (modified from Raven, 1963, and Thorne, 1969). In contrast the floras of other floristically related islands contain an even smaller proportion of introduced plants. Guadalupe has about 42 introduced taxa, which comprise 20 percent of its flora; and Cedros has about 22 introduced taxa, only 10 percent of its flora (Moran, 1967).

In addition to the 28 non-native plants that are considered to have been introduced to Santa Barbara Island, there are also a number that are native to the mainland and yet quite possibly should be treated as recently introduced to this island. For example, *Daucus pusillus* was not collected until 1963 and has never been found away from the Landing Cove area where supplies and people are usually put ashore.

1901. G. P. Kanakoff collected only one specimen, a *Lotus*.
    [2] According to Kellogg's description of *Coreopsis* (Proc. Calif. Acad. Sci. 4:198–199, 1873).

Endemic Plants

Roughly 100 vascular plants are restricted to the California off-shore islands and have not been found on the mainland. Fourteen of these insular endemics are native to Santa Barbara Island and constitute the most notable feature of its flora. Three endemics, *Eriogonum giganteum* var. *compactum, Dudleya traskiae,* and *Platystemon californicus* var. *ciliatus,* are known only from this island (figs. 4–6).

Fig. 4. A low shrub of the endemic *Eriogonum giganteum* var. *compactum (B68–77)* flowering at the Santa Barbara Botanic Garden, September 1970.
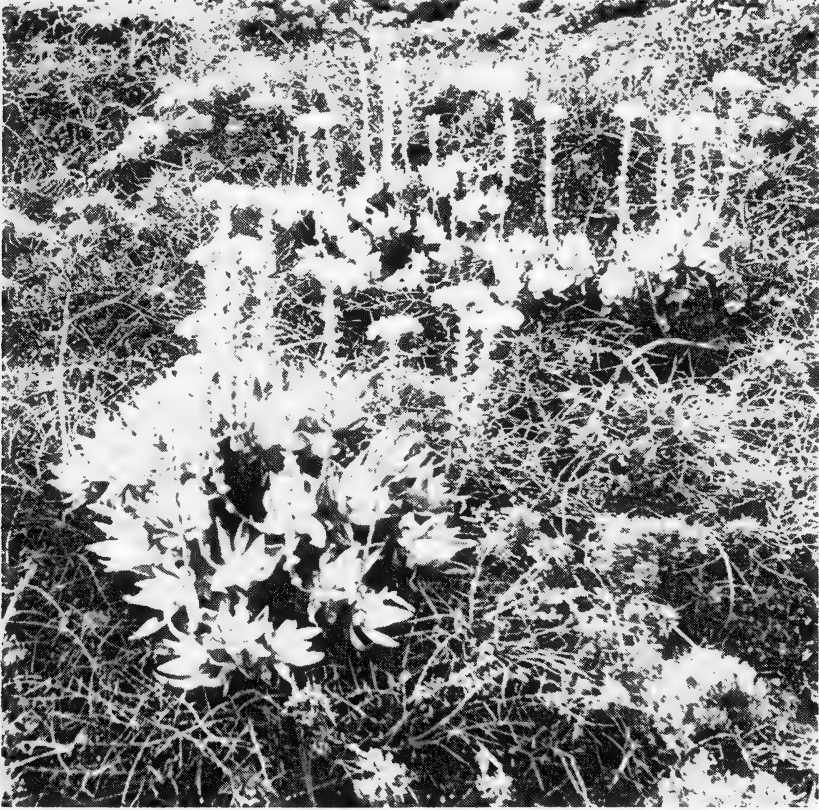
Fig. 5. *Dudleya traskiae (Philbrick & Benedict B66-403)*, taxonomically the most distinctive endemic of Santa Barbara Island. Shown here, 22 May 1966, on the southwest sea bluff between Cat Canyon and Signal Peak. Last seen in the wild in 1968.

The evolution of these endemics, whether on Santa Barbara Island or some similar land mass, is quite probably associated with Pleistocene fluctuations in land area—increase in number and diversity of available habitats as land area expanded and an intense selection during periods of restricted land area.

FLORISTIC RELATIONSHIPS

One of the interesting questions to be asked about an island flora concerns the location of its nearest relatives. Such relationships provide a clue as to how the island was botanically populated. Sixty-eight plants presently reported from Santa Barbara Island are known to be part of the native flora of California (modified from Munz, 1959 & 1968) and are presumed to be native to this island. Some of these plants are shared

Fig. 6. Pressed specimens of *Platystemon californicus* var. *ciliatus (Dunkle 7400)*, endemic to Santa Barbara Island. Vigorous individuals frequently measure 25 cm across and produce 50 or more flowers at one time.

with San Miguel Island (unpublished data at the Santa Barbara Botanic Garden), San Nicolas Island (Foreman, 1967; unpublished data at the Santa Barbara Botanic Garden), Santa Catalina Island (modified from Thorne, 1967 & 1969), San Clemente Island (modified from Raven, 1963, and Thorne, 1969), and Guadalupe Island (Reid Moran, personal communication, 1969). The native plants of the other California islands are not considered in this particular connection because comprehensive data are still being accumulated. Eventually the relationships between the native floras of all these islands should be investigated.

On the basis of the known number of shared native vascular plants (fig. 7), Santa Barbara Island shows its closest relationship to San Clemente Island (61 taxa shared) and Santa Catalina Island (57 taxa shared). The floristically related Guadalupe Island shares 38 taxa with Santa Barbara Island in spite of the two being separated by several hundred kilometers. San Miguel and San Nicolas both share 34 taxa with Santa Barbara.

A similar pattern of relationship is shown by examining the insular endemic plants that Santa Barbara Island shares with other islands (fig. 8, table 1). San Clemente and Santa Barbara share 10 of these taxa; Santa Catalina and Santa Barbara, eight; San Nicolas and Santa Barbara, six. The distant Guadalupe Island shares five with Santa Barbara Island. Anacapa, the nearest of the northern islands, shares four. Santa Cruz, the second nearest northern island, shares three. Santa Rosa, farther up the coast, and Los Coronados, to the south, each share two with Santa Barbara. All other of the California islands, as far south
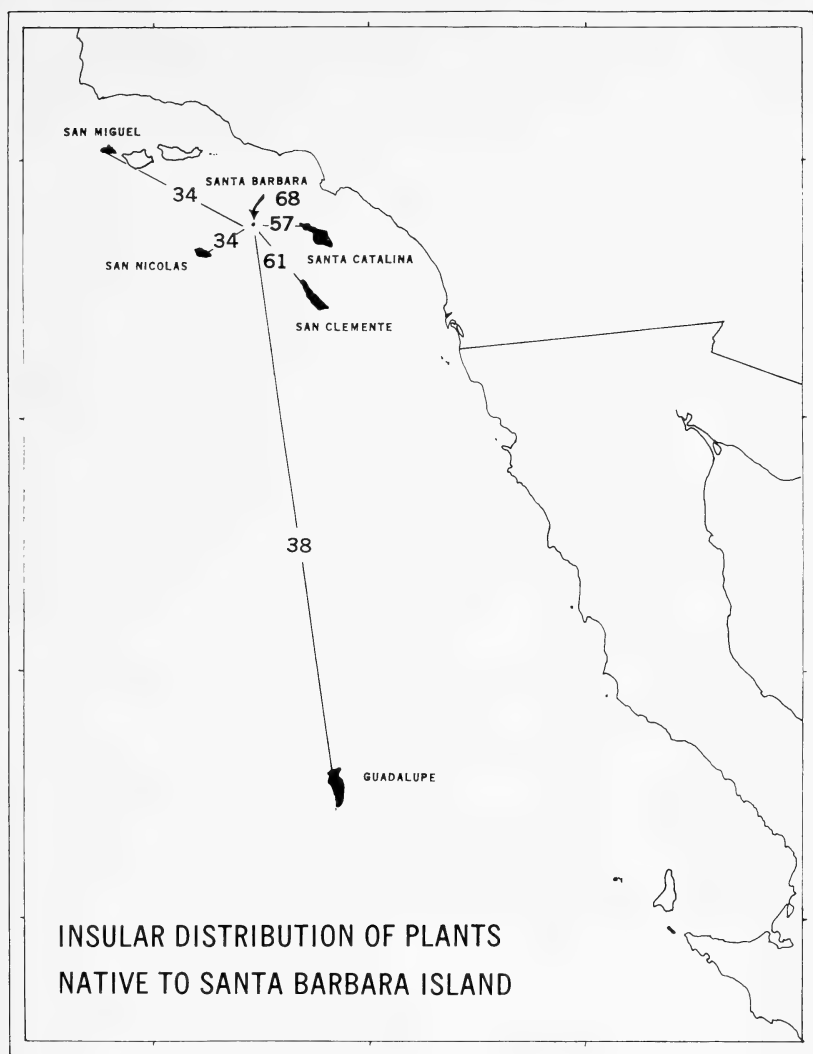
FIG. 7. All but 7 of the 68 native vascular plants known from Santa Barbara Island are a part of the relatively large flora of San Clemente Island. Santa Barbara Island also shares many plants with Santa Catalina Island. Present data indicate that the floristic affinities of Santa Barbara Island are with the southern islands. The numbers shared with islands not labeled on this map have yet to be determined.

as Natividad, share no more than a single insular endemic with Santa Barbara Island. Not one insular endemic is shared exclusively by Santa Barbara Island and any of the northern islands.

The *Phacelia* of Santa Barbara Island is of particular interest; it combines characteristics of the relatively widespread *P. distans* and the insular endemic *P. floribunda*. The former occurs on San Miguel and
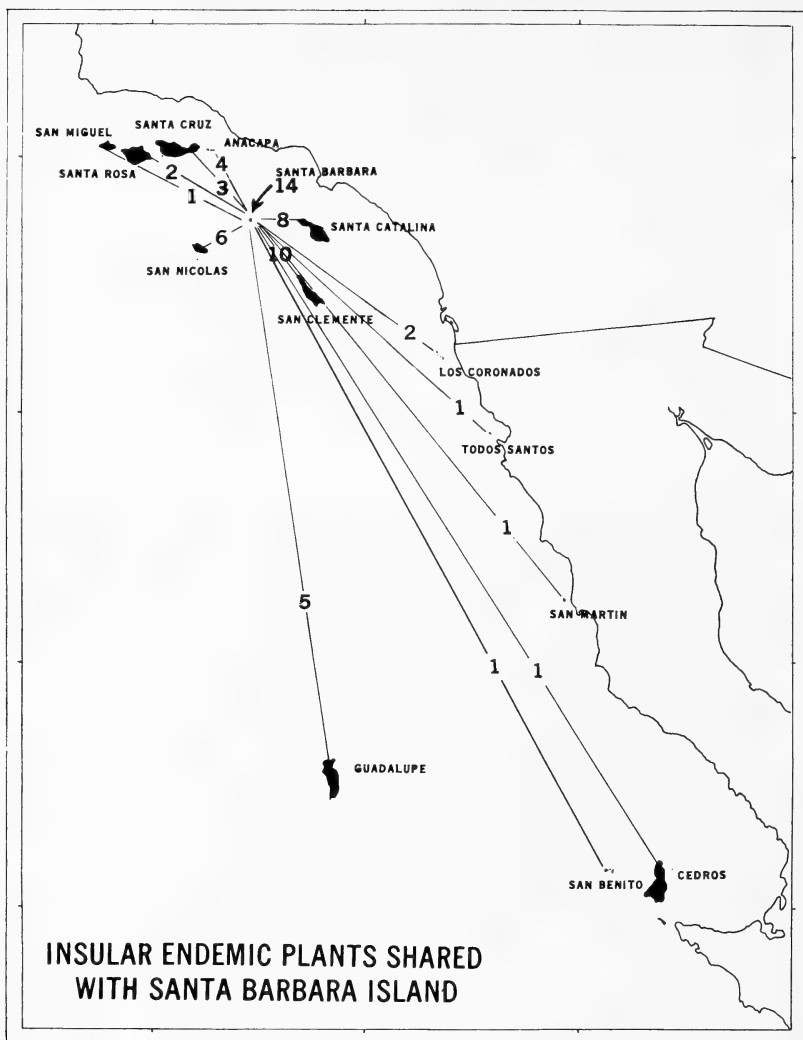
INSULAR ENDEMIC PLANTS SHARED
WITH SANTA BARBARA ISLAND

FIG. 8. Many vascular plants occur only on the California off-shore islands. Four-teen of these endemics are native to Santa Barbara Island. Ten of the 14 also occur on San Clemente Island thus indicating a close floristic relationship between these two islands. See also table 1.

Santa Catalina; *P. floribunda* occurs on Guadalupe; and both species occur on San Clemente. Although the Santa Barbara Island *Phacelia* apparently is restricted to the one island, it is not considered here as a stabilized endemic and is not included in the floristic tabulations of this paper. In addition to this *Phacelia,* the only native plants not shared with San Clemente Island are *Hutchinsia procumbens, Astragalus trask-*

TABLE 1. KNOWN DISTRIBUTIONS OF INSULAR ENDEMIC PLANTS OCCURRING ON SANTA BARBARA ISLAND

Eriogonum giganteum compactum	—	—	—	—	SBa	—	—	—	—	—	—	—	—	—
Eschscholzia ramosa	—	SR	SCr	—	SBa	—	SCa	SCl	LC	TS	—	G	SBe	C
Platystemon californicus ciliatus	—	—	—	—	SBa	—	—	—	—	—	—	—	—	—
Dudleya traskiae	—	—	—	—	SBa	SN	—	—	—	—	—	—	—	—
Astragalus traskiae	—	—	—	—	SBa	SN	SCa	SCl	—	—	—	G	—	—
Lotus argophyllus ornithopus	—	—	—	—	SBa	SN	SCa	SCl	—	—	—	G	—	—
Trifolium palmeri	—	—	—	—	SBa	SN	SCa	SCl	—	—	—	G	—	—
Calystegia macrostegia macrostegia	SM	SR	SCr	A	SBa	SN	SCa	SCl	—	—	SMa	G	—	—
Gilia nevinii	—	—	—	—	SBa	—	SCa	SCl	—	—	—	G	—	—
Galvezia speciosa	—	—	—	—	SBa	SN	SCa	SCl	—	—	—	—	—	—
Artemisia californica insularis	—	—	—	—	SBa	SN	—	SCl	—	—	—	—	—	—
Eriophyllum nevinii	—	—	—	—	SBa	—	SCa	SCl	—	—	—	—	—	—
Hemizonia clementina	—	—	A	A	SBa	SN	SCa	SCl	—	—	—	—	—	—
Malacothrix foliosa	—	—	A	A	SBa	—	—	SCl	LC	—	—	—	—	—
Totals	1	2	3	4	14	6	8	10	2	1	1	5	1	1

Fourteen insular endemic plants are native to Santa Barbara Island. An *Eriogonum*, *Platystemon*, and *Dudleya* occur nowhere else. An *Eschscholzia* and a *Calystegia* are relatively widespread; each is known from at least 10 islands. The remaining endemics are particularly indicative of a close floristic relationship among the southern islands.

Abbreviations refer to San Miguel, Santa Rosa, Santa Cruz, Anacapa, Santa Barbara, San Nicolas, Santa Catalina, San Clemente, Los Coronados, Todos Santos, San Martín, Guadalupe, San Benito, and Cedros islands. This tabulation is the basis of the map shown in figure 8.

iae, Coreopsis gigantea, and the three endemic taxa restricted to Santa Barbara Island.

The overall floristic relationship among most of the southern islands is indicative of relatively close proximity, similar climatic conditions, and colonization from similar plant sources by means of bird migrations, wind patterns, ocean currents, and human visitation.

PRESENT-DAY VEGETATIONAL CHANGES

Most of the dispersal of the plants making up this flora has taken place over many thousands of years; however, changes are still going on. To date five species have been eliminated from the flora of Santa Barbara Island. These are two maritime plants that were collected only once, *Camissonia cheiranthifolia* subsp. *cheiranthifolia* and *Galvezia speciosa,* and three marginally adapted introduced weeds, *Bromus diandrus, Brassica nigra,* and *Xanthium spinosum.* It now seems probable that the Santa Barbara Island endemic *Dudleya traskiae* has also been eliminated.

During the past 30 or so years, 20 species have been added to this flora. *Phyllospadix scouleri, Vulpia octoflora, Hesperocnide tenella, Opuntia littoralis* sensu stricto, and *Amsinckia spectabilis* are presumed to be native but are either inconspicuous or taxonomically difficult and probably were overlooked by previous botanists. Ten others were introduced to California or are more or less weedy California natives, which are not surprising additions to disturbed areas; these are *Avena barbata, Bromus mollis, Hordeum pusillum, Parapholis incurva, Cannabis sativa, Thelypodium lasiophyllum* var. *lasiophyllum, Daucus pusillus, Centaurea melitensis, Silybum marianum,* and *Sonchus tenerrimus.* The remaining five, *Calandrinia ciliata* var. *menziesii, Hutchinsia procumbens, Pholistoma auritum* var. *auritum, Microseris linearifolia,* and *Rafinesquia californica,* are perhaps the most significant of the recent arrivals.

During the same 30 years, changes in distribution and frequency have been more conspicuous than additions and deletions. The populations of *Coreopsis gigantea,* which already had been nearly eliminated from the upper terraces by farming prior to Dunkle's study, now have been reduced to isolated colonies (figs. 9–12b), primarily by the burrowing and gnawing of introduced rabbits. The drastic reduction of this plant may be responsible for the apparent extinction of the Santa Barbara Island song sparrow, which was abundant prior to 1940 and was intimately associated with the *Coreopsis* thickets (Townsend, 1890, p. 139; Sumner & Bond, 1939, pp. 9–10; Dunkle, 1950, p. 280; Sumner, 1958, p. 3). Elsewhere this succulent-stemmed arborescent shrub with easily breakable branches has persisted only in scattered locations on the Southern California coast and the off-shore islands.

Greatly increased, on the other hand, is the area covered by the South African iceplant, *Mesembryanthemum crystallinum.* Dunkle (1950, p. 359) mapped this species as occupying major areas on the two peaks of the island and as coexisting with *Suaeda californica* in sev-
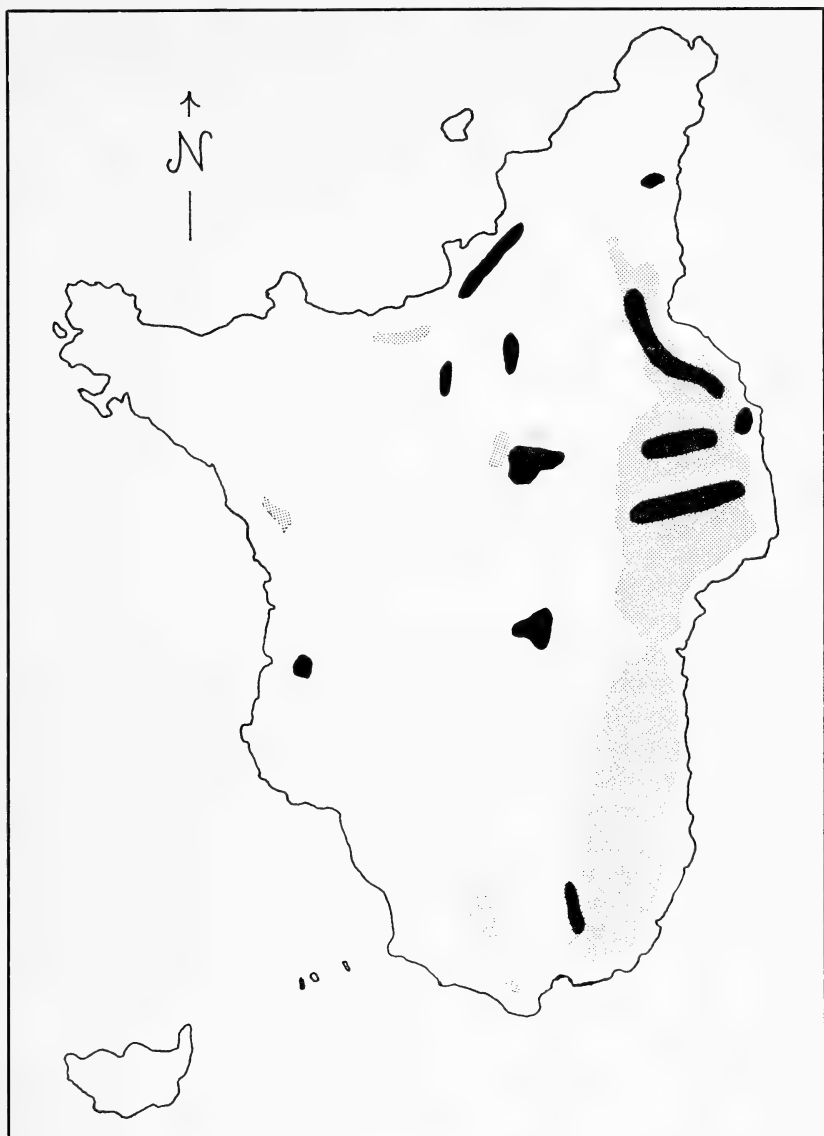
FIG. 9. Changes in the distribution of *Coreopsis gigantea* on Santa Barbara Island. Distribution for 1939–1941 is mapped in gray (from Dunkle, 1950, p. 359). Distribution for 1969–1970 is mapped in black. The reduction in the area occupied by this species is primarily the result of gnawing and tunneling by introduced rabbits.

eral sea gull nesting areas. Since that time, the iceplant has carpeted a much larger portion of the island, excluding other vegetation by physical or physiological means. When wind or other disturbance opens up small areas within this carpet, the soil often remains bare or is invaded only

by weedy introduced plants, such as *Malva parviflora* and *Erodium cicutarium*.

The major patches of *Suaeda californica,* particularly those on the West Slope, have been greatly reduced in area and density since 1968. Previous associations of *Suaeda* and *Mesembryanthemum* in gull nesting sites are now dominated by *M. crystallinum* with only a few scattered plants of *Suaeda*. From this pattern it is suggested that the gull may be important in the introduction of this iceplant and that, once established, the iceplant may contribute to the decline of the *Suaeda*. The introduced rabbits, which previously burrowed in the dense *Suaeda* patches, undoubtedly have contributed to this decline.

A third important change involves the restricted endemic *Dudleya traskiae*. By 1961 there were already in evidence many dead plants of this species (E. R. Blakley, personal communication, 1969). In 1968 only a few healthy *Dudleya* plants could be found on the island. In 1970 no live rosettes were found in any of the four locations where this plant had been previously collected. Again the major destruction is apparently due to gnawing by rabbits.

Man's Effect on the Vegetation

There are only fragmentary indications of early human activities on Santa Barbara Island. A few conspicuous shell mounds give evidence of former Indian visitation. The first suggestion of danger to the vegetation is based on an implication by T. J. Farnham that goats were placed on the island prior to 1846. He wrote: "Farther off shore and southward, are the islands of Santa Barbara, San Nicolas and San Clemente. . . . They are densely populated with goats" (Farnham, 1849, p. 107).

Feral house cats were extremely abundant shortly before 1896 (H. Bay Webster interview with Don Meadows, 1940). By 1908 these persistent wild cats were again numerous enough to be blamed for the drastic reduction in the nesting populations of Xantus' murrelet and the once abundant Cassin's auklet (Howell, 1917, pp. 20–22).

Britton (1897, pp. 192, 194) noted "ice-plant", "a field of malva weed", a lobsterman's "hut of lath and canvas", and "scattered . . . skulls and hoofs of sheep put on the island as a business venture some years ago". Additional introduced weeds, such as *Chenopodium murale,* were first collected in 1901 by R. E. Snodgrass.

About 1915 a group headed by the Alvin Hyder family moved to the island[1]. At times this group numbered as many as 17 people. A total of 11 structures were built, and a series of catch basins and reservoirs were set up to store rainwater and water hauled from the mainland. They brought with them two mules and two horses for plowing and other farm chores. For the first three years they concentrated on raising barley

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[1] The history of the Hyder activities on Santa Barbara Island is reported on the basis of a 1970 interview with Denton O. Hyder, the only son of Alvin Hyder.

FIG. 10a. Vegetation of East Slope, Santa Barbara Island, as photographed by Lowell Sumner on 15 April 1939. The foreground is dominated by introduced *Hordeum glaucum* and native *Coreopsis gigantea*. His original notation: "the broad mesa of Santa Barbara Island where exotic weeds . . . struggle with native species".

FIG. 10b. Same location as in figure 10a on 21 March 1970. In the foreground are scattered rosettes of *Mesembryanthemum crystallinum* on a carpet of dried plants of this same introduced species, the patch of *Coreopsis* obviously lost the "struggle".

Fig. 11a. A dense stand of *Coreopsis gigantea* in lower Cave Canyon, Santa Barbara Island. Photograph by Lowell Sumner, 14 April 1939.

Fig. 11b. Same location as in figure 11a on 21 March 1970. Note complete disappearance of *Coreop*sis from the south-facing slope in the foreground and the conspicuous thinning of the stand on the opposite slope.

Fig. 12a. A slope with short but healthy *Coreopsis gigantea* plants on Santa Barbara Island just west of North Peak summit. Photograph by Don Meadows, 19 March 1940.

Fig. 12b. Thirty years later, 21 March 1970, at the same location as in figure 12a. Introduced *Mesembryanthemum crystallinum* has replaced the native *Coreopsis* on this west-facing slope.

hay in a large field on the East Slope just east of Signal Peak. Sheep became the primary agricultural concern during the remaining seven years of the lease. A maximum of about "200 sheep" were kept on the island at one time. The Hyders also brought approximately "2,000 Belgian hares" [*Oryctolagus*] from various sources in the Santa Ana area. Although it is estimated that the number of these rabbits might have "doubled" temporarily, this venture soon was considered a failure; and the blame was again placed on the cats. Various other animals were raised; these included geese, ducks, chickens, turkeys, pigs, and up to "25 goats". Gull eggs were systematically harvested; only one egg was taken from each nest.

Farming necessitated clearing of both the *Coreopsis* and *Mesembryanthemum*. The former was pulled up by hand; and the latter was cut, allowed to dry, and burned. These fires took place each year between about 1917 and 1921. They resulted in the burning over of nearly all the tillable portion of the island. Several acres of corn and potatoes were raised near the southern edge of the upper West Slope.

Occasional sacks of grain and a few bales of hay were brought to the island. All major landings of materials, animals, and people were confined to the Landing Cove. The conspicuous agricultural weeds of this time were "oats, mustard, foxtail, and filaree". A "castor-bean" shrub, *Ricinus*, persisted at the Landing Cove for a short time. Of all the animals that were introduced by the Hyders only the rabbit persisted, and this probably not beyond the 1940's when a different rabbit was introduced. By 1926 the Hyder group had moved off Santa Barbara Island, but during that year D. O. Hyder returned for two months to graze sheep from his family's H-A Ranch in the Cuyama Valley of northern Santa Barbara County.

In 1931 *Mesembryanthemum* was the major vegetation over most of the island; but the *Coreopsis* was in good condition, especially at the top of the cliffs on the east side of the island (I. L. Wiggins, personal communication, 1970). At that time additional introduced weeds *(Atriplex semibaccata, Medicago polymorpha* var. *polymorpha, Sonchus oleraceus,* and *Xanthium spinosum)* were documented by the collections of LeRoy Abrams and I. L. Wiggins.

By 1939 several two- to three-meter *Eucalyptus* trees had grown for a time near the Landing Cove (Sumner & Bond, 1939, p. 15). Sumner & Bond (1939, p. 10) noted droppings of "former temporarily resident dogs". Cats were comparatively common, but only three rabbits were seen on the island (Sumner, 1958, p. 7; Reddick, 1939, p. 2). "Coreopsis in the unfarmed areas was at that time much more luxuriant than later" (Sumner, 1958, p. 4). During the spring of 1941 Mr. and Mrs. Clarence Fry spent one month on the island; they saw a total of 13 cats and two rabbits (Sumner, 1958, p. 7).

From 1942 through 1946 the island served as an aircraft early warning outpost and subsequently as a photographic tracking station; motor

vehicles were in use and an increase in dirt roadways resulted (G. H. Bowen, personal communication, 1968). Barracks, miscellaneous buildings, and additional boat loading facilities were constructed; even a few sheep were again placed temporarily on the island (Sumner, 1958, p. 7). At this time "New Zealand Red" rabbits were introduced (Sumner, 1958, p. 7). However, several years passed before these rabbits, *Oryctolagus,* caused any noticeable destruction of the vegetation.

In 1949 the island continued to support vigorous thickets of *Coreopsis* at about the same time as the road system was expanded to the Webster Point area and the currently-existing timber landing platform and cable car track were constructed (Reid Moran photographs, February 1949). *Coreopsis* to "a height of 8 or 10 feet" were noted at Landing Cove; "the whole east side of the island, up to an elevation of about 400 feet" was "covered with a dense forest" of these plants (P. C. Orr field notes, 9–11 February 1949). The following year, in 1950, only one cat and two rabbits were observed as Lowell Sumner began several years of observation on the interaction of Santa Barbara Island plants and animals. He reported that

> . . . the ecological effects of this new rabbit introduction were as yet scarcely evident. Two sub-adult rabbits were seen but the native "jungle" had reached such a peak of recovery that rabbit trails were almost invisible. . . . Large areas of Coreopsis which had been waist high in 1939 were head high in 1950. A younger generation was recapturing the old hayfield. . . . Extensive cactus patches . . . had been overwhelmed . . . by the spreading Coreopsis, morning glory, . . . and box thorn . . . (Sumner, 1958, p. 8).

Sumner's observations (1958, p. 4) indicate that 1952 was the approximate date of the rapid and destructive increase in the second rabbit population. The resulting decrease in *Coreopsis* and *Calystegia* and the related increase in *Mesembryanthemum* are shown in figure 13.

In 1953 the rabbits were conspicuously abundant, and the vegetation had seriously declined.

> Rabbits, all of the New Zealand Red strain, ran about in great numbers. The Coreopsis "jungle" had a stricken aspect. Many of the trees had been girdled and felled by the rabbits. . . . Throughout the thinning stands of survivors, bare ground showed everywhere through a shriveled carpet of dying vegetation. . . . This was because nearly all of the "forest" understory of low annuals, and of perennials such as the trailing morning glory, had been killed by the rabbits (Sumner, 1958, pp. 8–9).

There had been previous unofficial rabbit shooting on the island, and in October 1954 a rabbit control program was begun by the National Park Service and the U.S. Fish and Wildlife Service. At that time the

vegetation, even on nearly inaccessible cliffs, was spectacularly reduced by the gnawing of an estimated 712 rabbits.

> Living vegetation was so sparse that rabbit shooters could walk almost anywhere through the withering jungle. The rabbit population now so far exceeded the available burrows and concealing thickets that scores of the animals crouched in plain sight on the bare ground, taking advantage of any slight shade afforded by the surviving Coreopsis. Acres of box thorn [and] island sagebrush . . . had been exterminated. The giant morning glory was reduced to a few leafless, prostrate runners except where an occasional plant had been able to put out a few leaves beyond reach of the rabbits by climbing to the top of a still-standing Coreopsis (Sumner, 1958, p. 10).

In 1955 the estimated rabbit population reached 2,621; and the iceplant, *Mesembryanthemum crystallinum*, was rapidly increasing (fig. 13). That same year the rabbit control program was expanded to include strychnine poisoning.

> Iceplant . . . had staged a conspicuous, large-scale invasion of previously denunded ground and extended even beneath the Coreopsis, where it replaced the native wildflowers of earlier years (Sumner, 1958, p. 12).

Although the 1956 rabbit estimate was down to 727, this was still far too many; and the native vegetation declined even further while the introduced iceplant continued to spread.

> Coreopsis had been reduced by 25 to 30 percent through beavering, girdling and undermining. Wild cucumber, formerly common but not a preferred rabbit food, was reduced to an occasional small green runner. Morning glory, the best indicator of rabbit pressure, was so far gone that in three days the writer found only one plant that showed slight signs of current life. Small wild flowers seemed almost non-existent, and even the hardy Mediterranean grasses were greatly reduced. . . . Iceplant continued to spread enormously, forming dense carpets on most of the open ground outside of the Coreopsis patches. By now it had replaced most of the native plants and had even to a large extent replaced the dense wild oat stands in the former hayfield (Sumner, 1958, pp. 13–14).

The last known evidence of cats on Santa Barbara Island (Sumner, 1958, p. 17) is for the year 1957. During that year a continuation of the annual shooting and poisoning reduced the rabbit population to an estimated 560. Still the number was too high, and the vegetation continued to decline.
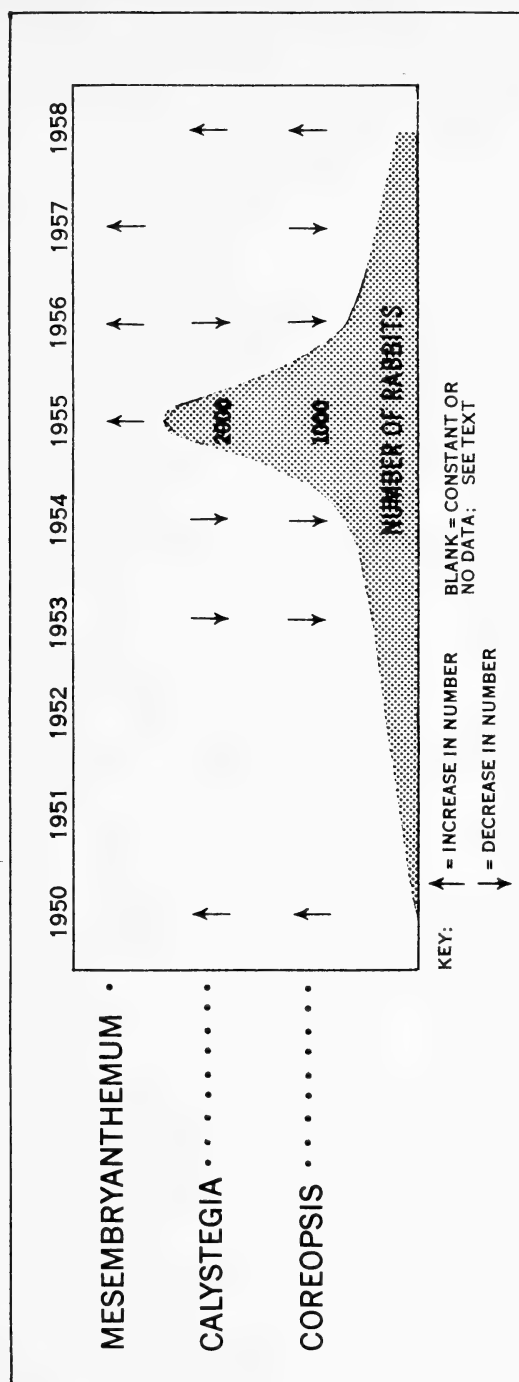
Fig. 13. Increase and decrease of three selected plants in relation to changes in the number of introduced rabbits on Santa Barbara Island. The rabbit population increased between 1950 and 1955. These animals drastically reduced the native populations of *Coreopsis gigantea* and *Calystegia macrostegia* thus allowing the area occupied by the relatively rabbit-resistant *Mesembryanthemum crystallinum* to increase spectacularly from 1955 through 1957. Rabbit poisoning was begun in 1955; this, in addition to increased rainfall, allowed the native vegetation to begin a modest recovery in 1958. (Data from Sumner, 1958, pp. 8–21.)

The vegetation . . . had suffered a decline even more pronounced than that of the rabbits. Approximately 50 percent of the Coreopsis was dead and prostrate. The bulk of the morning glories had been able to keep no leaves or runners, and appeared nearly dead. . . . Acres of box thorn appeared to be nearly dead. Even the brome grasses and wild oats were sparse; cheat grass was now the dominant surviving grass but had attained an average height of only 6 inches. . . . Iceplant had continued to make enormous gains, occupying nearly all ground laid bare by the rabbits. More than half the surface of the island now appeared covered by it . . . (Sumner, 1958, pp. 15–16).

In 1958 Sumner noted that the "song sparrows were still holding their own" (Sumner, 1958, p. 19); this is the last known field report of this endemic bird. Yet heavy rainfall and a further reduction in the number of rabbits combined to allow the vegetation to begin to recover (fig. 13).

Surviving Coreopsis were putting on a blazing show of golden yellow. . . . The first new young plants of this species since the rabbit outbreak were now observed. The number of such young plants was considerably less than $\frac{1}{2}$ of 1 percent of the total stand, and some of them had been partly eaten by rabbits. . . . Morning glory had revived appreciably, even in areas where most of the plants had, during the previous two years, appeared virtually lifeless. . . . Box thorn showed the first extensive development of new leaves in years, though approximately 35 percent of the original stand was dead. Island sagebrush exhibited strong recovery. Wild cucumber had revived. Annual wildflowers seen rarely or not at all since 1950 were common to profuse. . . . Wild oats [were] . . . waist and shoulder high. . . . The foxtail and brome grasses experienced a comparable resurgence. . . . Iceplant had attained astounding luxuriance and density, forming on 50 percent or more of the island a tough, slippery, wet barrier twelve to eighteen inches deep (!) very difficult for human beings to wade through and impenetrable to the rabbits (Sumner, 1958, pp. 17–18).

Then in the summer of 1959 an accidental fire covered most of the island. "It burned nearly all the vegetation from water's edge on the east shore of the island to the crest of the ridge where it was halted by the strong winds from the west slope. . . . Two-thirds of the island was denuded right down to mineral soil. . . . There were perhaps 30 rabbits left on the vegetated west slope; the others either were killed outright or could find nothing to eat" (Lowell Sumner, personal communication, 1970).

The Park Service has continued efforts to control the introduced rabbits. However, as even selective poisoning increases the risk to the native animals of the island, the main emphasis is now on shooting. To date, the rabbits have not been exterminated, and destruction of the vegetation continues.

Fishermen have stopped at the island for many years, and the Coast Guard has operated a lighthouse near the northeast corner of the island since 1929 (U.S. Coast Guard, Light list 3:32, 1969). Established as a National Monument in 1938, the island now has several hundred visitors each year. To the untrained eye there are only a few clues to the history of man's activities on Santa Barbara Island, but it is quite certain that the island would look very different today if domestic animals had never been introduced there.

SUMMARY AND CONCLUSION

The small flora of Santa Barbara Island, although sharing elements with other portions of California (especially with San Clemente Island), is of interest because of the accumulation of several unique plants during a period of less than a million years. These endemic plants are varieties of *Eriogonum* and *Platystemon* and a species of *Dudleya*.

In the last few decades native species of *Suaeda, Dudleya, Coreopsis,* and other genera have been drastically reduced on this island. In large part, they have been replaced by expansion of an introduced *Mesembryanthemum*.

Hopefully this paper will do more than serve as a demonstration of the influence of man, weeds, and introduced animals. Perhaps it will help urge preservation of the native plants and animals of Santa Barbara Island so that they remain available for further study, particularly from an evolutionary and ecological point of view.

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Meryl B. Dunkle's pioneer botanical study of Santa Barbara Island provided the major background for the present work.

LIST OF VASCULAR PLANTS

The specimens cited for each taxon are arranged geographically, starting with Arch Point, at the northeast corner of the island, and continuing more or less clockwise to Webster Point. Those cited without collector were collected by the author; those without herbarium are at the Santa Barbara Botanic Garden (SBBG). The angiosperm families are arranged according to Dalla Torre and Harms.

Polypodiaceae

POLYPODIUM CALIFORNICUM Kaulf.   Known only from Cave and Middle canyons. Rare, north exposure, rocky ledge, first canyon south [Cave Canyon], 20 March 1940, *Dunkle 7440* (LAM); triangular-shaped colony about 8 by 11 feet, upper of two populations, with *Marah, Coreopsis, Melica,* rock covered with few inches of soil, north-facing slope, middle Cave Canyon, 15 March 1969, *Philbrick & Ricker B69-34;* lower of two populations, north-facing slope, middle Cave Canyon, 15 March 1969, *Philbrick & Ricker B69-33;* about 50 yards from mouth of Middle Canyon, 5 May 1963, *Piehl 63-162* (SBBG, US). By transposition of column headings for Santa Catalina and Santa Barbara islands Dunkle (1950, p. 293) accidentally indicated several other ferns in the genera, *Polypodium, Pityrogramma, Adiantum, Pellaea,* and *Cheilanthes* as occurring on Santa Barbara Island.

Zosteraceae

PHYLLOSPADIX SCOULERI Hook.   Not reported by Dunkle or Sumner & Bond. Tidal pool below mouth of Graveyard Canyon, 22 May 1966, *Philbrick & Benedict B66-418;* low tide level, exposed surf, southwest portion of the Hook, Webster Point peninsula, 21 March 1970, *Philbrick & Benedict B70-35a.*

PHYLLOSPADIX TORREYI S. Wats.   Reported by Dunkle (1940, p. 2).

Low tide level, exposed surf, southwest portion of the Hook, Webster Point peninsula, 21 March 1970, *Philbrick & Benedict B70-35* (RSA, SBBG), determined by R. F. Thorne, 1970. One or both of the above species also have been collected near Cliff Canyon, Landing Cove, and Cave Canyon; however, positive identification could not be made from the material obtained. These taxa are very similar but differ in length of pistillate flowering stems, number of pistillate spadices per flowering stem, and shape of mature nutlets.

Gramineae

Avena barbata Pott ex Link.   Not reported by Dunkle or Sumner & Bond. Less common than *A. fatua,* exposed cliffs, Landing Cove, 5 May 1963, *Piehl 63-177;* scattered, north slope of Signal Peak, 4 May 1963, *Blakley 5674* (DS, SBBG).

Avena fatua L. (*A. f.* var. *glabrata* Peterm.).   Sumner & Bond (1939, pp. 12–13) indicated "noticeably abundant" or "dominant in some areas". Dunkle (1940, p. 2) reported: "A common grass on the east slopes where it forms large, well-defined colonies. It grows particularly rank above the head of the landing cove." This grass is still very common with *Amsinckia intermedia* over most of the East Slope of the island. No definite locality, 14 April 1939, *Bond 402* (SBM 14906, 14907); abundant, deep soil, Landing Cove, 21 March 1940, *Dunkle 7454* (LAM); middle of east-facing slope, Landing Cove, 18 March 1968, *B68-46* (MICH, RSA, SBBG, SD); south-facing slope, middle Cave Canyon, 15 March 1969, *Philbrick & Ricker B69-44.*

Bromus arizonicus (Shear) Steb. (*B. catharticus* Vahl of Dunkle, 1940; *B. marginatus* Nees of Dunkle, 1942).   For *B. catharticus,* Dunkle (1940, p. 3) reported: "In deep soil of the landing cove". For *B. marginatus,* he (Dunkle, 1942, pp. 128–129) indicated "only one locality known". Several locations in the northern portion of the island now known for *B. arizonicus,* but nowhere is it abundant. Interrupted irregular patch 15 by 30 feet, west of Cliff Canyon, opposite Shag Rock, 15 March 1969, *Philbrick & Ricker B69-55* (MICH, SBBG, US); few in colony, mesa slope east of North Peak, 4 May 1963, *Piehl 63-128* (RSA, SBBG); uncommon, deep soil, Landing Cove, 21 March 1940, *Dunkle 7455* (AHFH, LAM), determined by G. L. Stebbins, 1969, as an unusual form with flattened spikelets and short awns; middle of east-facing slope, Landing Cove, 18 March 1968, *B68-42;* north-facing slope, upper third of Cave Canyon, 27 April 1968, *Philbrick & McPherson B68-219;* clump, 1 foot in diameter, with *Eriogonum, Astragalus, Trifolium palmeri,* summit area, North Peak, 29 April 1969, *B69-68.* Also seen at Middle Canyon and West Slope. Distinguished from *B. carinatus*

H. & A. by the length of the upper glume about equalling that of the lowest lemma and by the relatively glabrous or short-pubescent dorsal surface of the lemma between the midrib and margin (Stebbins *et al.,* Proc. Calif. Acad. Sci., ser. 4, 25:307–322, 1944).

BROMUS DIANDRUS Roth (*B. rigidus* Roth of some authors).   For *B. rigidus,* Dunkle (1940, p. 3)reported: "A few plants grow along the trail from the landing cove." No recent collections are known. Occasional, canyon bank, east side Landing, 30 May 1939, *Dunkle 8139* (AHFH, LAM); common, rocky bank, east side Landing, 30 May 1939, *Dunkle 8141* (AHFH, LAM).

BROMUS MOLLIS L. (*B. hordeaceus* L. of some authors).   Not reported by Dunkle or Sumner & Bond; presently restricted to Landing Cove and adjacent areas. Scattered, under *Coreopsis,* beach bluffs, Landing Cove, 4 May 1963, *Blakley 5685* (MICH, SBBG, US); just north of middle Cave Canyon, 19 March 1968, *B68-64.* The Santa Barbara Island plant is not the taxon which has been treated by some as *B. molliformis* Lloyd.

BROMUS RUBENS L. (*B. sterilis* L. of Sumner & Bond, 1939; *B. orcuttianus* Vasey of Dunkle, 1940).   Sumner & Bond (1939, p. 12) indicated "noticeably abundant" or "dominant in some areas" for both *B. rubens* and *B. sterilis.* For *B. rubens,* Dunkle (1940, p. 3) reported: "A few plants along the trail from the landing"; for *B. orcuttianus,* he reported (1940, p. 3): ". . . shaded parts of canyon bottoms". No definite locality, 14 April 1939, *Bond 373* (SBM), as *"B. sterilis?";* no definite locality, 14 April 1939, *Bond 395* (SBM); short plants, dominant with *Avena fatua,* mesa slope east of North Peak, 4 May 1963, *Piehl 63-127* (SBBG, US); infrequent, rocky bluff, east side Landing, 30 May 1939, *Dunkle 8142* (AHFH); common, shaded bottom, second canyon south [Middle Canyon], 19 March 1940 *Dunkle 7423* (AHFH, LAM); south-facing slope, base of small rock cliff below fork of Graveyard Canyon, 27 April 1968, *Philbrick* & *McPherson B68-228;* common, with *Mesembryanthemum,* sides of Cat Canyon, 4 May 1963, *Blakley 5656* (MICH, SBBG); common, top of Signal Peak, 4 May 1963, *Blakley 5665* (CAS, SBBG, SD). Also seen at Cliff Canyon, Cave Canyon, North Peak, and West Slope.

{*Bromus sterilis* L.   Cited by Sumner & Bond (1939, p. 12), but this is probably based on *Bond 373,* which is *B. rubens.* According to Dunkle (1942, pp. 128–129) "only one locality known" for *B. sterilis;* this occurrence not confirmed although the species is reported for Santa Catalina Island.}

BROMUS TRINII Desv. [*B. vulgaris* (Hook.) Shear of Dunkle, 1940].

Presently confined to the northeast portion of the island. Scattered, exposed cliffs, Landing Cove, 5 May 1963, *Piehl 63-173;* near center of Cave Canyon, 4 May 1963, *Blakley 5619* (CAS, MICH, SBBG, US); infrequent, shaded side, second canyon south [Middle Canyon], 19 March 1940, *Dunkle 7424* (AHFH, LAM), as *B.. vulgaris;* south-facing slope, lower Middle Canyon, 15 March 1969, *Philbrick & Ricker B69-46* (MICH, SBBG, US).

HORDEUM GLAUCUM Steud. (*H. stebbinsii* Covas; *H. murinum* L., in part).   For *H. murinum,* Sumner & Bond (1939, p. 12) indicated "noticeably abundant" or "dominant in some areas". Dunkle (1940, p. 3) reported: "The most common and widespread grass on the island where it forms a vast mat on the eastern open slopes". Although abundant, this grass is now far less conspicuous than *Avena fatua* on the eastern half of the island. No definite locality, 14 April 1939, *Bond 400* (SBM); dominant plant of island, slopes, east side, 28 May 1939, *Dunkle 8108* (AHFH, LAM); few, mesa slope east of North Peak, 4 May 1963, *Piehl 63-126;* with *Avena, Bromus rubens,* middle of east-facing slope, Landing Cove, 18 March 1968, *B68-48;* terrace just south of lower Middle Canyon, 15 March 1969, *Philbrick & Ricker B69-38* (RSA, SBBG); forming large grassy areas, north slope of Signal Peak, 4 May 1963, *Blakley 5673* (CAS, SBBG); west-facing slope between North Peak and Signal Peak, 12 June 1964, *B64-10* (MICH, SBBG, US). Also seen at Cliff Canyon, Cave Canyon, North Peak, West Slope, and Webster Point. Distinguished from *H. leporinum* Link, by length of cilia on rachis segment margin and by length of prolongation of lateral spikelet rachilla (Covas, Madroño 10:1–21, 1949).

HORDEUM PUSILLUM Nutt.   Not reported by Dunkle or Sumner & Bond. Primarily restricted to the terrace slopes near the eastern canyons. North of middle Cave Canyon, west of buildings, 19 March 1968, *B68-65;* few, exposed cliffs, Landing Cove, 5 May 1963 *Piehl 63-172;* head of Graveyard Canyon near road, 27 April 1968, *Philbrick & McPherson B68-232.*

LAMARCKIA AUREA (L.) Moench.   Infrequent, open slope, east side, 28 May 1939, *Dunkle 8124* (LAM); few, scattered, mesa slope east of North Peak, 4 May 1963, *Piehl 63-125* (MICH, SBBG); terrace just north of Landing Cove, 18 March 1968, *B68-29* (CAS, SBBG, US); uncommon, openings among *Coreopsis* near Camp [Landing Cove], 21 March 1940, *Dunkle 7458* (LAM); few, scattered, sea cliff, mouth of Middle Canyon, 5 May 1963, *Piehl 63-154;* between Middle and Graveyard canyons, 21 May 1966, *Philbrick & Benedict B66-365.* Also seen in Cave Canyon.

MELICA IMPERFECTA Trin.   Presently confined to Cave and Middle

canyons. Common, north[-facing] slope, head of Cave Canyon, 4 May 1963, *Blakley 5611* (DS, SBBG); common, north[-facing] slope near center of Cave Canyon, 4 May 1963, *Blakley 5620* (DS, SBBG); common locally, shaded bottom, second canyon south [Middle Canyon], 20 March 1940, *Dunkle 7438* (LAM).

MUHLENBERGIA MICROSPERMA (DC.) Kunth.   Presently restricted to the eastern portion of the island. No definite locality, 14 May 1940, *Bond 506* (SBM); rocky ledge, northern edge of upper Landing Cove, 18 March 1968, *B68-30;* few, canyon bottom, head of Cave Canyon, 4 May 1963, *Blakley 5614;* common, south exposure, second canyon south [Middle Canyon], 19 March 1940, *Dunkle 7421* (LAM); south-facing slope, north fork of Graveyard Canyon, 27 April 1968, *B68-230;* southwest-facing slope, east of Sutil Island, 16 March 1969, *Philbrick & Ricker B69-60* (CAS, SBBG, US).

PARAPHOLIS INCURVA (L.) C. E. Hubb.   Only one location known; not reported by Dunkle or Sumner & Bond. Luxuriant, interrupted patch, 3 by 25 feet, oriented along contour at irregular narrow interface above *Lasthenia* and below *Mesembryanthemum crystallinum,* northwest-facing slope, north base of Webster Point peninsula between point and North Peak, 29 April 1969, *B69-81* (CAS, MICH, SBBG, US), *B69-82* (SBBG).

PHALARIS MINOR Retz.   "Noticeably abundant" or "dominant in some areas" (Sumner & Bond, 1939, pp. 12–13). Few, small eroded gully, Landing Cove, 4 May 1963, *Blakley 5680* (CAS, SBBG, SD); southwest of buildings between Landing Cove and Cave Canyon, 21 May 1966, *Philbrick & Benedict B66-370;* north-facing slope, middle of Cave Canyon, 27 April 1968, *Philbrick & McPherson B68-211* (MICH, SBBG, US). Also seen in Middle Canyon.

POLYPOGON MONSPELIENSIS (L.) Desf.   To date found only in the Landing Cove area. Rare, lava crevices above high tide, east Landing, 30 May 1939, *Dunkle 8148* (AHFH); few, north[-facing] cliff near tramway track, Landing Cove, 21 October 1961, *Blakley 4791;* north-facing rocky cliff just east of wooden platform, Landing Cove, 21 March 1970, *Philbrick & Benedict B70-44.*

STIPA PULCHRA Hitchc. [*S. lepida* Hitchc. var. *andersonii* (Vasey) Hitchc. of Dunkle, 1940].   Now known only from scattered locations in the central portion of the island. With *Calystegia, Amblyopappus, Opuntia prolifera,* above fork in upper Graveyard Canyon, 19 March 1968, *B68-83* (MICH, SBBG, US); canyon head [Cat Canyon], south side, 28 May 1939, *Dunkle 8109* (LAM); west-facing slope between North Peak and Signal Peak, 12 June 1964, *B64-7.*

VULPIA MEGALURA (Nutt.) Rydb. (*Festuca megalura* Nutt.).   Primarily confined to the eastern canyon area. Common, rocky bank, east side Landing, 30 May 1939, *Dunkle 8140* (LAM); beach bluffs, Landing Cove, 4 May 1963, *Blakley 5684* (DS, SBBG); trough of Cave Canyon, 5 May 1963, *Piehl 63-150a;* common, bottom of center Middle Canyon, 4 May 1963, *Blakley 5643* (DS, SBBG); north-facing slope, extreme upper north fork, Graveyard Canyon, 27 April 1968, *Philbrick & McPherson B68-231.*

VULPIA OCTOFLORA (Walt.) Rydb. (*Festuca octoflora* Walt.).   Not reported by Dunkle or Sumner & Bond. Now known from the eastern canyons. More or less exposed cliff, Landing Cove, 4 May 1963, *Piehl 63-144* (MICH, SBBG, US); dense colony, sea cliff, mouth of Middle Canyon, 5 May 1963, *Piehl 63-156* (MICH, SBBG, US). For both of these specimens the maximum hair length on the dorsal surface of the lemma is 0.2 mm, as opposed to about 0.3 mm for San Clemente Island and about 0.1 mm for San Miguel Island.

Liliaceae

DICHELOSTEMMA PULCHELLUM (Salisb.) Heller [*Brodiaea pulchella* (Salisb.) Green, *B. capitata Benth.*].   For *B. capitata,* Dunkle (1940, p. 4) reported: "Rather generally scattered over the entire island". Today known primarily from the eastern portion of the island. West of Cliff Canyon, opposite Shag Rock, 15 March 1969, *Philbrick & Ricker B69-56;* south-facing slope, lower-middle Cliff Canyon, 15 March 1969, *Philbrick & Ricker B69-49;* Landing Cove, 18 March 1968, *B68-59;* north-facing slope near mouth of Middle Canyon, 15 March 1969, *Philbrick & Ricker B69-39;* junction of forks, Graveyard Canyon, 15 March 1969, *Philbrick & Ricker B69-35;* abundant, hillside, west end, 18 March 1940, *Dunkle 7419* (AHFH, LAM). Also seen at Cave Canyon and North Peak.

Moraceae

CANNABIS SATIVA L.   Not reported by Dunkle or Sumner & Bond. Tight cluster of two-leafed seedlings germinating from apparent animal seed cache, north-facing slope, lower Middle Canyon, 23 March 1968, *B68-76.*

Urticaceae

HESPEROCNIDE TENELLA Torr.   Not reported by Dunkle or Sumner

& Bond. Found only in Cave Canyon. Noted only once, under other vegetation, south bank of Cave Canyon, 5 May 1963, *Piehl 63-152.*

PARIETARIA HESPERA Hinton *(P. floridana* Nutt. of some authors).
Known primarily from the northeast portion of the island. Cliff Canyon, 18 March 1968, *B68-36;* east-facing slope just south of Landing Cove, 15 March 1969, *Philbrick & Ricker B69-43;* few, shade, crevices of rocky cliff near center of Cave Canyon, 4 May 1963, *Blakley 5624* (CAS, SBBG); infrequent-rare, shade of *Coreopsis,* bottom of second canyon south [Middle Canyon], 19 March 1940, *Dunkle 7422* (AHFH, LAM); common, cactus patch, head of Graveyard Canyon, 21 March 1940, *Dunkle 7448* (AHFH, LAM); with *Crassula,* upper northwest slope of North Peak, 13 February 1970, *B70-2.* For information on two proposed varieties of this species, see Hinton (Sida 3:293–297, 1969).

Polygonaceae

{*Eriogonum arborescens* Greene.   Reported by Davidson & Moxley (Flora S. Calif., p. 111, 1923) for "Santa Barbara and Santa Cruz Islands". The occurrence on the former island is doubtful.}

ERIOGONUM GIGANTEUM var. COMPACTUM Dunkle (*E. giganteum* subsp. *giganteum* of Raven, Proc. Symp. Biol. Calif. Islands, p. 60, 1967).
See figure 4 in introductory text. "On sea bluffs, especially common on the north-west side" (Dunkle, 1940, p. 4). "Locally common on north, south, and east bluffs" (Dunkle, 1950, p. 327). Known primarily from the more inaccessible sea cliffs. No definite locality, August 1901, *Snodgrass s.n.* (DS 491714); no definite locality, 3 July 1931, *Abrams & Wiggins 311* (DS); low compact shrub about ⅓ to ½ m high, with *Cryptantha maritima, Atriplex californica,* east-facing sea bluff north of Cliff Canyon, 27 April 1968, *Thorne 37545* (SD); shallow soil, bluff, Landing Cove, 27 September 1941, *Dunkle 8704* (LAM, type); with *Coreopsis,* shady beach bluff, Landing Cove, 22 October 1961, *Blakley 4812* (MICH, SBBG, SD); few, rocky outcropping, mouth of Middle Canyon, 22 October 1961, *Blakley 4815* (MICH, SBBG, US); rare, rocky sea bluff, south end, 28 May 1939, *Dunkle 8103* (LAM); rounded shrub about 2 feet tall, common, undisturbed area, south slope [of Signal Peak], 10 February 1949, *Moran 3157* (DS, SD, UC); regenerating plant having only small new leaves, with few normal individuals nearby, upper northwest slope of North Peak, 13 February 1970, *B70-5;* base of south side of Webster Point, 4 May 1963, *Piehl 63-119;* south-facing slope, halfway up west ridge, Sutil Island, 20 March 1968, *B68-86.* Endemic taxon restricted to Santa Barbara Island but closely related to the subspecies of Santa Catalina (*E. g.* subsp. *giganteum*) and of San Clemente (*E. g.* subsp. *formosum*) islands. "This plant formerly reported

as *E. giganteum* Wats. has such differing characteristics from the species as to warrant raising it to the varietal rank. The plant differs from the species in being lower, 4–6 dm. tall, much more compacted and with the pubescence at the base of the plant, the lower side of the leaves, and the inflorescence much more densely white-wooly. The peduncle is first 3-branched, then usually 2-branched, with the ultimate branches very short, .2–2.5 cm. long. The inflorescence is compacted into from 3 to 9 very compacted, subcapitate clusters. The involucres are sessile. Dunkle No. 8704" (Dunkle, 1942, p. 130, type description).

{*Eriogonum grande* Greene.   Accidentally indicated (Dunkle, 1950, p. 293) as dominant on Santa Barbara Island by transposition of column headings for Santa Catalina and Santa Barbara islands. Not known for the latter island.}

Pterostegia drymarioides F. & M.   Known primarily from the northern portion of the island. Frequent, cliff, Landing Cove, 4 May 1963, *Piehl 63-145;* common, around rocks and under *Coreopsis,* head of Cave Canyon, 4 May 1963, *Blakley 5616;* infrequent, hillside, west end, 18 March 1940, *Dunkle 7414* (LAM). Also seen at Cliff Canyon, Middle Canyon, Graveyard Canyon, and North Peak.

Chenopodiaceae

Aphanisma blitoides Nutt. ex Moq. (*Atriplex rosea* L. of Dunkle, 1940).   Reported by Jepson (Flora Calif. 1:430, 1914). The two collections, which Dunkle (1940, p. 5) cited for *Atriplex rosea,* are *Aphanisma blitoides.* The latter species was also reported by Dunkle (1940, p. 4) but apparently on the basis of these same two collections. *Aphanisma blitoides* is now known from scattered south- and west-facing locations. Uncommon, dry south exposure, Landing Cove, 21 March 1940, *Dunkle 7459* (AHFH, LAM), as *Atriplex rosea;* few colonies, open slope, Landing Cove, 4 May 1963, *Piehl 63-142* (SBBG, SD); scattered, south[-facing] slope, Cave Canyon, 4 May 1963, *Blakley 5612* (MICH, RSA, SBBG); just south of Graveyard Canyon, 19 March 1968, *B68-81;* west-facing slope, Cat Canyon, 22 May 1966, *Philbrick & Benedict B66-413;* rare, flat terrace, west end, 18 March 1940, *Dunkle 7416* (AHFH, LAM), as *Atriplex rosea.* Also seen at East Slope and Middle Canyon.

Atriplex californica Moq.   Known from widely scattered locations; most conspicuous in the Cliff Canyon area. Common, rocky sea bluff, east coast, 28 May 1939, *Dunkle 8119* (LAM); forming mats, scattered, east terrace, 21 October 1961, *Blakley 4810;* gray clumps, common, rocky areas, Cliff Canyon, 5 May 1963, *Blakley 5698;* one

plant among rocks and chollas, between Cat Canyon and Signal Peak, 4 May 1963, *Blakley 5659* (MICH, SBBG); abundant, cliff ledge, "Brewster Point" [Webster Point], 18 March 1940, *Dunkle 7410* (LAM). Also seen at Landing Cove.

ATRIPLEX SEMIBACCATA R. Br.   No definite locality, 3 July 1931, *Abrams* & *Wiggins 287* (DS); abundant, slope, east side, 28 May 1939, *Dunkle 8123* (AHFH); scattered, cliff west of Arch Point, 21 October 1961, *Blakley 4792* (CAS, SBBG, US); Cliff Canyon, 18 March 1968, *B68-23* (SBBG, SD); terrace just north of Landing Cove, near shell mound, 18 March 1968, *B68-27* (MICH, SBBG); scattered, near center of Middle Canyon, 4 May 1963, *Blakley 5644* (RSA, SBBG); bluff due north of North Peak, 21 May 1966, *Philbrick* & *Benedict B66-378* (RSA, SBBG); south-facing slope just below summit, Sutil Island, 20 March 1968, *B68-90* (MICH, SBBG, US). Also seen at Cave Canyon, Cat Canyon, West Slope, Webster Point, and rock off Webster Point. By transposition of column headings Dunkle (1950, p. 293) accidentally indicated three additional species of *Atriplex* as occurring on Santa Barbara Island.

{*Chenopodium album* L.   Cited by Sumner & Bond (1939, p. 13); this occurrence is doubtful.}

CHENOPODIUM CALIFORNICUM (S. Wats.) S. Wats.   Known primarily from the northeast portion of the island. Infrequent, north slope, east side, 28 May 1939, *Dunkle 8116* (LAM); common, deep soil, Landing Cove, 21 March 1940, *Dunkle 7453* (LAM); north[-facing] slope near center of Cave Canyon, 4 May 1963, *Blakley 5621;* semi-shade under *Coreopsis,* rocky north[-facing] slope, Middle Canyon, 22 October 1961, *Blakley 4816.*

CHENOPODIUM MURALE L.   No definite locality, August 1901, *Snodgrass s.n.* (DS 16844), determined by H. A. Wahl, 1965; no definite locality, 3 July 1931, *Abrams* & *Wiggins 291* (DS), determined by H. A. Wahl, 1965; locally common, grassy terraces with *Mesembryanthemum crystallinum,* east side, 28 May 1939, *Dunkle 8100* (AHFH, LAM); few, edge of cliff, west of Arch Point, 21 October 1961, *Blakley 4795* (CAS, SBBG); abundant, deep soil, Landing Cove, 21 March 1940, *Dunkle 7456* (LAM); scattered, north[-facing] slope, base of cliff, mouth of Cave Canyon, 4 May 1963, *Blakley 5631* (RSA, SBBG); scattered, north[-facing] slope, Graveyard Canyon, 21 October 1961, *Blakley 4806* (SBBG, SD); scattered, rocky top of beach bluff between Graveyard and Cat canyons, 4 May 1963, *Blakley 5654;* west-facing slope between North Peak and Signal Peak, 12 June 1964, *B64-8;* south-facing slope just below summit, Sutil Island, 20 March 1968, *B68-89*

(MICH, SBBG, US). Also seen at Cliff Canyon, Middle Canyon, Cat Canyon, Webster Point, and rock off Webster Point.

SUAEDA CALIFORNICA S. Wats. (*S. c.* var. *pubescens* Jeps., *S. taxifolia* Standl.).   For *S. californica* var. *pubescens,* Dunkle (1940, p. 5) reported: "Forms large clumps in various parts of the mesa". The number and vigor of these populations have declined since 1968. Dry hillsides, 12 August 1938, *Elmore 302* (AHFH); abundant, sea cliff summits, east side, 28 May 1939, *Dunkle 8114* (AHFH, LAM); mesa slope east of North Peak, 4 May 1963, *Piehl 63-129* (CAS, SBBG), subglabrous; bluff between Cat Canyon and Sutil Island, 22 May 1966, *Philbrick & Benedict B66-417* (CAS, SBBG); few, top of Signal Peak, 4 May 1963, *Blakley 5664* (MICH, RSA, SBBG); west-facing slope between North Peak and Signal Peak, 12 June 1964, *B64-9* (SBBG, SD); summit of North Peak, 21 May 1966, *Philbrick & Benedict B66-382* (RSA, SBBG), very pubescent; common, west terrace near Webster Point, 21 October 1961, *Blakley 4800* (MICH, SBBG); south-facing slope just above sea spray, Sutil Island, 20 March 1968, *B68-85* (MICH, SBBG). Also seen in Cliff Canyon. Specimens differ conspicuously in amount of pubescence.

Nyctaginaceae

MIRABILIS LAEVIS (Benth.) Curran.   Restricted to the southern portion of the island. Rare, rock bluff, south end, 28 May 1939, *Dunkle 8107* (LAM); locally common, rocky sea bluffs, south point, 19 March 1940, *Dunkle 7433* (LAM); south-facing slope just east of middle Cat Canyon, 19 March 1968, *B68-80* (RSA, SBBG); few, rocky crevices, west side of Cat Canyon, 4 May 1963, *Blakley 5657* (MICH, SBBG, US).

Aizoaceae

MESEMBRYANTHEMUM CRYSTALLINUM L. [*Cryophytum crystallinum* (L.) N.E. Br., *Gasoul crystallinum* (L.) Rothm.].   See figure 10b in introductory text. Although Dunkle (1940, p. 5) reported *M. crystallinum* as "abundant on all slopes" and "forming large colonies that may be seen as dark patches from many miles at sea", this species now is dominant over even larger portions of the island. See discussion in introductory text. No definite locality, 3 July 1931, *Abrams & Wiggins 307* (DS); abundant, covering large areas, open slope, east side, 30 May 1939, *Dunkle 8146* (AHFH, LAM); common, among *Coreopsis,* many more dead than living plants, slope east of North Peak, 4 May

1963, *Piehl 63-139;* cliff west of Arch Point, common all over the island, 21 October 1961, *Blakley 4793;* lower part of small canyon between Landing Cove and Cliff Canyon, 15 March 1969, *Philbrick & Ricker B69-47;* abundant, forming dense colonies, south side of North Peak, 5 May 1963, *Blakley 5711;* west-facing slope between North Peak and Signal Peak, 12 June 1964, *B64-12;* south-facing slope, rocky ledge just east of summit, Sutil Island, 20 March 1968, *B68-91.* Also seen at Cliff Canyon, Landing Cove, Cave Canyon, Middle Canyon, Cat Canyon, Signal Peak, Webster Point, and rock off Webster Point. The correct generic name for this and the following species is uncertain. Pending a decision involving typification and possibly conservation, the best known name has been used here. "Ice-plant" on Santa Barbara Island was mentioned by Britton (1897, p. 194) and by Grinnell (Pasadena Acad. Sci. Publ. 1:5, 1897). Except for Anacapa and San Nicolas, islands which were not extensively worked by the earlier collectors, *M. crystallinum* was reported for all of the islands from San Miguel to Natividad by the year 1900. *Mesembryanthemum nodiflorum,* on the other hand, spread more slowly.

MESEMBRYANTHEMUM NODIFLORUM L. [*Mesembryanthemum* sp. of Sumner & Bond, 1939; *Cryophytum nodiflorum* (L.) L. Bolus; *Gasoul nodiflorum* (L.) Rothm.]. For *M.* sp., Sumner & Bond (1939, pp. 12–13) indicated "noticeably abundant" or "dominant in some areas". No definite locality, 3 July 1931, *Abrams & Wiggins 289* (DS); dry field, 12 August 1938, *Elmore 310* (AHFH); common, old road, east coast, 28 May 1939, *Dunkle 8121* (AHFH); abundant, open slopes, east side, 30 May 1939, *Dunkle 8147* (AHFH, LAM); few, cliff west of Arch Point, 21 October 1961, *Blakley 4794;* scattered colonies, exposed cliffs, Landing Cove, 5 May 1963, *Piehl 63-182;* common in bare areas, ridge top between North Peak and Signal Peak, 5 May 1963, *Blakley 5708;* west-facing slope between North Peak and Signal Peak, 12 June 1964, *B64-13;* south-facing slope, rocky ledge just east of summit, Sutil Island, 20 March 1968, *B68-92.* Also seen at Cat Canyon and Signal Peak. Much less abundant than *M. crystallinum* on this island and less adapted or slower to reach many of the off-shore islands. On the basis of the published record, *M. nodiflorum* reached the Southern California islands of San Nicolas, Santa Catalina, and San Clemente before 1899 but probably did not reach the more northern islands from San Miguel to Santa Barbara until 1930 to 1950. It was reported about the same time, 1932 to 1949, from Guadalupe, San Benito, and Cedros islands but apparently did not reach Los Coronados, Todos Santos, or Natividad until approximately 1968 to 1971 when it was first collected on these three islands by the Santa Barbara Botanic Garden. This plant is not yet known to have been documented from San Martin or San Geronimo. It is probable, therefore, that *M. nodiflorum* is still extending its range in this portion of the world.

Portulacaceae

CALANDRINIA CILIATA var. MENZIESII (Hook.) Macbr.   Not reported by Dunkle or Sumner & Bond. To date known only from the northeast portion of the island. Few plants, head of Cliff Canyon, 4 May 1963, *Piehl 63-134;* tops eaten off, rare, rocky ledge, beach bluffs, Landing Cove, 4 May 1963, *Blakley 5688;* east-facing slope, north edge of Landing Cove, 15 March 1969, *Philbrick & Ricker B69-54* (MICH, SBBG, US).

CALANDRINIA MARITIMA Nutt.   Found only in the eastern portion of the island. Infrequent, gravelly soil, north ridge, 17 March 1940, *Dunkle 7406* (LAM); one plant, head of Cliff Canyon, 4 May 1963, *Piehl 63-133;* south-facing slope, upper Cave Canyon, 19 March 1968, *B68-67;* between Middle and Graveyard canyons, 19 March 1968, *B68-73;* uncommon, dry rocky soil, southeast bluffs, 19 March 1940, *Dunkle 7432* (LAM). Also seen in Middle and Graveyard canyons.

CLAYTONIA PERFOLIATA Donn [*Montia perfoliata* (Donn) Howell]. Known primarily from the northern portion of the island. Infrequent, rocky shallow soil, north exposure, east canyons, 17 March 1940, *Dunkle 7407* (LAM); common, shady bank, Landing Cove, 21 March 1940, *Dunkle 7457* (LAM); exposed cliffs, Landing Cove, 5 May 1963, *Piehl 63-168;* few, north[-facing] slope, rock crevices near center of Cave Canyon, 4 May 1963, *Blakley 5623.* Also seen at Cliff Canyon, Middle Canyon, Graveyard Canyon, North Peak, and West Slope.

Caryophyllaceae

SILENE GALLICA L.   Dunkle (1940, p. 5) reported: "Common along the trail from the landing cove"; and this species was not seen beyond that portion of the island until 1970. Infrequent, rocky bluff, east side Landing, 30 May 1939, *Dunkle 8143* (AHFH, LAM); few, shade under *Coreopsis,* beach bluffs, Landing Cove, 4 May 1963, *Blakley 5693;* largest flowers white, 11 mm diameter, smallest flowers pink, 4 mm diameter, probably open pink and age white as petals expand, exposed north-facing slope just above wooden platform, Landing Cove, 21 March 1970, *Philbrick & Benedict B70-32* (RSA, SBBG); with *Microseris, Rafinesquia, Pholistoma a.* var. *auritum,* north-facing slope, trough of middle-lower Middle Canyon, 22 March 1970, *Philbrick & Benedict B70-48.*

SPERGULARIA MACROTHECA (Hornem.) Heynh. var. MACROTHECA. Known only from a few locations. Rare, dry terrace, east side, 28 May 1939, *Dunkle 8110* (AHFH); 20 plants seen, east terrace, opposite

Shag Rock, 21 March 1970, *Philbrick* & *Benedict B70-33;* rare, about 8 plants, bare exposed rocky soil, Arch Point, 5 May 1963, *Blakley 5703* (MICH, SBBG, SD); infrequent, grassy slope, west side, 29 May 1939, *Dunkle 8130* (AHFH, LAM). By transposition of column headings Dunkle (1950, p. 293) accidentally indicated another species of *Spergularia* as occurring on Santa Barbara Island.

Papaveraceae

ESCHSCHOLZIA RAMOSA (Greene) Greene (*E. elegans* Greene of Dunkle, 1942, 1950).   For *Eschscholzia elegans,* Dunkle (1942, pp. 128, 131) indicated "not found in recent years or very local". In 1950 (p. 327) he reported: "A single plant on south exposure of Cave Canyon". Now known from both Cave and Graveyard canyons. Rare, arroyo south of east Landing [Cave Canyon], 27 April 1941, *Moran 829* (DS); few plants, south-facing slope, middle Cave Canyon, 18 March 1968, *B68-68,* determined by W. R. Ernst, 1968; south-facing slope, base of small rock cliff below fork in Graveyard Canyon, 27 April 1968, *Philbrick* & *McPherson B68-229.* According to W. R. Ernst (personal communication, 1968) *E. ramosa* is distinguished from *E. elegans* by its "shorter divisions of the leaves which diverge at a broader angle", by the ultimate leaf divisions which are "more likely to be quite blunt distally", and by the corollas which tend "to be smaller than in *E. elegans".*. Both of these taxa are insular endemics, and both occur on Guadalupe Island. *E. elegans* is restricted to that island while *E. ramosa* has been documented for all but four of the islands from Santa Rosa to Cedros (excluding Anacapa, San Nicolas, San Martin, and San Geronimo).

PLATYSTEMON CALIFORNICUS var. CILIATUS Dunkle (*P. ornithopus* Greene of Jepson, Flora Calif. 1:557, 1922; *P. aculeolatus* Greene; *P. setosus* Greene).   See figure 6 in introductory text. Presently known only from the northeast portion of the island. No definite locality, "only plant found: the flora was mostly seed", May 1901, *Trask s.n.* (CAS 969), type or isotype of *P. aculeolatus;* no definite locality, "infrequent, but many dried plants. fl's cream", May 1902, *Trask 11* (CAS 971, ND-G 3727), type and isotype of *P. setosus;* locally common, gravelly soil, northwest coast, 17 March 1940, *Dunkle 7400* (LAM); common locally, not found elsewhere, head of Cliff Canyon, 4 May 1963, *Piehl 63-130* (MICH, SBBG); few, bare rocky area near beach bluff, Arch Point, 5 May 1963, *Blakley 5700* (CAS, RSA, SBBG, SD, US); down-wind from main population, with *Amsinckia,* between North Peak and mouth of Cliff Canyon, 30 April 1969, *B69-98.* The collections from Santa Barbara Island all represent the same taxon, which is endemic to a portion of this small island. However, the original descriptions of

P. aculeolatus (Greene, Pittonia 5:167, 1903), *P. setosus* (Greene, Pittonia 5:194, 1903), and *P. californicus* var. *ciliatus* (Dunkle, Bull. S. Calif. Acad. Sci. 39:177, 197, 1940) are each inaccurate to a certain degree; they occasionally disagree with the specimens being described or emphasize only a part of the total variation existing in the population. The plants cited above may be described in part as follows: Usually a branched cespitose leafy annual; leaves sparsely ciliate-denticulate, usually with scattered hairs of less than 1 mm on the upper and lower surface; pedicels with similar scattered hairs, less than 7 cm long, usually over-topping the foliage by less than 3 cm; flower diameter 10 to 17 mm; sepals dorsally pubescent to subglabrous; petals white or very light cream; mature fruit torulose, 5 to 11 mm long, with up to 8 joints in each of 8 to 12 carpels. *Platystemon californicus* is a notoriously complex and variable species; however, *P. c.* var. *ciliatus* is distinct both morphologically and geographically.

STYLOMECON HETEROPHYLLA (Benth.) G. Tayl. [*Papaver heterophyllum* (Benth.) Greene of Sumner & Bond, 1939, and Dunkle, 1942, 1950].
Reported by Sumner & Bond (1939, p. 13), otherwise known only from two locations in the northeast portion of the island. North-facing slope, Landing Cove, 28 April 1968, *Philbrick & Thorne B68-240*. Also photographed in upper Cliff Canyon by M. R. Benedict (personal communication, 1971).

Cruciferae

BRASSICA NIGRA (L.) Koch.   "One plant along the trail above the cabin" (Dunkle, 1940, p. 6). One plant only, gentle slope, Camp [Landing Cove], 21 March 1940, *Dunkle 7445* (AHFH, LAM). Known only from this collection, which consists of a few shoots (the longest of which is 33 cm), a few small clusters of flower buds, and one flower. Without fruit, the determination is uncertain.

HUTCHINSIA PROCUMBENS (L.) Desv.   Not reported by Dunkle or Sumner & Bond. So far known only from one collection in Landing Cove. Shallow soil, level excavated area immediately west of landing platform, Landing Cove, 22 March 1970, *Philbrick & Benedict B70-45*, determined by C. L. Hitchcock, 1970.

LEPIDIUM NITIDUM Nutt. var. NITIDUM.   Conspicuous in several scattered locations. Few plants, mesa slope east of North Peak, 4 May 1963, *Piehl 63-124;* dense tufts, base of Arch Point, 4 May 1963, *Piehl 63-141;* common, grassy protected areas near top of Signal Peak, 4 May 1963, *Blakley 5667* (CAS, MICH, RSA, SBBG); few, with weedy

grasses, ridge top between North Peak and Signal Peak, 5 May 1963, *Blakley 5707;* common, hillside, west end, 18 March 1940, *Dunkle 7413* (LAM). Also seen in Graveyard Canyon.

THELYPODIUM LASIOPHYLLUM (H. & A.) Greene var. LASIOPHYLLUM [*Caulanthus lasiophyllum* (H. & A.) Payson]. Not reported by Dunkle or Sumner & Bond, but apparently now spreading throughout the eastern portion of the island. Terrace just north of Landing Cove, near shell mound, 18 March 1968, *B68-24* (MICH, SBBG, US); north rim of lower Graveyard Canyon, 21 May 1966, *Philbrick & Benedict B66-383;* east of Signal Peak, between Graveyard Canyon and Cat Canyon, 19 March 1968, *B68-78.* Also seen in Middle Canyon.

Resedaceae

OLIGOMERIS LINIFOLIA (Vahl) Macbr. (*O. subulata* Del. ex Webb). Reported by Dunkle (1950, p. 311). Now known from scattered locations throughout much of the island, but most conspicuous in the northeast portion. Rare, sun, exposed beach bluff north side of North Peak, 5 May 1963, *Blakley 5704* (SBBG, SD); wind-stunted, just southeast of lighthouse between Arch Point and Cliff Canyon, 18 March 1968, *B68-22;* bluff due west of mouth of Cliff Canyon, 21 May 1966, *Philbrick & Benedict B66-376* (SBBG, US); scattered, northern sea cliff, mouth of Middle Canyon, 5 May 1963, *Piehl 63-157* (CAS, MICH, SBBG); first small canyon north of Graveyard Canyon, 21 May 1966, *Philbrick & Benedict B66-368* (MICH, SBBG); few, bare eroded area near top of Signal Peak, 4 May 1963, *Blakley 5662* (RSA, SBBG); west mesa between Webster Point and Arch Point, 4 May 1963, *Piehl 63-120.* Some doubt has been raised that California is within the native range of *O. linifolia;* however, according to H. C. D. de Wit (personal communication, 1970) *O. linifolia* "very certainly is indigenous in California".

Crassulaceae

CRASSULA ERECTA (H. & A.) Berger (*Tillaea erecta* H. & A.). Noted only in the northern portion of the island. Small dense reddish mats, abundant, beach bluffs, Landing Cove, 4 May 1963, *Blakley 5689;* few, north[-facing] slope, head of Middle Canyon, 4 May 1963, *Blakley 5636;* with *Parietaria,* upper northwest slope of North Peak, 13 February 1970, *B70-3;* common, slope, west end, 18 March 1940, *Dunkle 7411* (LAM). Also seen in Cave Canyon.

DUDLEYA TRASKIAE (Rose) Moran [*Stylophyllum traskae* Rose; *Coty-*

ledon traskeae (Rose) Fedde; *Echeveria traskae* (Rose) Berger; *E. greenei* (Rose) Berger of Dunkle, 1940, 1950; *E. albida* (Rose) Berger of Dunkle, 1940, 1942]. See figure 5 in introductory text. Moran (Ph.D. Thesis, Univ. Calif., Berkeley, p. 73, 1951) "saw only two colonies, one on the south slope and one on the west"; Dunkle (1950, p. 328) also reported only these same two populations. Subsequently this plant was found in the eastern canyons; the western population was eliminated prior to 1962. This taxon has been found only on Santa Barbara Island, and it is now thought to be extinct in the wild because all attempts to locate live plants failed in 1970. South-facing slope, lower Cave Canyon, 27 April 1968, *Philbrick & McPherson B68-207;* local and rare, with *Opuntia,* side of Middle Canyon, 22 October 1961, *Blakley 4819;* infrequent, rocky sea bluffs, south end, 28 May 1939, *Dunkle 8102* (LAM); south slope [of Signal Peak], 10 February 1949, *Moran 3158* (SD), grown at Berkeley; west-facing slope west of Cat Canyon, southeast of Signal Peak, 22 May 1966, *Philbrick & Benedict B66-402* (SBBG), *B66-403* (MICH, SBBG); west side, 26–27 April 1941, *Moran 823* (DS, SD). This Santa Barbara Island endemic shows considerable variation in color, shape, and size of the leaves, both in the field and when grown in the garden. However, all of these plants have been determined by Reid Moran as *D. traskiae* and have nearly identical flowers in cultivation. Information on the type follows. ". . . corolla bright canary-yellow, . . . the lobes somewhat spreading; carpels inclined to spread" (Rose, Bull. N.Y. Bot. Gard. 3:34, 1903, part of type description). "Only known from material collected by Blanche Trask on Santa Barbara Island . . ., May, 1901. The plant was distributed as *Cotyledon lanceolata,* from which of course it is very distinct" (Rose, *loc. cit.,* p. 34). "The type specimen consists of fragments from and a photograph of an herbarium specimen. Presumably the original of the photograph was destroyed with the bulk of Mrs. Trask's collections in the San Francisco fire of 1906" (Moran, *loc. cit.,* p. 73).

Leguminosae

ASTRAGALUS TRASKIAE Eastw. [*A. leucopsis* (T. & G.) Torr. of Eastwood, 1941; *A. nevinii* Gray of Jepson, Flora Calif. 2:369, 1936, and Eastwood, 1941]. "Common on north and west slopes where windswept. There is a very sharp line of demarcation on the summit of the ridge, indicating that it does not like the competition of other plants, particularly the grasses" (Dunkle, 1940, p. 7). Now most conspicuous at bare windy areas between Arch Point and Signal Peak. Reported by Munz (1935, p. 269). No definite locality, 3 July 1931, *Abrams & Wiggins 308* (DS); tufts, bare rocky areas, Arch Point, 5 May 1963, *Blakley 5699* (CAS, MICH, RSA, SBBG, SD, US); prostrate shrub, head of Cliff Canyon, 4 May 1963, *Piehl 63-131* (MICH, SBBG);

common, gravelly soil, north ridge, 17 March 1940, *Dunkle 7405* (AHFH, LAM); forming low mounds, corolla ivory colored, brink of south cliff, 5 May 1941, *Moran 826* (DS), determined by R. C. Barneby; south slope, 350 feet, 26 April 1941, *Moran 822* (UC), grown at Rancho Santa Ana Botanic Garden; south slope, 10 February 1949, *Moran 3158* (UC), grown at Berkeley; tuff, exposed sea bluff, Signal Peak, 19 March 1940, *Dunkle 7436* (AHFH, LAM), abundant where exposed to wind; with *Eriogonum*, summit area, North Peak, 29 April 1969, *B69-72* (SBBG, SD); frequent, cliff summits, west side, 29 May 1939, *Dunkle 8132* (AHFH, LAM); west slope, 350 feet, 27 April 1941, *Moran 823* (UC). Endemic to Santa Barbara and San Nicolas islands and very similar to *A. nevinii*, which is restricted to San Clemente Island. By transposition of column headings Dunkle (1950, p. 293) accidentally indicated two other species of *Astragalus* as occurring on Santa Barbara Island.

Lotus argophyllus subsp. ornithopus (Greene) Raven (*Syrmatium ornithopum* Greene). "Occasional on southern bluffs and southern canyon exposures, with one plant on western cliff break" (Dunkle, 1950, p. 328); now quite rare on this island. Ottley (Univ. Calif. Publ. Bot. 10:238, 1923) cites a Trask specimen from Santa Barbara Island. Only eight plants observed, near center of Middle Canyon, 4 May 1963, *Blakley 5639* (MICH, SBBG, US); south-facing slope, lower third of Middle Canyon, 27 April 1968, *Philbrick & McPherson B68-225;* locally common, sea bluff, Signal Peak, 19 March 1940, *Dunkle 7435* (LAM); "Brewster Point" [Webster Point], 18 March 1940, *Dunkle 7409* (LAM). Insular endemic subspecies, reported also from San Nicolas, Santa Catalina, San Clemente, and Guadalupe islands. Closely related to mainland taxa and to the more restricted subspecies from Santa Cruz Island (*L. a.* subsp. *niveus*) and from San Clemente Island (*L. a.* subsp. *adsurgens*). The Santa Barbara Island plants are characterized by peduncles which are much shorter than those of the plants from the other four islands where this subspecies occurs.

Medicago polymorpha L. var. polymorpha (*M. hispida* Gaertn.). For *M. hispida,* Dunkle (1940, p. 6) reported: "Between the cabin and the landing cove." No definite locality, 3 July 1931, *Abrams & Wiggins 313* (DS); common, north exposure, Landing Cove, 21 March 1940, *Dunkle 7463* (AHFH, LAM); north-facing slope, Landing Cove, 28 April 1968, *Philbrick & McPherson B68-239;* few, grassy areas among *Coreopsis*, north slope, Signal Peak, 4 May 1963, *Blakley 5669*. Latter two specimens examined by J. P. Simon. Also seen at North Peak and West Slope. *Medicago polymorpha* occurs on all the islands from San Miguel to San Clemente; but the taxon with only short prickles on the fruit, *M. p.* var. *brevispina,* has been documented only for the larger islands, Santa Rosa, Santa Cruz, Santa Catalina, and San Clemente.

TRIFOLIUM PALMERI S. Wats. [*T. gracilentum* var. *palmeri* (S. Wats.) McDer. of Dunkle, 1940].   For *T. gracilentum* var. *palmeri,* Dunkle (1940, p. 7) reported: "Infrequent on hillsides". Currently scattered in the eastern portion of the island. East-facing slope, terrace between Cave Canyon and North Peak, 29 April 1969, *B69-87* (MICH, SBBG, SD); head of Landing Cove, 30 April 1969, *B69-90;* beach bluff, Landing Cove, 4 May 1963, *Blakley 5690;* cliff of headland just south of Landing Cove, 30 April 1969, *B69-104;* with *Coreopsis, Calystegia,* north-facing slope near mouth of Cave Canyon, 30 April 1969, *B69-112;* edge of cactus patch, head of Graveyard Canyon, 21 March 1940, *Dunkle 7449* (LAM); with *Eriogonum, Astragalus, Malacothrix foliosa,* summit area, North Peak, 29 April 1969, *B69-69.* An insular endemic reported also for San Nicolas (Eastwood, Proc. Calif. Acad. Sci., ser. 3, 1:101, 1898), Santa Catalina, San Clemente, and Guadalupe islands. Distinguishable in the field from *T. tridentatum* by the absence of an involucre and by a preference for drier habitats.

TRIFOLIUM TRIDENTATUM Lindl. (*T. microdon* H. & A. of Dunkle, 1940). Known only from the eastern portion of the island. Common, bluff, east side, 28 May 1939, *Dunkle 8115* (AHFH, LAM); north-facing slope, Landing Cove, 18 March 1968, *B68-62* (MICH, SBBG); north-facing slope, upper third of Cave Canyon, 27 April 1968, *Philbrick & McPherson B68-220;* common, north exposure, second canyon south [Middle Canyon], 19 March 1940, *Dunkle 7425* (AHFH, LAM); rare, with grass in shade of *Coreopsis,* north slope of Signal Peak, 4 May 1963, *Blakley 5678* (CAS, RSA, SBBG).

Geraniaceae

{*Erodium botrys* (Cav.) Bertol.   "Noticeably abundant" or "dominant in some areas" according to Sumner & Bond (1939, pp. 12–13), who also listed the two documented species of *Erodium* with similar notations for their frequency. This listing was the basis of Dunkle's inclusion of *E. botrys* in 1942 (p. 133) as "rare", and in 1950 (p. 329) as "reported only by Bond". This occurrence not confirmed. }

ERODIUM CICUTARIUM (L.) L'Her.   "Noticeably abundant" or "dominant in some areas" (Sumner & Bond, 1939, pp. 12–13). Common, grassy slope, east coast, 28 May 1939, *Dunkle 8120* (AHFH); head of Cliff Canyon, 4 May 1963, *Piehl 63-136;* terrace just north of Landing Cove, near shell mound, 18 March 1968, *B68-26;* common, north open slope, Landing Cove, 21 March 1940, *Dunkle 7462* (AHFH, LAM); few, sun, between Graveyard and Cat canyons, 4 May 1963, *Blakley 5653* (RSA, SBBG); between Cat Canyon and Sutil Island, 22 May, 1966, *Philbrick & Benedict B66-405;* summit of North Peak, 21 May

1966, *Philbrick* & *Benedict B66-384;* common, summit, open north ridge, 29 May 1939, *Dunkle 8134* (AHFH, LAM). Also seen at Middle Canyon, Graveyard Canyon, Cat Canyon, Signal Peak, and West Slope. The Santa Barbara Island expression of this *Erodium* does not fit any of the subspecies described in the treatment by Webb & Chater (Flora Europaea 2:203, 1968). It is characterized by: herbage glandular or non-glandular; leaflets cut about 4/5 of distance to midrib; petals equal or subequal, lavender or nearly white; mericarp 4.3 to 5.4 mm; maximum diameter of apical pit 0.6 to 0.7 mm; single conspicuous or inconspicuous furrow below apical pit.

ERODIUM MOSCHATUM (L.) L'Her.   "Noticeably abundant" or "dominant in some areas" (Sumner & Bond, 1939, pp. 12–13); "only found on protected slope in Landing Cove Canyon" (Dunkle, 1940, p. 7). No definite locality, 3 July 1931, *Abrams* & *Wiggins 301* (DS); common locally, beach bluff, Arch Point, 5 May 1963, *Blakley 5702;* head of Cliff Canyon, 4 May 1963, *Piehl 63-135;* terrace just north of Landing Cove, near shell mound, 18 March 1968, *B68-25;* abundant, open slopes among *Coreopsis,* Camp [Landing Cove], 21 March 1940, *Dunkle 7466* (AHFH, LAM); north-facing slope, upper third of Cave Canyon, 27 April 1968, *Philbrick* & *McPherson B68-221* (RSA, SBBG); abundant, with *Mesembryanthemum,* side of Cat Canyon, 4 May 1963, *Blakley 5655.* Also seen at Middle Canyon, Signal Peak, North Peak, and West Slope.

Euphorbiaceae

{*Euphorbia misera* Benth.   Erroneously indicated as occurring on Santa Barbara Island by Dunkle (1950, p. 294).}

Anacardiaceae

{*Rhus integrifolia* (Nutt.) Benth. & Hook.   Accidentally indicated, by transposition of column headings (Dunkle, 1950, p. 293), as occurring on Santa Barbara Island rather than on Santa Catalina. This genus is not known from the former island.}

Rhamnaceae

{*Ceanothus crassifolius* Torr.   Erroneously reported as occurring on Santa Barbara Island by Axelrod (Carnegie Inst. Wash. Publ. 516: 119, 1939).}

{*Rhamnus pirifolia* Greene (*R. crocea* var. *insularis* Sarg.).   Munz

(1935, p. 299) reported *R. crocea* var. *insularis* for "Catalina and Santa Barbara Is.". This occurrence on Santa Barbara Island is doubtful.}

Malvaceae

{*Lavatera assurgentiflora* Kell.   Reported erroneously by Raven (Proc. Symp. Biol. Calif. Islands, p. 62, 1967).}

MALVA PARVIFLORA L.   "Occasional on slopes, particularly about former habitations" (Dunkle, 1940, p. 7). No definite locality, 3 July 1931, *Abrams & Wiggins 295* (DS); common, slopes, east side, 28 May 1939, *Dunkle 8117* (LAM); seasonal dominant of patches in grassland, with *Sonchus oleraceus,* seedling *Amblyopappus,* east terrace just north of head of Graveyard Canyon, 13 February 1970, *B70-4;* common, near top of Signal Peak, 4 May 1963, *Blakley 5666* (RSA, SBBG, SD). Also seen at Cliff Canyon, Landing Cove, North Peak, West Slope, Webster Point, and rock off Webster Point.

{*Sidalcea malvaeflora* (DC.) A. Gray ex Benth.   Reported by Munz (1935, p. 305) for ". . . Santa Barbara Is.". This occurrence doubtful.}

Cactaceae

OPUNTIA LITTORALIS (Engelm.) Cockerell.   Confused with *O.. oricola* in much of the literature prior to 1964. All opuntias were intentionally not collected by Dunkle or Sumner & Bond; undoubtedly this species was present at that time. Large clump, some stem joints semi-spinose, normal flower buds with light pink style and (atypically) without apiculate projections on stigma lobes, aborted flower buds also present, sterile fruit green; with *O. oricola, O. prolifera, Marah, Amblyopappus;* top of sea cliff, east of buildings between Landing Cove and mouth of Cave Canyon, elevation about 175 feet; 21 May 1966; *Philbrick O-628* (MICH, SBBG). Known from all of the islands from San Miguel to Todos Santos, but extremely rare on the former. On Santa Barbara Island it is the least common *Opuntia,* occurring only below 300 feet elevation from Landing Cove to Graveyard Canyon and in Cat Canyon. Distinguished from *O. oricola* by having more elliptical mature stem joints (at least 1.5 times as long as broad), outer perianth parts with entire margins, broader inner perianth parts (less than 1.8 times as long as broad), pink style, and fruit obpyriform (Philbrick, Ph.D. Thesis, Cornell Univ., Ithaca, 1963).

OPUNTIA ORICOLA Philbr.   Confused with *O. littoralis* in much of

the literature prior to 1964. Not collected by Dunkle or Sumner & Bond, but present at that time. No definite locality, 3 July 1931, *Abrams & Wiggins 305* (DS); scattered, terrace, Landing Cove, 5 May 1963, *Blakley 5713;* spines straw colored, scattered, most of colony dead, Middle Canyon, 22 October 1961, *Blakley 4818* (SBBG, paratype; MICH); Sutil Island, 20 March 1968, *Philbrick O-703.* Now documented for all the islands from San Miguel to Todos Santos, plus Cedros Island. On Santa Barbara Island it occurs from Cliff Canyon to Cat Canyon. Distinguished from *O. littoralis* by having more circular mature stem joints (less than 1.5 times as long as broad), outer perianth parts with erosely denticulate margins, narrow inner perianth parts (more than 1.8 times as long as broad), red style, and subspherical fruit (Philbrick, Cactus Succulent J. 36:163–165, 1964).

OPUNTIA PROLIFERA Engelm.　　"Infrequent in the Coreopsis belt, but small, depauperate forms are plentiful on the bluffs of the south point" (Dunkle, 1940, p. 8). Intentionally not collected by Dunkle or Sumner & Bond. Now especially common on south-facing slopes at lower elevations on the eastern portion of the island. No definite locality, 3 July 1931, *Abrams & Wiggins 306* (DS); 3 feet tall, many young plants around its base, Landing Cove, 5 May 1963, *Blakley 5712;* scattered, semi-shade, north [-facing] slope with *Coreopsis*, Middle Canyon, 22 October 1961, *Blakley 4817* (MICH, SBBG); common, beach bluff south side of Signal Peak, 21 October 1961, *Blakley 4808;* Sutil Island, 20 March 1968, *Philbrick O-704.* Also seen in Cliff, Cave, Graveyard, and Cat canyons. Reported for all the islands from Santa Rosa to Los Coronados, plus San Martin, Guadalupe, San Benito, Cedros, and Natividad; however, several of these populations are conspicuously different and suggest the need for a detailed study.

Onagraceae

CAMISSONIA CHEIRANTHIFOLIA (Hornem. ex Spreng.) Raimann subsp. CHEIRANTHIFOLIA *(Oenothera cheiranthifolia* Hornem. ex Spreng. var. *cheiranthifolia).*　　Known only from one collection, which P. H. Raven (personal communication, 1970) has suggested might possibly be in error. However, an appropriate northwest beach habitat was known to D. O. Hyder (personal communication, 1970) as late as 1926. No definite locality, no date, *Henry Hemphill s.n.* (UC 172325), "Brandegee Herbarium", determined by P. A. Munz in August 1927, determined by P. H. Raven in 1966–1967. Specimen consists of one small seedling plus three separate branches (17–23 cm long); each portion is with flowers or fruit. Hemphill collected on Anacapa Island in 1901.

Umbelliferae

DAUCUS PUSILLUS Michx.   Not reported by Dunkle or Sumner & Bond. To date known only from Landing Cove. Rare, shade under *Coreopsis,* beach bluffs, Landing Cove, 4 May 1963, *Blakley 5687;* north-facing slope, Landing Cove, 28 April 1968, *Philbrick & McPherson B68-238.*

Convolvulaceae

CALYSTEGIA MACROSTEGIA (Greene) Brummitt subsp. MACROSTEGIA *(Convolvulus occidentalis* var. *macrostegius* Munz).   For *Convolvulus occidentalis* var. *macrostegius,* Dunkle (1940, p. 8) reported: "Common about the island, especially in the Coreopsis belt". Now primarily confined to the eastern canyons. No definite locality, 3 July 1931, *Abrams & Wiggins 296* (DS), determined by S. M. Walters & D. A. Webb, 1960; occasional, brushy slopes, east side, 29 May 1939, *Dunkle 8138* (LAM); scandent vine visited by bees and beetles, slopes near center of Cave Canyon, 4 May 1963, *Blakley 5622;* scandent on *Coreopsis,* few, mouth of Cave Canyon, 21 October 1961, *Blakley 4804* (CAS, SBBG); north-facing slope, upper Middle Canyon, 22 May 1966, *Philbrick & Benedict B66-408;* with *Stipa, Amblyopappus, Opuntia prolifera,* upper Graveyard Canyon, 19 March 1968, *B68-84;* heavy woody base, corolla cream with light purple outside, near head of Graveyard Canyon, 5 May 1963, *Piehl 63-165.* These morning-glories are considered here as an insular endemic subspecies (see Brummitt, Ann. Missouri Bot. Gard. 52:214–216, 1965) occurring on all of the islands from San Miguel to San Clemente, plus San Martin and Guadalupe. They are morphologically approached by certain plants of a closely related subspecies from the Santa Barbara–Carpinteria area of the mainland. The insular taxon differs by having large coreaceous leaves, thick stems, long peduncles with several flower buds each, large flowers, large bracts, and pollen grains of 80 to 116 microns (vs. 80 to 88 microns for the Santa Barbara–Carpinteria plants). The genus should be more closely studied on Santa Catalina Island where both insular and mainland taxa occur.

Polemoniaceae

GILIA NEVINII A. Gray [*G. gilioides* (Benth.) Greene of Dunkle, 1940, 1950].   For *G. gilioides,* Dunkle (1940, p. 8) reported: "Very rare and occurring only in a depauperate state on grassy slopes. Identification uncertain." Now known from several locations in and near the eastern canyons. East-facing slope, north edge of Landing Cove, 15 March 1969, *Philbrick & Ricker B69-51;* corolla lavender, trail from shore,

Landing Cove, 5 May 1963. *Piehl 63–178;* rare, shaded side, second canyon south [Middle Canyon], 19 March 1940, *Dunkle 7429* (LAM), as *G. gilioides;* flower purplish, anthers blue, rare, rocky north [-facing] slope near junction of forks, Graveyard Canyon, 4 May 1963, *Blakley 5650;* north-facing slope, second small canyon south of Graveyard Canyon, 28 April 1968, *Philbrick & McPherson B68-243b.* This insular endemic occurs on Santa Cruz, Anacapa, Santa Barbara, Santa Catalina, San Clemente, and Guadalupe islands. The occurrence on the latter three islands has been previously recognized (Munz, 1935, p. 394; Grant, Aliso 6:72, 1966); and the occurrence on the more northern three islands is based on specimens at the Santa Barbara Botanic Garden, including: *Philbrick, Benedict & Smith B65-713, B65-730, B65-785,* 20–21 April 1965; *Blakley 4950, 4975, 4984,* 31 March & 1 April 1962, determined by Alva Day in August 1963; *Philbrick B65-517, B65-525,* 28 March 1965. As are many gilias, this species is somewhat difficult to identify. We have emphasized the following characters in distinguishing it from related species: maximum plant size larger than *G. angelensis,* stem pubescent throughout, leaf 2- to 3-pinnate, calyx narrow-cylindrical, corolla relatively large and lavender at base, pollen marked with meandering nongeometric lines.

Hydrophyllaceae

PHACELIA DISTANS Benth. approaching P. FLORIBUNDA Greene *(P. distans* Benth. of Dunkle, 1940; *P. floribunda* Greene of Dunkle, 1942, 1950; *P. hispida* Gray of Eastwood, 1941, and Dunkle, 1942, 1950).   In and near the eastern canyons. No definite locality, 3 July 1931, *Abrams & Wiggins 298* (DS, UC); no definite locality, 14 May 1940, *Bond s.n.* (UC 637185); infrequent, north slope, east coast, 28 May 1939, *Dunkle 8122* (LAM); mesa slope east of North Peak, 4 May 1963, *Piehl 63-122* (CAS, SBBG); fairly common, south exposure, Landing Cove, 21 March 1940, *Dunkle 7460* (LAM); arroyo south of east Landing [Cave Canyon], 27 April 1941, *Moran 828* (UC); common, shaded bottom, second canyon south [Middle Canyon], 20 March 1940, *Dunkle 7441* (AHFH, LAM); terrace just south of lower Middle Canyon, 15 March 1969, *Philbrick & Ricker B69-37;* infrequent in few colonies, open gentle slope above head of Graveyard Canyon, 5 May 1963, *Piehl 63-164;* bottom of lower Graveyard Canyon, 27 April 1968, *Philbrick & McPherson B68-233;* east-facing slope, head of first small gully south of Graveyard Canyon, 28 April 1968, *Philbrick & McPherson B68-244.* This *Phacelia* forms a series of somewhat variable populations on Santa Barbara Island. Although a few plants in the drier locations *(Philbrick & Ricker B69-37)* exhibit the consistently pinnatifid sepals of *P. floribunda* (as known from Guadalupe and San Clemente islands), even these individuals have larger seeds and longer anthers than are characteristic

of the insular species. The Santa Barbara Island plants have: a variable proportion of glandular hairs on the stem (all less glandular than *P. flori-bunda* and insular *P.. distans*), variable sepals (from all sepals entire to one few-lobed sepal per flower, to all pinnatifid sepals), dried anther lengths of 0.6 to 1.0 mm, and mature seeds of 1.7 to 2.5 mm in length. Particular attention should also be given to the shape and attachment position of the scales at the base of the anthers. The relationship beween *P. floribunda* and *P. distans* is worthy of detailed study on this island.

PHOLISTOMA AURITUM (Lindl. ex Lindl.) Lilja var. AURITUM.   Not reported by Dunkle or Sumner & Bond. To date known only from Cave and Middle canyons. Bottom, upper Cave Canyon, 16 March 1969, *Philbrick & Ricker B69-57, B69-58;* north-facing slope, middle Cave Canyon, 19 March 1968, *B68-69;* with *Phacelia,* trough just below dry falls, middle Middle Canyon, 22 March 1970, *Philbrick & Benedict B70-56* (RSA, SBBG); with *Silene, Microseris, Rafinesquia,* north-facing slope, trough of middle-lower Middle Canyon, 22 March 1970, *Philbrick & Benedict B70-51.*

PHOLISTOMA RACEMOSUM (Nutt.) Const. *(Nemophila racemosa* Nutt. ex A. Gray).   Known only from the eastern canyons. Trail from east Landing, 27 April 1941, *Moran 832* (CAS); few, trough of Cave Canyon, 5 May 1963, *Piehl 63-150* (SBBG, US); south-facing slope lower Middle Canyon, 19 March 1968, *B68-74;* locally common, shaded bottom, Graveyard Canyon, 20 March 1940, *Dunkle 7443* (LAM).

Boraginaceae

AMSINCKIA INTERMEDIA F. & M. *(A. spectabilis* F. & M. of Dunkle, 1940).   Sumner & Bond (1939, pp. 12, 14) indicated "noticeably abundant" or "dominant in some areas". Dunkle (1940, p. 9) reported *A. spectabilis* as "occasional on grassy slopes"; however, in 1942 he (Dunkle, pp. 128, 134) indicated *A. intermedia* as "abundant" or "usually dominant". Both of Dunkle's observations probably refer to *A.. intermedia,* which is now common throughout much of the island. No definite locality, 14 April 1939, *Bond 383* (SBM); common, grassy terrace, east side, 28 May 1939, *Dunkle 8112* (LAM); prostrate, flowers orange, scattered, Cliff Canyon, 5 May 1963, *Blakley 5697* (RSA, SBBG); common, open slopes, Landing Cove, 21 March 1940, *Dunkle 7461* (LAM), as *7451* in Dunkle (1940, p. 9); very prickly, corolla yellow, some with orange spots, Landing Cove, 5 May 1963, *Piehl 63-171;* flowers orange, common, head of Cave Canyon, 4 May 1963, *Blakley 5615* (SBBG, SD); southwest-facing slope just east of Sutil Island, 16 March 1969, *Philbrick & Ricker B69-59,* also very conspicuous over nearly all of east slope; flowers orange, common, grassy area

south side of North Peak, 5 May 1963, *Blakley 5710* (MICH, SBBG);
low, somewhat decumbent, corolla small, yellow, among *Coreopsis,* slope
east of North Peak, 4 May 1963, *Piehl 63-138;* prostrate, exposed to
strong wind, common, north side of North Peak, 5 May 1963, *Blakley
5705* (CAS, SBBG); with *Suaeda, Mesembryanthemum crystallinum,
M. nodiflorum, Hordeum glaucum, Lasthenia,* north base of Webster
Point peninsula, 29 April 1969, *B69-76.* Also seen at Arch Point, Mid-
dle Canyon, Graveyard Canyon, Cat Canyon, and Signal Peak. Above
determinations verified by E. R. Chandler. The following characteristics
are useful in distinguishing this species from *A. spectabilis.* The calyx
lobes are always free, while at least one pair is frequently united in
A. spectabilis. The mature nutlet is usually greater than 2.5 mm in
length, has pronounced irregular ridges and tubercles on its dorsal sur-
face and a transverse ventral keel that intersects an ovate attachment
scar above its widest point (Ray & Chisaki, Amer. J. Bot. 44:530,
1957).

AMSINCKIA SPECTABILIS F. & M.   The two collections, which Dunkle
(1940, p. 9) cited for *A. spectabilis,* are *A. intermedia.* More delicate
habit than *A. intermedia,* two to three calyx lobes united for more
than half their length, homostylic, locally common, terrace about 40
feet west of sea cliff, just west of Arch Point, 21 March 1970, *Philbrick
& Benedict B70-34* (RSA, SBBG).

CRYPTANTHA CLEVELANDII Greene var. CLEVELANDII [*C. traskae* John-
ston of Dunkle, 1940; *C. c.* var. *hispidissima* (Greene) Johnston of
Dunkle, 1940; *C. c.* var. *florosa* Johnst.; *C. leiocarpa* (F. & M.) Greene
of some authors; *C. brandegei* Johnst.; *C. abramsii* Johnst.].   Re-
ported as *C. clevelandii* and in error as *C. traskae* by Dunkle (1940,
p. 9). Apparently confined to the eastern portion of the island. No
definite locality, 14 April 1939, *Bond 386* (SBM); Landing Cove, 21
March 1940, *Dunkle 7446-b* (AHFH), as *C. traskiae* [corrected spell-
ing]; common, south[-facing] slope, head of Cave Canyon, 4 May
1963, *Blakley 5613* (CAS, SBBG, SD); uncommon, shaded side, sec-
ond canyon south [Middle Canyon], 19 March 1940, *Dunkle 7428*
(LAM); common locally, cactus clump, head of Graveyard Canyon, 21
March 1940, *Dunkle 7447* (LAM); rare, rocky bluffs, south end, 28
May 1939, *Dunkle 8106* (AHFH); uncommon, gravelly soil, Signal
Peak, 21 March 1940, *Dunkle 7446* (LAM), as *C. traskiae;* among
Coreopsis, slope east of North Peak, 4 May 1963, *Piehl 63-140* (SBBG,
SD); common, exposed to strong wind, north side of North Peak, 5 May
1963, *Blakley 5706* (CAS, MICH, RSA, SBBG). According to E. R.
Chandler (personal communication, 1969) *C. clevelandii* seems to be
composed of several morphologically distinct ecological races. The Santa
Barbara Island material is similar to that from the mainland coast of
Ventura. For this taxon, the habit of growth is sprawling to subprostrate

with relatively thin stems; the mature stem pubescence is composed of both thin short appressed hairs without pustulate bases and longer stouter spreading hairs with pustulate bases; some of the inflorescences have a few bracts toward their bases; the larger hairs on the midrib of the mature calyx lobes are relatively few and usually from 1.5 to 2.0 mm in length; the flower is relatively small (maximum corolla diameter 1.7 to 2.3 mm); the combined height of style and gynobase does not exceed that of the mature nutlet (0.7 to 0.8 times nutlet height).

{*Cryptantha intermedia* (A. Gray) Greene.   Reported by Dunkle (1942, p. 134; 1950, p. 330) without voucher specimen; this occurrence is doubtful.}

CRYPTANTHA MARITIMA (Greene) Greene.   Johnston (Contr. Gray Herb., *n.s.,* 74:48, 1925) cites a Trask specimen from Santa Barbara Island as *C. maritima* var. *genuina.* Currently restricted to the eastern portion of the island. Scattered, Cliff Canyon, 5 May 1963, *Blakley 5694;* terrace just north of Landing Cove, near shell mound, 18 March 1968, *B68-28;* rocky ledges, mouth of Cave Canyon, 4 May 1963, *Blakley 5628* (MICH, SBBG, SD); common, rocky ledges, mouth of Middle Canyon, 4 May 1963, *Blakley 5646;* between Middle and Grave-yard canyons, 19 March 1968, *B68-72;* with *Amblyopappus, Opuntia prolifera, Calandrinia maritima,* dry exposed southeast-facing slope, upper Graveyard Canyon, 19 March 1968, *Philbrick s.n.* (SBBG 29583); infrequent, rocky bluffs, cliffs, south end, 17 March 1940, *Dunkle 7403* (AHFH, LAM); east-facing slope, mouth of Cat Canyon, 28 April 1968, *Philbrick & McPherson B68-245;* bluff between Cat Canyon and Sutil Island, 22 May 1966, *Philbrick & Benedict B66-415.* The relationship to mainland taxa and to *C. cedrosensis* is under study.

Solanaceae

LYCIUM CALIFORNICUM Nutt. ex A. Gray.   "Widespread and frequent-ly dominant on all terraces, southern bluffs, and western headlands; fre-quently a component of the *Suaeda-Larus* biome" (Dunkle, 1950, p. 330). Presently scattered over much of the island, but most of the stands are thin and small. Gradually disappearing from many of the California off-shore islands. Thickets about 12 inches high, dry fields, 12 August 1938, *Elmore 295* (AHFH); common, slopes, east side, 28 May 1939, *Dunkle 8125* (AHFH); scattered colonies 2 feet tall, east terrace, 21 October 1961, *Blakley 4809;* south-facing slope, middle Cave Canyon, 21 May 1966, *Philbrick & Benedict B66-363* (SBBG, SD); 2 feet by 4 feet, scattered, ridge between North Peak and Signal Peak, 5 May 1963, *Blakley 5709* (MICH, RSA, SBBG); with *Amsinckia, Amblyo-pappus, Hordeum glaucum, Mesembryanthemum nodiflorum, M. crystal-*

linum, rocky west-facing slope, north base of Webster Point peninsula, 29 April 1969, *B69-80;* abundant, flat terrace, west end, 18 March 1940, *Dunkle 7418* (LAM); rocks, southwest-facing slope, west terrace near southwest coast, between the Hook and *Suaeda* swale, 29 April 1969, *B69-83;* west ridge, Sutil Island, 20 March 1968, *B68-87.* Also seen at Cliff Canyon, Middle Canyon, Landing Cove, and Webster Point.

Scrophulariaceae

GALVEZIA SPECIOSA (Nutt.) A. Gray.   Known only from the following fragmentary specimen, which was brought to our attention by Roman Gankin and L. R. Heckard. No definite locality, "plant from Santa Barbara I.", May 1863, *J. G. C[ooper] s.n.* (UC 26766). Specimen consists of a total of 16 cm of inflorescence. The lower portion has four subglabrous leaves; the upper has three corollas. This taxon is an insular endemic known otherwise only from Santa Catalina and San Clemente islands. A similar taxon is known from Guadalupe Island, but the Guadalupe plant differs in frost hardiness, habit of growth, and characters of the leaf, flower, and fruit. Detailed study will undoubtedly show the latter taxon to constitute a distinct subspecies. J. G. Cooper made zoological collections on Santa Barbara Island for six weeks in May and June 1863 (Cooper, Proc. Calif. Acad. Sci. 4:80, 1870; Howell, 1917, p. 20); and his specimen indicates a logical range extension from the larger, floristically related southern islands. The Cooper collection is dated 38 years before the next known botanical specimens were taken from the island, and it seems quite possible that *Galvezia* might have become extinct or extremely rare during those years. Although there is no doubt about the identification of the specimen and the label information is accepted here as originally given, it should be mentioned that the collection data might possibly have been confused; for at about the same time Cooper also visited Santa Catalina and San Clemente islands (Howell, 1917, pp. 25, 55, 78), and his specimen matches material from either of these islands. It may be relevant that the accuracy of Cooper's zoological collection data is placed in some doubt by Howell (1917, p. 6) and by reference to Cooper's own list of island fauna (Cooper, Proc. Calif. Acad. Sci. 4:77, 1870).

Plantaginaceae

{*Plantago maritima* L.   Reported by Dunkle (1942, p. 135) without documenting specimen, and omitted from his more comprehensive 1950 publication. This occurrence is doubtful.}

PLANTAGO OVATA Forssk. (*P. insularis* Eastw.).   Known only from

the southern portion of the island. Near cliff just north of mouth of Graveyard Canyon, 22 March 1970, *Philbrick* & *Benedict B70-58;* common locally, exposed rocky sea bluff, southeast point, 19 March 1940, *Dunkle 7430* (LAM); west-facing slope, upper Cat Canyon, 19 March 1968, *B68-79;* few, scattered among rocks and *Opuntia prolifera,* between Cat Canyon and Signal Peak, 4 May 1963, *Blakley 5658* (DS, SBBG); few, edge of bare spots near top of Signal Peak, 4 May 1963, *Blakley 5661* (DS, MICH, SBBG). Morphological and palynological studies indicate that *P. ovata* of the Old World and *P. insularis* of North America are conspecific, the American populations being introduced (Bassett & Baum, Can. J. Bot. 47:1865–1868, 1969). For cytogenetic evidence emphasizing the differences between these two populations, see Stebbins & Day (Evolution 21:409–428, 1967).

Rubiaceae

{*Galium angustifolium* Nutt.   Munz (1959, p. 1043) reported *G. angustifolium* var. *foliosum* for ". . . Santa Cruz, Santa Rosa, Anacapa, Santa Barbara ids.". The possible primary sources suggested by P. A. Munz (personal communication, 1969) have been checked without giving evidence of any *Galium,* other than *G. aparine,* on Santa Barbara Island. It is possible that the above quote was intended to mean "on Santa Cruz, Santa Rosa, and Anacapa of the Santa Barbara Islands". *Galium angustifolium* var. *foliosum* is known only for the more northern islands, Santa Rosa, Santa Cruz, and Anacapa; the tetraploid, *G. a.* var. *angustifolium,* occurs on Santa Catalina Island (Lauramay T. Dempster, personal communication, 1969). The occurrence of either of these varieties on Santa Barbara Island is doubtful.}

GALIUM APARINE L.   Low cropped-off plant, mesa slope east of North Peak, 4 May 1963, *Piehl 63-123;* exposed cliffs, Landing Cove, 5 May 1963, *Piehl 63-169* (CAS, SBBG), frequent on east side of island; scattered, scandent on grass, base of cliff, north [-facing] slope, mouth of Cave Canyon, 4 May 1963, *Blakley 5632,* determined by L. T. Dempster; few, scandent below rocky cliff, north [-facing] slope near junction of north and south forks, Graveyard Canyon, 4 May 1963, *Blakley 5648* (CAS, MICH, SBBG, US), determined by L. T. Dempster; common, with *Lycium,* flat terrace, west end, 18 March 1940, *Dunkle 7417* (AHFH, LAM). Also seen in Middle Canyon.

Cucurbitaceae

MARAH MACROCARPUS (Greene) Greene *(Echinocystis fabacea* Naud. of Dunkle, 1940; *E. macrocarpa* Greene).   Known only from the

eastern portion of the island. No definite locality, 14 April 1939, *Bond 401* (SBM); small canyon between Landing Cove and Cliff Canyon, 18 March 1968, *B68-37* (MICH, SBBG); bluff, Landing Cove, 4 May 1963, *Blakley 5686* (SBBG, SD); common, first canyon south [Cave Canyon], 20 March 1940, *Dunkle 7439* (LAM); sea cliff north of North Peak, 21 May 1966, *Philbrick & Benedict B66-380.* Also seen in Cliff, Middle, Graveyard, and Cat canyons. On the basis of Stocking's publication (Madroño 13:113–137, 1955) and study of the specimens at the California Academy of Sciences, Santa Barbara Museum of Natural History, and Santa Barbara Botanic Garden, E. R. Chandler (personal communication, 1969) has considered the following characteristics of *M. macrocarpus* in distinguishing it from *M. fabaceus*: flowers larger, more or less cup-shaped; small free tips of calyx usually projecting between corolla lobes; filaments usually longer than anthers; scale-like staminodia usually present; stigmas rounded; styles evident. Variation and relationship within and between the species are being studied further.

Compositae

ACHILLEA BOREALIS Bong. [*A. millefolium* var. *lanulosa* (Nutt.) Piper of Dunkle, 1940, 1942, 1950; *A. lanulosa* Nutt. of Eastwood, 1941].
For *A. millefolium* var. *lanulosa,* Dunkle (1940, p. 11) reported: "Common about the island. It grows very short and compact on the inaccessible north cliffs . . . ." Still scattered throughout much of the island. No definite locality, 3 July 1931, *Abrams & Wiggins 294* (DS), determined as *A. borealis* subsp. *californica* (Pollard) Keck by F. Ehrendorfer, 1952; dry hillside, 12 August 1938, *Elmore 308* (AHFH); common, north slopes, east side, 28 May 1939, *Dunkle 8118* (AHFH); to 1 foot tall, scattered, rocky beach bluff with *Coreopsis,* Landing Cove, 21 October 1961, *Blakley 4788* (RSA, SBBG); scattered in grass, north [-facing] slope near center of Middle Canyon, 4 May 1963, *Blakley 5645;* to 14 inches tall, scattered, grassy north slope of Signal Peak, 4 May 1963, *Blakley 5671* (MICH, SBBG); with *Coreopsis, Amsinckia intermedia, Thelypodium, Malacothrix foliosa, Hordeum glaucum,* east-facing slope, North Peak, 29 April 1969, *B69-66.* Also seen on East Slope and West Slope. For a discussion of the subspecies of *A. borealis* see Clausen, Keck, & Heisey (Carnegie Inst. Wash. Publ. 520:298–299, 1940). Treated as varieties of *A. millefolium* by Nobs (*In* Abrams & Ferris, Illus. Flora Pacific States 4:390–391, 1960).

AMBLYOPAPPUS PUSILLUS H. & A.   Common throughout much of the island. No definite locality, 14 April 1939, *Bond 371* (SBM); no definite locality, 14 May 1940, *Bond 508* (SBM); common, widely distributed, grassy terrace, east side, 28 May 1939, *Dunkle 8111* (AHFH, LAM);

bluff half-way between Landing Cove and Cliff Canyon, 21 May 1966, *Philbrick & Benedict B66-372;* few, under *Coreopsis,* shady beach bluff, Landing Cove, 22 October 1961, *Blakley 4813* (RSA, SBBG); vigorous erect plants, near buildings just south of Landing Cove, 22 May 1966, *Philbrick & Benedict B66-412* (MICH, SBBG), 32 cm high; sea bluffs, south end, 19 March 1940, *Dunkle 7434* (LAM); common, bare areas, north slope of Signal Peak, 4 May 1963, *Blakley 5676;* summit area, North Peak, 29 April 1969, *B69-71;* bluff due north of North Peak, 21 May 1966, *Philbrick & Benedict B66-379.* Also seen at Cliff Canyon, Middle Canyon, Graveyard Canyon, West Slope, and Webster Point.

{*Ambrosia chamissonis* (Less.) Greene.   Indicated as occurring on Santa Barbara Island by Foreman (1967, p. 70). This occurrence is doubtful.}

ARTEMESIA CALIFORNICA var. INSULARIS (Rydb.) Munz (*A. nesiotica* Raven).   Scattered in the eastern portion of island. No definite locality, 3 July 1931, *Abrams & Wiggins 299* (DS, UC); common, lower terrace slope, east side, 28 May 1939, *Dunkle 8126* (AHFH, LAM); eastern slope between Cave and Middle canyons, 19 March 1968, *B68-70* (SBBG, US); mesic habitate with *Mesembryanthemum crystallinum,* rocky northeast-facing slope south of Landing Cove, 30 April 1969, *B69-106;* scattered, sun, mouth of Cave Canyon, 21 October 1961, *Blakley 4802* (MICH, SBBG), *4803* (SBBG, SD); 3 feet tall, 4 feet in diameter, few, head of Middle Canyon, 4 May 1963, *Blakley 5647;* top of cliff, south of Signal Peak, opposite Sutil Island, 22 May 1966, *Philbrick & Benedict B66-407* (RSA, SBBG). An insular endemic also occurring on San Nicolas and San Clemente islands. Plants of *B68-70* grown at Santa Barbara Botanic Garden have up to 12 ray flowers and 35 disk flowers per head.

BACCHARIS PILULARIS subsp. CONSANGUINEA (DC.) C. B. Wolf. Listed for terraces of Santa Barbara Island by Dunkle (1950, p. 292) but no documenting specimen found and not included in his "Annotated List of the Vascular Plants of Santa Barbara Island" (1950, pp. 326–331). Now known only from a single shrub in Middle Canyon. Single plant, south edge of canyon bottom, lower third of Middle Canyon, just above point where canyon narrows, 27 April 1968, *Philbrick & McPherson B68-224* (CAS, MICH, SBBG, SD).

CENTAUREA MELITENSIS L.   Not reported by Dunkle or Sumner & Bond; so far found only in the Landing Cove area. Rosettes only, exposed cliffs, Landing Cove, 5 May 1963, *Piehl 63-176* (SBBG); north of buildings, south of Landing Cove, 28 April 1968, *Philbrick & McPherson B68-235* (RSA, SBBG).

COREOPSIS GIGANTEA (Kell.) Hall.   See figures 11a–12a in intro-
ductory text. About 1871 Kellogg or Harford noted "This plant is . . .
found on Santa Barbara Island, in some ravines, reaching to 10 feet in
height; on exposed cliffs and plateaus it rarely exceeded 5 feet . . ."
(Proc. Calif. Acad. Sci. 4:199, 1873). In 1940 Dunkle (p. 10) reported:
"The most characteristic growth on the island. Grotesque and tree-like,
much more arborescent than the plants elsewhere, growing from 4 to 8
feet high with stout branches at right angles. It forms dense thickets on
the east slopes and bluffs from 30 to 250 feet. It is scattered elsewhere
over the island. On the north bluffs the Pelicans use the stubby plants
as a foundation for their high nests." In 1950 he referred to this species
as "the dominant plant of the island" (p. 279) and added: "Common
in all but the most extremely wind-swept areas; dominant on the lower
eastern terrace, bluffs, and canyons. Undoubtedly dominant over more
extensive areas before cultivation of the terraces" (p. 330). This plant
is now reduced to scattered, relatively thin patches within the distribu-
tion described here. See introductory text and figure 9 for further details
of distribution. No definite locality, August 1901, *Snodgrass s.n.* (DS
492439); dry canyon walls and rocky hillsides, 12 August 1938, *Elmore
297* (AHFH); with *Mesembryanthemum crystallinum* (dominant),
*Perityle, Atriplex semibaccata, Opuntia prolifera, Chenopodium murale,
Sonchus oleraceus, Malacothrix foliosa, Amblyopappus, Amsinckia, Mal-
va,* south-facing slope, lower-middle Cliff Canyon, 30 April 1969, *B69-94;*
extremely abundant, open gentle slope, Camp [Landing Cove], 21 May
1940, *Dunkle 7444* (AHFH, LAM); 4 to 8 feet high, near Landing, 10
February 1949, *Moran 3161* (DS, SD, UC), ". . . forming forest over
much of east slope of island"; 3 feet tall, common, beach bluffs, Landing
Cove, 4 May 1963, *Blakley 5692* (MICH, SBBG); gnawed by rabbits,
with *Trifolium palmeri, Malacothrix foliosa,* headland cliff just south of
Landing Cove, 30 April 1969, *B69-103;* 1 to 2 meters tall, 2 to 4 inches
diameter at breast height, rocky north-facing slope, lower Cave Canyon,
27 April 1968, *Thorne 37529* (SD); waist high, dominating small open
Coreopsis patch, with *Bromus rubens, Hordeum glaucum, Atriplex semi-
baccata, Thelypodium, Amsinckia intermedia, Achillea, Malacothrix
foliosa,* seedling *Coreopsis,* east-facing slope, North Peak, 29 April 1969,
B69-64; common, north slope, North Peak, 1 October 1961, *Blakley
4798;* extremely common, ridge above sea, northwest side, 29 May 1939,
Dunkle 8129 (AHFH, LAM).

ERIOPHYLLUM NEVINII A. Gray.   Primarily confined to the less ac-
cessible sea cliffs. Dry hillside, 12 August 1938, *Elmore 300* (AHFH);
few, upper beach bluff west of Arch Point, 21 October 1961, *Blakley
4797* (CAS, RSA, SBBG, SD); rocks near east Landing, 27 April 1941,
Moran 883 (DS); east-facing slope, first small gully south of Landing
Cove, east of Quonset huts, 30 April 1969, *B69-101* (MICH, SBBG);
to 12 inches tall, south[-facing] slope, windswept rocky ledge, mouth of

Cave Canyon, 4 May 1963, *Blakley 5629* (MICH, SBBG, US); rocky sea bluffs, south end, 28 May 1939, *Dunkle 8101* (LAM); common, sea cliffs, "northwest rock" [there is no other known evidence that Dunkle might have collected on Shag Rock], 28 May 1939, *Dunkle 8128* (LAM); west ridge, Sutil Island, 20 March 1968, *B6888.* Endemic to Santa Barbara, Santa Catalina, and San Clemente islands. Each of the three populations is modally distinct, at least in characteristics of the foliage.

{*Gnaphalium purpureum* L.   Reported by Munz (1935, p. 541) for "... Santa Barbara and Santa Rosa I." and by Munz (1959, p. 1259) for "... Santa Catalina, Santa Rosa, and Santa Barbara ids.". No other evidence is known; a documenting specimen has not been seen for Santa Barbara Island.}

{*Haplopappus venetus* (HBK.) Blake [*Aplopappus venetus* (HBK.) Blake].   By transposition of column headings for Santa Catalina and Santa Barbara islands Dunkle (1950, p. 293) accidentally indicated two varieties of *Aplopappus venetus* as occurring on Santa Barbara Island. This genus is not known from the latter island.}

HEMIZONIA CLEMENTINA Brandeg. (*H. c.* "forma erecta" of Dunkle, 1950, *H. c.* "forma prostrata" of Dunkle, 1950).   *"Astragalus trask-iae, Malacothrix foliosa, Hemizonia clementina,* and *Baeria hirsutula* are dominants of the windiest areas" (Dunkle, 1950, p. 274). Hall (Univ. Calif. Publ. Bot. 3:150–151, 1907) cited the Trask specimen from Santa Barbara Island. Presently throughout much of the island. No definite locality, no date, *Trask s.n.* (UC 89558); no definite locality, August 1901, *Snodgrass s.n.* (DS 492422); narrow-leaved form, no definite locality, 3 July 1931, *Abrams & Wiggins 300* (DS); no definite locality, 3 July 1931, *Abrams & Wiggins 302* (DS, UC); dry hillside, 12 August 1938, *Elmore 299* (AHFH); abundant, rocky sea cliffs, east side, 28 May 1939, *Dunkle 8113* (LAM), maximum cauline leaf length 8.4 cm; to 1 foot tall, few, under *Coreopsis,* north[-facing] slope, Landing Cove, 21 October 1961, *Blakley 4790* (CAS, SBBG), maximum cauline leaf length 1.7 cm; to 1 foot tall, few, under *Coreopsis,* Middle Canyon, 22 October 1961, *Blakley 4822* (RSA, SBBG); abundant, sea bluffs, south end, 19 March 1940, *Dunkle 7437* (AHFH, LAM); 1 foot tall, 2 feet in diameter, scattered, between Cat Canyon and Signal Peak, 4 May 1963, *Blakley 5660;* 2 feet in diameter, scattered, north slope of Signal Peak, 4 May 1963, *Blakley 5672;* 6 inches high, 11 inches in diameter, summit of North Peak, 21 May 1966, *Philbrick & Benedict B66-381* (SBBG, SD); prostrate, bluff due north of North Peak, 21 May 1966, *Philbrick & Benedict B66-377;* 1 foot tall, few, west terrace near Webster Point, 21 October 1961, *Blakley 4799* (SBBG, US). An insular endemic species reported also from Anacapa, San Nicolas, Santa

Catalina, and San Clemente islands. Its nearest relatives are probably the species of the Baja California off-shore islands (see Carlquist, Island Life, pp. 115–118, 1965). Both the size and shape of leaf and the pubescence of herbage are conspicuously modified by time of year and by habitat.

HEMIZONIA FASCICULATA (DC.) T. & G. subsp. FASCICULATA [*H. f.* var. *ramosissima* (Benth.) Gray of Eastwood, 1941, and Dunkle, 1942, 1950]. To date known only from the northeast portion of the island. No definite locality, 3 July 1931, *Abrams* & *Wiggins 303* (DS), two small plants shorter than 18 cm determined as "*H. ramosissima* Benth. toward *fascic.*" by D. D. K[eck], 1953; rare, canyon bank, east side, 29 May 1939, *Dunkle 8137* (LAM); east-facing slope, terrace between Cave Canyon and North Peak, 29 April 1969, *B69-84;* southwest of buildings between Landing Cove and Cave Canyon, 21 May 1966, *Philbrick & Benedict B66-369* (MICH, SBBG).

{*Hieracium argutum* Nutt. Reported by Eastwood (1941, p. 73). No other evidence for the occurrence of this genus on Santa Barbara Island is known. The validity of this report is doubtful.}

LASTHENIA CHRYSOSTOMA (F. & M.) Greene (*Baeria hirsutula* Greene of Dunkle, 1940, 1942, 1950; *B. chrysostoma* F. & M.). "*Astragalus traskiae, Malacothrix foliosa, Hemizonia clementina,* and *Baeria hirsutula* are dominants of the windiest areas" (Dunkle, 1950, p. 274). At least since 1968 *Lasthenia* has produced the most conspicuous patches of spring flowers seen on the island; these have been noted in the Cliff and Cat canyon areas, on North and Signal peaks, and near the north shore between Webster Point and North Peak. Ornduff (Univ. Calif. Publ. Bot. 40:58, 1966) cites a specimen collected by Evermann in 1918. Very succulent, locally abundant, head of Cliff Canyon, 27 April 1968, *Philbrick & McPherson B68-201;* abundant, side of Cliff Canyon, 5 May 1963, *Blakley 5695* (CAS, MICH, RSA, SBBG, SD, US); open north exposure, Landing Cove, 21 March 1940, *Dunkle 7464* (LAM); rocky soil, south high point [Signal Peak], 17 March 1940, *Dunkle 7402* (LAM); forming large yellow areas, north slope of Signal Peak, 4 May 1963, *Blakley 5675* (RSA, SBBG, US); with *Eriogonum, Astragalus, Trifolium palmeri,* summit area, North Peak, 29 April 1969, *B69-73;* with *Suaeda, Mesembryanthemum crystallinum, M. nodiflorum, Hordeum glaucum, Amsinckia intermedia,* north base of Webster Point peninsula, 29 April 1969, *B69-75;* hillside, west end, 18 March 1940, *Dunkle 7412* (LAM). Also seen at East Slope and Arch Point.

MALACOTHRIX FOLIOSA A. Gray [*M. insularis* var. *squalida* (Greene) Ferris of Ferris *In* Abrams & Ferris, Illus. Flora Pacific States 4:576, 1960; *M. clevelandii* Gray of Gentry, Publ. Allan Hancock Pacific

Exped. 13:40, 1949].   The Trask specimen from Santa Barbara
Island is cited by Hall (Univ. Calif. Publ. Bot. 3:266, 1907) with the
date "May, 1901". Dunkle (1950, p. 293) accidentally indicated this
species as occurring on Santa Catalina rather than Santa Barbara Island.
Presently abundant to scattered throughout much of the island. No def-
inite locality, no date. *Trask s.n.* (UC 133516), annotated by H. M. H[all],
June 1906, determined by W. S. Davis, 1965; no definite locality, August
1901, *Snodgrass s.n.* (DS 492421), determined as *M. indecora* by W. S.
Davis, 1965; no definite locality, 3 July 1931, *Abrams &Wiggins 304* (DS,
UC), determined by W. S. Davis, 1965, part determined as *"M. foliosa?
approaching M. insularis squalida"* by R[oxanna] S. F[erris]; no definite
locality, 19 April 1938, *Bilderback s.n.* (SD 21229), determined by W.
S. Davis, 1965; no definite locality, 12 August 1938, *Elmore 370*
(AHFH), determined by Elizabeth Williams, 1948, much branched plant
with small cauline leaves; no definite locality, 14 April 1939, *Bond 372*
(SBM), *387* (SBM); no definite locality, 14 May 1940, *Bond s.n.*
(UC 637181), determined by W. S. Davis, 1965; with *Coreopsis,
Amsinckia intermedia, Achillea, Thelypodium, Hordeum glaucum,* east-
facing slope, North Peak, 29 April 1969, *B69-67;* dense low-growing
mound, bluff due west of mouth of Cliff Canyon, 21 May 1966, *Philbrick
& Benedict B66-373;* abundant, gravelly soil, north ridge, 17 March
1940, *Dunkle 7404* (AHFH, LAM); dwarfed by wind, field of spring
annuals, head of Cliff Canyon, 30 April 1969, *B69-96;* forming mats on
rocky canyon side, Cliff Canyon, 5 May 1963, *Blakley 5696* (MICH,
RSA, SBBG); small canyon between Landing Cove and Cliff Canyon,
18 March 1968, *B68-32* (CAS, SBBG), cauline leaves large with wide
lobes; small canyon between Landing Cove and Cliff Canyon, 18 March
1968, *B68-33,* cauline leaves small with narrow lobes; infrequent, rocky
bluff, east side Landing, 30 May 1939, *Dunkle 8144* (AHFH, LAM),
small plants with small cauline leaves; gnawed by rabbits, with *Coreop-
sis, Trifolium palmeri,* cliff of headland just south of Landing Cove,
30 April 1969, *B69-102;* few, north[-facing] slope, base of rocky cliff
near center of Cave Canyon, 4 May 1963, *Blakley 5625* (SBBG, SD),
determined by W. S. Davis, 1965; erect, variable as to size, loses leaves
early, mouth of Middle Canyon, 5 May 1963, *Piehl 63-158* (MICH,
SBBG); infrequent, rock bluffs, south end, 28 May 1939, *Dunkle 8105*
(AHFH, LAM); scattered, north slope of Signal Peak, 4 May 1963,
Blakley 5677, determined by W. S. Davis, 1965; common, west side,
27 April 1941, *Moran 824* (DS, UC), determined by W. S. Davis, 1965,
determined as *M. insularis* var. *squalida* by [R.S.] Ferris, 1954. Also
seen at Cat Canyon and North Peak. *Malacothrix foliosa* is an insular
endemic, which also has been collected on Anacapa, San Clemente, and
Los Coronados (W. S. Davis, personal communication, 1970). It is
similar to certain annual *Malacothrix* of San Miguel, Santa Cruz, and
San Nicolas. The Santa Barbara Island plants are extremely variable
in habit and foliage characteristics; they are most similar to the popu-

lations from San Clemente Island, the type locality. The achene length is from 1.2 to 1.7 mm, and the mature style extends well beyond the apex of the anthers. This complex, including both *M. foliosa* and *M. indecora,* is currently under further study by W. S. Davis; and his preliminary suggestions have been valuable here.

{*Malacothrix indecora* Greene [*M. foliosa* var. *indecora* (Greene) E. W. Williams].   The *Malacothrix* of Santa Barbara Island has been studied in the field and herbarium; particular attention has been given to the leaf lobing, receptacle, phyllaries, style, and achene. The probable isotypes of Greene's *M. indecora* have been examined (CAS, DS, ND-G). Even though this species is reported from Santa Barbara Island by W. S. Davis (personal communication, 1970), it is presently felt that none of the Santa Barbara Island material seen can be placed in this taxon without reservation.}

Microseris linearifolia (Nutt.) Sch.-Bip. [*M. lindleyi* (DC.) A. Gray of some authors].   Not reported by Dunkle or Sumner & Bond. Currently known only from Cave and Middle canyons. North-facing slope, upper Cave Canyon, 27 April 1968, *Philbrick & McPherson B68-216;* with *Silene, Rafinesquia, Pholistoma a.* var. *auritum,* north-facing slope, trough of middle-lower Middle Canyon, 22 March 1970, *Philbrick & Benedict B70-49.*

Perityle emoryi Torr. (*P. greenei* Rose).   Known only from the eastern portion of the island. With *Mesembryanthemum crystallinum, Coreopsis, Opuntia prolifera, Amblyopappus,* south-facing slope, lower-middle Cliff Canyon, 30 April 1969, *B69-95;* to 8 inches tall, scattered, mouth of Cave Canyon, 4 May 1963, *Blakley 5626* (RSA, SBBG); rocky dry soil, southeast bluffs, 19 March 1940, *Dunkle 7431* (LAM); infrequent, rocky sea bluffs, south end, 28 May 1939, *Dunkle 8104* (LAM). Also seen at Landing Cove and Middle Canyon.

Rafinesquia californica Nutt.   Not reported by Dunkle or Sumner & Bond. To date found only in lower Middle Canyon. With *Sonchus,* south bank near mouth of Middle Canyon, 5 May 1963, *Piehl 63-157a;* north-facing slope, lower Middle Canyon, 27 April 1968, *Philbrick & McPherson B68-226.*

{*Senecio lyonii* A. Gray.   Reported by Gentry (Publ. Allan Hancock Pacific Exped. 13:41, 1949) for "the Channel Islands of San Clemente, Santa Barbara, Santa Cruz". No other evidence for this occurrence on Santa Barbara Island is known; a documenting specimen has not been seen.}

Silybum marianum (L.) Gaertn.   Not reported by Dunkle or

Sumner & Bond. Found only in Cliff Canyon; and in an attempt to eradicate this introduced weed, all remaining plants were destroyed after each collection was made. Four plants, severe insect damage, bottom of middle-lower Cliff Canyon, 18 March 1968, *B68-20* (SBBG, US); only two plants seen, bottom of middle-lower Cliff Canyon, 15 March 1969, *Philbrick & Ricker B69-48* (RSA, SBBG).

Sonchus oleraceus L. [*S. asper* (L.) Gars. of Sumner & Bond, 1939].
"Common, particularly in regions previously cultivated" (Dunkle, 1940, p. 10). No definite locality, 3 July 1931, *Abrams & Wiggins 297* (DS); dry hillside, 12 August 1938, *Elmore 304* (AHFH); no definite locality, 14 April 1939, *Bond 378* (SBM), as *S. asper;* common, open slopes, east slope, 21 March 1940, *Dunkle 7450* (AHFH, LAM); south-facing slope, lower-middle Cliff Canyon, 15 March 1969, *Philbrick & Ricker B69-50;* scattered, exposed cliffs, Landing Cove, 5 May 1963, *Piehl 63-180;* few, north[-facing] slope, base of small cliff, mouth of Cave Canyon, 4 May 1963, *Blakley 5630* (RSA, SBBG); grazed, infrequent, mouth of Middle Canyon, 5 May 1963, *Piehl 63-160;* common, widespread, open slopes, west side, 29 May 1939, *Dunkle 8131* (LAM). Also seen at Signal Peak and Webster Point.

Sonchus tenerrimus L.		Not reported by Dunkle or Sumner & Bond. Currently spreading in the eastern portion of the island. Lower terrace just south of Middle Canyon, 15 March 1969, *Philbrick & Ricker B69-45,* apparently more common than in 1968; terrace east of Signal Peak, between Cat and Graveyard canyons, 19 March 1968, *B68-82* (MICH, SBBG); terrace east of upper Cat Canyon, 28 April 1968, *Philbrick & McPherson B68-247;* north-facing slope near mouth of Cave Canyon, 30 April 1969, *B69-111.* Linear leaf lobes and more rugose achenes distinguish this taxon from the similar *S. oleraceus.*

Xanthium spinosum L.		Known only from one collection. No definite locality, 3 July 1931, *Abrams & Wiggins 293* (DS).

{*Xanthium strumarium* L. (*X. pennsylvanicum* Wallr.).		*Xanthium pennsylvanicum* reported for Santa Barbara Island by Eastwood (1941, p. 74). No other evidence is known; a documenting specimen has not been located.}

Selected Bibliography

Bartholomew, G. A. 1967. Seal and sea lion populations on the California Islands. *In* R. N. Philbrick, ed., Proc. Symp. Biol. Calif. Islands, pp. 229–244. Santa Barbara Bot. Gard., Santa Barbara.

Britton, J. R. 1897. Our summer isles. Land of Sunshine 7:192–197.

Corey, W. H. 1954. Tertiary basins of Southern California. Calif. Dept. Nat. Resources, Div. Mines Bull. 170 (chap. 3):73–83.

Diamond, J. M. 1969. Avifaunal equilibria and species turnover rates cn the Channel Islands of California. Proc. Natl. Acad. Sci. U.S.A. 64:57–63.

DUNKLE, M. B. [Unpubl. 1940]. Los Angeles Museum—Channel Islands Biological Survey, Santa Barbara Island report, botany. 11 pp.

————. 1942. Contributions from the Los Angeles Museum—Channel Islands Biological Survey. 27. Flora of the Channel Islands National Monument. Bull. S. Calif. Acad. Sci. 41:125–137.

————. 1950. Plant ecology of the Channel Islands of California. Publ. Allan Hancock Pacific Exped. 13:247–386.

EASTWOOD, A. 1941. The islands of Southern California and a list of the recorded plants. 2. Leafl. W. Bot. 3:54–78.

EMERY, K. O. 1960. The sea off Southern California, a modern habitat of petroleum. Wiley & Sons, New York. 366 pp.

FARNHAM, T. J. 1849. Life, adventures, and travels in California, to which are added the conquest of California, travels in Oregon, and history of the gold regions. Nafis & Cornish, New York. 468 pp.

FOREMAN, R. E. 1967. Observations on the flora and ecology of San Nicolas Island. U.S. Naval Radiol. Defense Lab. TR–67–8:1–79.

GRINNELL, J., and A. H. MILLER. 1944. The distribution of the birds of California. Cooper Ornith. Club, Pacific Coast Avifauna 27:1–608.

HOWELL, A. B. 1917. Birds of the islands off the coast of Southern California. Cooper Ornith. Club, Pacific Coast Avifauna 12:1–127.

KEMNITZER, L. E. 1933. Geology of San Nicolas and Santa Barbara islands, Southern California. M.S. Thesis, Calif. Inst. Tech., Pasadena. 45 pp.

LIPPS, J. H., J. W. VALENTINE, and E. MITCHELL. 1968. Pleistocene paleoecology and biostratigraphy, Santa Barbara Island, California. J. Paleontol. 42:291–307.

MORAN, R. 1967. Discussion of the flora of Guadalupe Island. *In* R. N. Philbrick, ed., Proc. Symp. Biol. Calif. Islands, pp. 69–70. Santa Barbara Bot. Gard., Santa Barbara.

MUNZ, P. A. 1935. A manual of Southern California botany. Claremont Coll., Claremont. 642 pp.

————. 1959. A California flora. Univ. Calif. Press, Berkeley & Los Angeles. 1681 pp.

————. 1968. Supplement to a California flora. Univ. Calif. Press, Berkeley & Los Angeles. 224 pp.

RAVEN, P. H. 1963. A flora of San Clemente Island, California. Aliso 5:289–347.

REDDICK, T. [Unpubl. 1939]. Notes on the Channel Islands Biological Survey of the Los Angeles Museum, Santa Barbara Island. 3 pp.

SAVAGE, J. M. 1967. Evolution of the insular herpetofaunas. *In* R. N. Philbrick, ed., Proc. Symp. Biol. Calif. Islands, pp. 219–227. Santa Barbara Bot. Gard., Santa Barbara.

SUMNER, E. L., JR. [Unpubl.] 1958. The rabbits of Santa Barbara Island, a progress report and summary. 21 pp.

————., and R. M. BOND. [Unpubl. 1939]. An investigation of Santa Barbara, Anacapa, and San Miguel islands, California. 73 pp.

THORNE, R. F. 1967. A flora of Santa Catalina Island, California. Aliso 6:1–77.

————. 1969. A supplement to the floras of Santa Catalina and San Clemente islands, Los Angeles County, California. Aliso 7:73–83.

TOWNSEND, C. H. 1890. Scientific results of explorations by the U.S. Fish Commission steamer Albatross. 14. Birds from the coasts of western North America and adjacent islands, collected in 1888–'89, with descriptions of new species. Proc. U.S. Natl. Mus. 13:131–142.

VALENTINE, J. W., and J. H. LIPPS. 1967. Late Cenozoic history of the Southern California Islands. *In* R. N. Philbrick, ed., Proc. Symp. Biol. Calif. Islands, pp. 21–35. Santa Barbara Bot. Gard., Santa Barbara.

VON BLOEKER, J. C., JR. 1967. Land mammals of the Southern California Islands. *In* R. N. Philbrick, ed., Proc. Symp. Biol. Calif. Islands, pp. 245–263. Santa Barbara Bot. Gard., Santa Barbara.

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RARE NATURAL HYBRIDIZATION IN PHORADENDRON (VISCACEAE)

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Natural hybridization is a characteristic of many groups of flowering plants. The mistletoes, however, appear to be an exception. The virtual absence of hybridization in *Phoradendron* was first mentioned by Wiens (1961). The same situation appears to prevail in the related genus *Arceuthobium* where extensive field work throughout the western United States, Mexico, Guatemala, and Honduras has failed to produce any evidence of natural hybridization (Wiens, 1968; Hawksworth and Wiens, 1971).

The near absence of hybridization is not limited to the North American viscaceous mistletoes but it apparently a world-wide phenomenon and characteristic of the loranthaceous mistletoes as well. During the course of field work in Mexico (Wiens, 1964a; Hawksworth and Wiens, 1965), Guatemala, Honduras, Costa Rica, Hispaniola, Ecuador, Chile, Malaya, and Ceylon (Barlow and Wiens, 1971; Wiens and Barlow, 1971), no evidence of natural hybridization has been observed in either mistletoe family.

The Australasian mistletoes also exhibit a near absence of natural hybridization (Barlow, 1966). Previous reports of both inter- and infra-generic hybridization in New Zealand Loranthaceae (Thomson, 1949; Smart, 1952; Cockayne and Allan, 1934) are strongly questioned by Barlow (1966).

Such apparent lack of hybridization in entire families is rare in the flowering plants. The apparent evolutionary and systematic consequences of such behavior are discussed in some detail with respect to the related viscoid genus *Arceuthobium* (Hawksworth and Wiens, 1971). In *Arceuthobium* these authors proposed that lack of hybridization has produced dendritic patterns of evolution typically associated with animals, whereas reticulate patterns of evolution are more common in flowering plants. Hawksworth and Wiens (1971) suggested that dendritic patterns produced relatively clear evolutionary lines with more clearly defined species than is generally typical of flowering plants.

The primary object of this report is to discuss natural hybridization between *Phoradendron juniperinum* Engelm. subsp. *juniperinum* and *P. bolleanum* (Seem.) Eichler subsp. *densum* (Torr.) Wiens. Another case of probable hybridization involves *P. tomentosum* (DC.) Engelm.

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ex Gray subsp. *macrophyllum* (Engelm.) Wiens and *P. villosum* (Nutt.) Nutt. subsp. *villosum* and is discussed later in the paper. Although the former hybrid combination has been briefly mentioned (Wiens, 1961; Vasek, 1966) the general rarity of hybridization in the mistletoes warrants better documentation and discussion of this hybrid combination.

ECOLOGICAL ASPECTS OF "JUNIPERINUM" $\times$ "DENSUM" HYBRIDIZATION

The parental taxa are members of section *Pauciflorae*, which is one of the most reduced and (presumably) highly derived species groups in the genus. Both species are widely distribtued parasites of juniper (occasionally cypress) in the western United States and Mexico; their distributions are among the most northerly in the section and in the genus as a whole. For a thorough discussion of the relationships, taxonomy, host preferences, and distribution of these taxa see Wiens (1964b). In southern California "juniperinum" and "densum" are primarily parasitic on *Juniperus occidentalis* and *J. californicum*, respectively. In other parts of their range, however, different species are the principal hosts.

Only two instances of hybridization between "juniperinum" and "densum" are known; both are in southeastern California. One hybrid population occurs in Inyo County on the northeastern edge of the Inyo Mountains above Whippoorwill Flat on the road between Big Pine and Saline Valley [a representative collection is *W 2667* (RSA)]. The other was discovered by Vasek (1966) in the vicinity of Rose Mine in the San Bernardino Mountains. In both instances "juniperinum" and 'densum" parasitize *Juniperus osteosperma*. All our observations are based on the Whippoorwill Flat population.

In this population both parental species are plentiful on *J. osteosperma* along the eastern slopes above the southern end of the flat. Both species of mistletoe grow freely on the same tree, frequently on the same branch, and often within a decimeter or two of one another. Although both mistletoes are prevalent in the area, "juniperinum" is seemingly more abundant than "densum", particularly with increasing elevation and/or on northfacing slopes. Vasek (1966) also reports that in the Rose Mine population "juniperinum" is more common when the two parental species occur together.

In the Whippoorwill Flat population the predominance of "juniperinum" is probably due to climatic factors. The total geographic distribution of the two mistletoes shows that "juniperinum" is adapted to a broader climatic amplitude than "densum" and generally occurs in regions with lower winter temperatures than does "densum". For example, in southern Arizona both "juniperinum" and "densum" are locally abundant south of the Mogollon Rim; however, only "juniperinum" occurs north of the rim and ranges as far north as east central Oregon, northern Utah, and western Colorado, well north of the dis-

tributional range of "densum". These apparent geographical climatic preferences are reflected elevationally in the Whippoorwill Flat area.

The slopes above the southeastern side of Whippoorwill Flat where the hybrid occurs, and in which "juniperinum" predominates quantitatively, occupies elevations from approximately 7250 to 7550 ft. South of Whippoorwill Flat the road descends to Saline Valley and to about 6800 ft. both parental mistletoes remain common. However, by approximately 6500 ft. only "densum" is present. This suggests an altitudinal overlap of about 600 ft. in which hybridization is possible.

Further generalized observations in the area also support the previously suggested altitudinal demarcations of "densum" and "juniperinum." Immediately north of Whippoorwill Flat are the headwaters of Marble Canyon where elevations quickly decrease to levels below which Pinyon-Juniper Woodland does not occur. The north end of the ridge bordering Whippoorwill Flat attains an altitude of approximately 7475 ft. In this location Pinyon-Juniper Woodland is well-developed, but the trees are perhaps somewhat smaller than in the area where the hybrids occur. "Juniperinum" was plentiful along this northern ridge from the summit to the fringes of juniper distribution at about 6600 ft. No "densum", however, was observed in the locality although it is lower than Whippoorwill Flat. This area is apparently exposed directly to storms moving eastward from the Sierra Nevada and probably subject to environmental extremes greater than those occurring on Whippoorwill Flat. This may explain both the absence of "densum" from this location and the apparent reduction in the size of the junipers. "Densum" appears to attain its highest altitudinal limits in areas where the Pinyon-Juniper Woodland is best developed; these areas probably correspond to locations not subjected to environmental extremes. This entire situation might provide an interesting opportunity to obtain precise quantitative data relating to environmental gradients associated with closely related species and their hybrid progeny.

In addition to the elevational preferences, the two mistletoes also appear to exhibit differences in flowering time. On the basis of bud sizes observed in June "juniperinum" probably reaches peak flowering time somewhat later than "densum" and the two species are probably weakly seasonally isolated. We have not observed the population during anthesis but we estimate that "densum" reaches peak flowering in early July, whereas "juniperinum" probably attains maximum flowering in late July. This would allow a period of perhaps two to three weeks during which cross pollination could occur.

Although Vasek (1966) states that hybrids are not difficult to find we have not observed a high frequency of hybrid individuals. We have not made actual counts but it seems unlikely that we have observed more than 15–25 hybrids in this population. The number of individuals forming the parental populations must certainly number into the thousands.

GENETIC ASPECTS OF THE "JUNIPERINUM" × "DENSUM" HYBRID

The most characteristic feature of the hybrid is the intermediate nature of the leaves. As indicated in Figure 1, "juniperinum" has leaves reduced to minute, connate scales about 1 mm long. "Densum" has well-developed leaves ca 10–13 mm long and ca 3–4 mm wide. The mature leaves of the hybrid are only ca 4–6 mm long, and ca 2 mm wide but they are clearly distinct. The nature of the leaves is the most readily identifying feature of the hybrids. There is relatively little morphological variation in the hybrids and none of our observations suggests the occurrence of backcrossing to either parental species. Furthermore, we have never found any fruit development on the hybrid individuals although abundant mature fruit has been observed on both parental
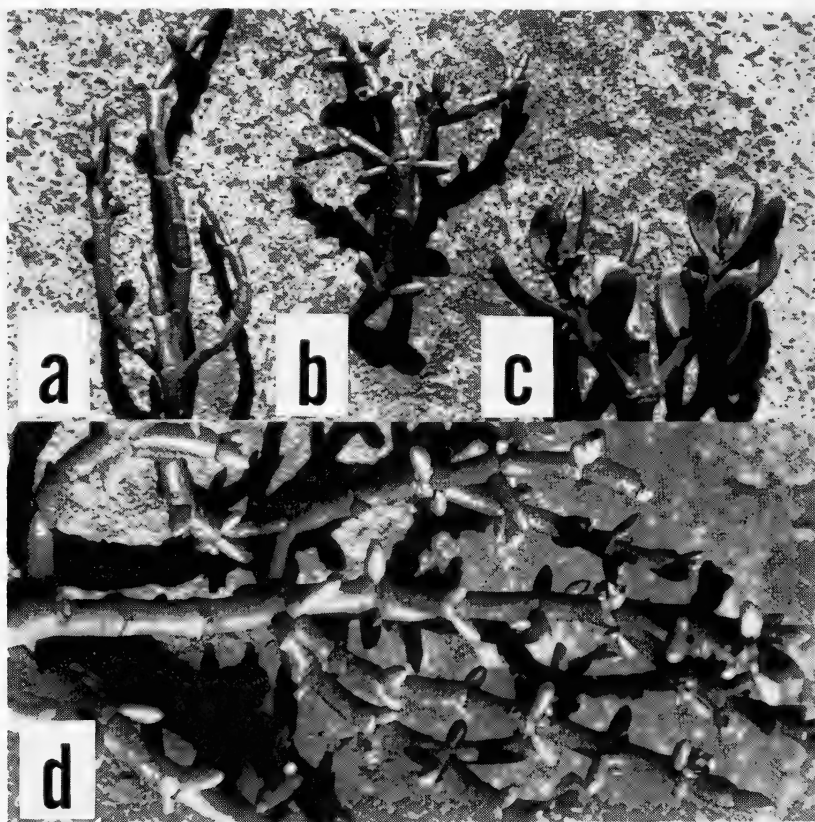

Fig. 1. Recognized species and their natural hybrid in *Phoradendron:* a. *P. juniperinum* ssp. *juniperinum;* b, *P. juniperinum* ssp. *juniperinum* × *P. bolleanum* ssp. *densum;* c, *P. bolleanum* ssp. *densum;* d, *P. juniperinum* ssp. *juniperinum* × *P. bolleanum* ssp. *densum.*

species. As previously mentioned we have never observed the population at anthesis and we have not determined if the flowers of the hybrid are functional or if they produce fertile pollen. Developing flowers of the hybrid, however, were studied perhaps a month prior to anthesis and attempts were made to observe the pairing relaitonships of the chromosomes during microsporogenesis. Dividing pollen mother cells were rare and the anthers themselves appears generally aberrant. The few meiotic cells observed suggested that there was little or no pairing of the chromosomes. Both parental species of this population are meiotically normal diploids with a chromosome number of $n = 14$ (Wiens, 1964a).

The generally consistent and intermediate morphology of the hybrids, their seemingly aberrant meiotic behavior, the complete absence of fruit formation, and finally, their low frequency of occurrence in the parental populations, strongly suggest that these plants are sterile F_1 hybrids. As such they have no evolutionary significance unless fertility could be regained through polyploidy, or sterility circumvented through agamospermy.

The hybrids, however, show a surprising resemblance to a poorly known Mexican species, *P. minutifolium* Urban, which is also a member of the *Pauciflorae*. The leaves are especially similar to the hybrid except that they are deciduous with age (Trelease, 1916, Pl. 16). This species is also typically several times larger than the hybrids. *Phoradendron minutifolium* was known only from the type locality on the Cofre de Perote in eastern Veracruz until it was discovered in other areas as distant as Durango (Wiens, 1964b). More recently it was collected by F. G. Hawksworth (pers. comm.) in the Sierra del Carmen in Coahuila, just south of the Texas border. At least in northern Mexico *P. minutifolium* is broadly sympatric with both *P. bolleanum* subsp. *bolleanum* and subsp. *densum* and *P. juniperinum* subsp. *juniperinum;* all are parasites on juniper.

It is tempting to speculate that *P. minutifolium* originated through hybridization between geographic elements of *P. bolleanum* and *P. juuiperinum*. The situation would appear to resemble that of a classical amphidiploid, but at least on the Cofre de Perote *P. minutifolium* has a normal haploid chromosome number of $n = 14$ (Wiens, 1964a) and highly fertile pollen. If the species did arise through hybridization between *P. bolleanum* and *P.. juniperinum* it must have been at the diploid level. This is rare in the flowering plants but a few cases have been reported. The hybrids at Whippoorwill Flat, however, are apparently highly sterile and this possibility does not seem likely. The morphological resemblance between *P. minutifolium* and hybrid could simply be fortuitous. Additional research is necessary to clarify the problem.

OTHER PUTATIVE HYBRIDS

Another case of possible natural hybridization involves *P. tomentosum* subsp. *macrophyllum* (= *P. flavescens* var. *macrophyllum*) and

P. villosum subsp. *villosum*. This situation, however, is not as definite as the former. The flowering times of the putative parental species are especially difficult to reconcile since "macrophyllum" flowers from approximately December to March and "villosum" from approximately July to September. Only two collections of this putative hybrid are known [representative collections are *W 970, 2672* (RSA)] from southern California, both on *Platanus racemosa*. One plant originated from upper Lytle Creek Canyon in San Bernardino Co. and the other from the mouth of Cobal Canyon above Claremont in Los Angeles Co.

The most unusual morphological feature of these presumed hybrids is the narrow leaf, which is beyond the range of variation in either of the suspected parental species (fig. 2). The supposed hybrid observed in obal Canyon occurred in a normal population of "macrophyllum" parasitizing *Platanus racemosa* along the canyon bottom, although "villosum" was present on *Quercus dumosa* several hundred yards above the canyon bottom. This plant was staminate and appeared to produce flowers at about the same time as "macrophyllum".

An analysis of microsporogenesis is this plant revealed a high incidence of irregularities generally associated with meiosis in species hybrids, viz. lack of pairing and lagging chromosomes at first metaphase and anaphase, and the production of micronuclei (fig. 3). Furthermore, observations of this apparent hybrid during one season revealed that

Fig. 2. Recognized species in *Phoradendron* and their putative hybrid: a, *P. tomentosum* ssp. *macrophyllum;* b, Putative *P. tomentosum* ssp. *macrophyllum* × *P. villosum* ssp. *villosum;* c. *P. villosum* ssp. *villosum.*
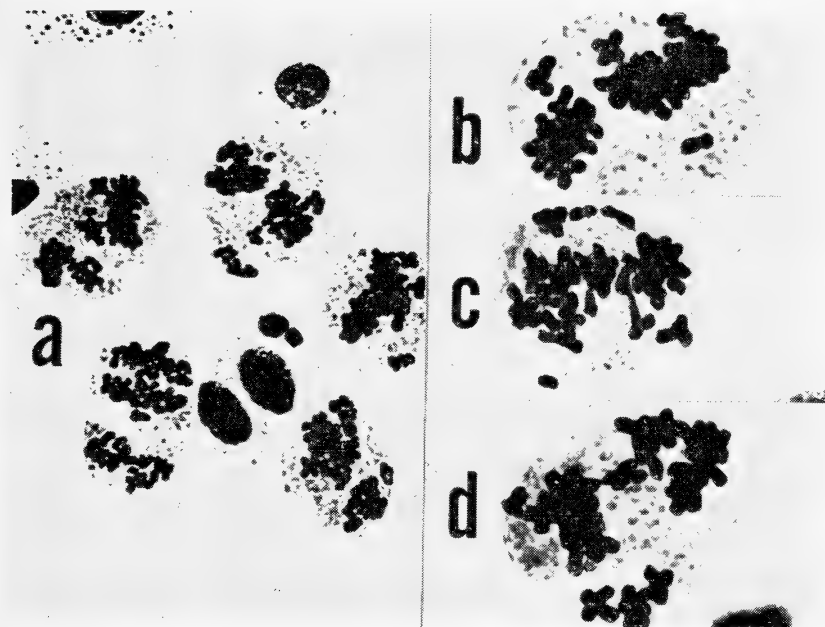
Fig. 3. Microsporogenesis in the putative hybrid *P. tomentosum* ssp. *macrophyllum* × *P. villosum* ssp. *villosum:* a, Irregular anaphase distributions with univalents and lagging chromosomes (upper cell), tetrad with micronuclei formation (lower cell), ca. × 400; b, Lagging univalent (lower right), ca × 600; c, Irregular distribution and high incidence of univalent formation, ca × 600; d, Irregular anaphase distributions, ca × 600.

although the floral buds developed normally, anthesis never occurred. This suggests an interesting case of hybrid inviability in which development is apparently complete except for the actual opening of the flowers.

As mentioned previously this is not a clear case of natural hybridization. The great disparity of flowering times between the potential parents and the lack of an intermediate morphology of the plants does not strongly support a hybrid origin of plants with this phenotype. The irregular meiosis, however, and the failure of anthesis do indicate a hybrid origin. Additional plants with this phenotype will have to be studied before the origin of this peculiar morphotype can be determined.

LITERATURE CITED

BARLOW, B. 1966. A revision of the Loranthaceae of Australia and New Zealand. Austral. J. Bot. 14:421–499.

BARLOW, B. and D. WIENS. 1971. The cytogeography of the loranthaceous mistletoes. Taxon 20:291–312.

COCKAYNE, L. and H. ALLAN. 1934. An annotated list of groups of wild hybrids in the New Zealand flora. Ann. Bot. 48:1–55.

HAWKSWORTH, F. G. and D. WIENS. 1965. *Arceuthobium* in Mexico. Brittonia 17:213–238.

————. 1971. The biology and classification of dwarf mistletoes *(Arceuthobium)*. U.S. Dept. of Agric. Handbook (in press).

SMART, C. 1952. The life history of *Tupeia* Cham. et Schlect. (Loranthaceae). Trans. Roy. Soc. N.Z. 79:459–466.

THOMSON, W. 1949. A natural hybrid between *Loranthus micranthus* and *Tupeia antarctica*. Trans. Roy. Soc. New Zealand 77:208.

TRELEASE, W. 1916. The genus *Phoradendron:* A monographic revision. Univ. of Illinois Press, Urbana.

VASEK, F. 1966. The distribution and taxonomy of three western junipers. Brittonia 18:350–372.

WIENS, D. 1961. A taxonomic study of the acataphyllous species of *Phoradendron*. Ph.D. Thesis, Claremont Graduate School and University Center, Honnold Library, Claremont, Calif.

————. 1964a. Chromosome numbers in North American Lorenthaceae: *Arceuthobium, Phoradendron, Struthanthus, Psittacanthus*. Amer. J. Bot. 51:1–6.

————. 1964b. Revision of the acataphyllous species of *Phoradendron*. Brittonia 16:11–54

————. 1968. Chromosomal and flowering characteristics in dwarf mistletoes *(Arceuthobium)*. Amer. J. Bot. 55:325–334.

WIENS, D. and B. BARLOW. 1971. The cytogeography and relationships of the viscaceous and eremolepidaceous mistletoes. Taxon 20:313–332.

NOTES AND NEWS

CRUPINA VULGARIS (COMPOSITAE: CYNAREAE), NEW TO IDAHO AND NORTH AMERICA. *Crupina vulgaris* Cass., native to the Mediterranean region of Europe, grows in Idaho. The discovery of a well-established colony of this species constitutes the first known record for North America. The plant is a coarse, rank annual that averages 120 cm. in height. Although *C. vulgaris* resembles some members of *Centaurea,* it can be readily distinguished by its inconspicuous flower (one to several per head) and its distinctive shuttlecock-like fruit. The fruit, a heavy-bodied achene, is topped by a conspicuous crown of dark brown pappus bristles which graduate in length from the very short outermost to 1.5 times longer than the body of the achene for the innermost. *C. vulgaris* was found July 26, 1969, in Idaho County, 6 miles ENE of Grangeville on the Sammy VonBargen ranch. The colony was located along State Highway 13 on the Harpster Grade 4.5 road miles from Harpster (NW ¼ Sec. 7, T. 30N., R. 4E., B.P.M.). The plants were growing in basalt lava river breaks on dry, steep southerly facing rangeland at 2,700 feet elevation. My initial collection (*Stickney 1928,* ID, MONT, MONTU, WS, WTU, US, and USFS) was identified by Dr. Charles Feddema of the Forest Service Herbarium, U.S. Department of Agriculture. Queries to seven herbaria in the Pacific Northwest and two in Washington, D.C., revealed no record of previous occurrence in Idaho or North America. A second collection (*Stickney 2118,* IDS, OSC, and NY in addition to those listed above) was made from the same location to secure flowering material. The area of the collection site has had a long history of livestock grazing and of noxious weed establishment and control. The present vegetation is composed principally of introduced ruderal species, among which *Potentilla recta, Bromus tectorum, Lactuca serriola,* and *Dipsacus sylvestris* are prominent. Mr. VonBargen first noticed *C. vulgaris* growing in a small roadside colony at the collection site in 1968. A cursory examination by me in 1970 revealed that a vigorous stand of this species dominated an area of at least 40 acres. *C. vulgaris* appears to be well able to maintain itself under conditions present in the highly disturbed vegetation of this former bunchgrass rangeland. Its capability to invade other types of vegetation has not been observed and remains as yet unknown.—PETER F. STICKNEY, Intermountain Forest & Range Experiment Station, Ogden, Utah 84401.

MOSSES OF UNUSUAL INTEREST FROM BAJA CALIFORNIA

HOWARD CRUM

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The arid lands of Baja California support, naturally, a limited moss flora. The few collections that have been made there include, however, a fair number of species of interest which indicate floristic ties with California and Arizona rather than an expected relationship with Mexico's Sierra Madre Occidental or central plateau. Insofar as it is known, the bryoflora has been completely documented by Koch and Crum (1950), Crum and Miller (1957), and Crum and Steere (1959).

The present report, listing nine mosses new to Baja California, three of them new to Mexico, is based on a few incidental collections made by Reid Moran in 1958, 1961, and 1968 and C. F. Harbison in 1957. A complete set of specimens is deposited at SD. Some duplicates are represented in MICH.

Following is a list of localities, giving some details not repeated in the citation of individual specimens:

Guadalupe Island: Rocky arroyo wall, Arroyo Mepomene, ca. 400 m. alt., 28° 55½′ N, 118° 15′ W, *Reid Moran*, 29 April 1958.

Gaudalupe Island: North slope at north end of island, ca. 1000 m. alt., 29° 09½′ N, 118° 19′ W, *C. F. Harbison*, 14 December 1957.

Sierra San Borja: Decomposed granite, east slope of mountains above El Terminal, 1100 m. alt., 28° N, 113° 36′ W, *Reid Moran*, 25 Nov. 1961.

San Pedro Mártir: East slope of Cerro "2828," on east rim, 2800 m. alt., 31° 02′ N, 115° 27′ W, *Reid Moran*, 24 August 1968.

Ceratodon stenocarpus BSG. North end of Guadalupe Island, *Harbison*, Dec. 14, 1957. Cerro 2828, Sierra San Pedro Mártir, *Moran 15414* in part.—A genus new to Baja California. Both specimens are sterile and, therefore, the specific designation may be in some question. Both *C. stenocarpus* and *C. purpureus* (Hedw.) Brid. occur in Mexico and in the southwestern United States, but *C. stenocarpus* is by far the more common. It ranges from the American Southwest to Bolivia and is common in similar latitudes in the Old World.

Encalypta vulgaris Hedw. Cerro 2828, Sierra San Pedro Mártir, *Moran 15414* in part.—A calciphile widespread in western North America but not previously known from Mexico. It is widely distributed in Europe, Asia, Australia, Tasmania, New Zealand, and New Guinea.

Bryoerythrophyllum recurvirostrum (Hedw.) Chen. Cerro 2828, Sierra San Pedro Mártir, *Moran 15413* in part, *15414* in part.—A very wide-ranging calciphile, occurring in Europe, Asia, and Africa, and also across northern North America and south to Mexico, Arkansas, Ohio, and New York.

Tortula bartramii Steere. On decomposed granite, above El Terminal,

Sierra San Borja, *Moran 8506* in part.—A rare species already known from Sonora and Chihuahua, as well as the southwestern United States.

Tortula mucronifolia Schwaegr. Rocky wall of Arroyo Mepomene, Guadalupe Island, *Moran 6731.*—A circumpolar calciphile, widespread from Alaska to Greenland and south to northern Mexico in the West, Nebraska, the Great Lakes, and Nova Scotia in the East.

Grimmia apocarpa Hedw. Cerro 2828, Sierra San Pedro Mártir, *Moran 15414* in part.—Nearly cosmopolitan but limited to upland or montane areas with outcropping rock.

Pohlia elongata Hedw. Cerro 2828, Sierra San Pedro Mártir, *Moran 15414* in part.—A montane species of wide, circumboreal distribution but rare and local. British Columbia to Arizona and New Brunswick to Minnesota and south to Georgia. These plants are autoicous and could therefore be referred to *P. acuminata* Hornsch. (which is permitted both paroicous and autoicous inflorescences), but I do not feel that the supposed differences justify differentiation of two species.

Mnium arizonicum Amann. Cerro 2828, Sierra San Pedro Mártir, *Moran 15413* in part.—Only a few plants were found, scattered in mixture with several other mosses, but enough to demonstrate the distinctive shape, serration, and areolation of the leaves of this rare species which ranges from Wyoming and Utah south to New Mexico and Arizona. A first record for Mexico.

Hypnum revolution (Mitt.) Lindb. Cerro 2828, San Pedro Mártir, *Moran 15413, 15414.*—Circumpolar; a characteristic calciphile of northern and Rocky Mountain distribution, already known from Mexico, from Puebla and Tamaulipas.

LITERATURE CITED

CRUM, H. and H. A. MILLER. 1957. Bryophytes from Guadalupe Island, Baja California. Southw. Naturalist 1:116–120. (1956).

CRUM, H. and W. C. STEERE. 1959. Some bryophytes from Baja California. Southw. Naturalist 3: 114–123. (1958).

KOCH, L. F. and H. CRUM. 1950. Mosses of Baja California. Rev. Bryol. Lichénol. 19: 188–192.

NOTES AND NEWS

NEW LOCALITY FOR LAVATERA VENOSA S. WATS. (MALVACEAE).—*Lavatera venosa* was described from the San Benito Islands, off the west coast of central Baja California, where it is common on all three islands. Brandegee (Zoe 5:25, 1900) reported it also from San Geronimo Island and from a rock at the mouth of San Bartolomé Bay. On tiny San Geronimo, a guano island mostly barren of plant life, only two plants of *L. venosa* were found in 1963; and the guano keeper, who knew every inch of the island, said there were no more (*Moran 10574,* SD).

In April 1971, I found a single plant of *L. venosa* on Isla Ascunción, about 53 miles southeast of San Bartolomé Bay. However, a small islet off the northeast shore was topped by a lush growth of what appeared through the binoculars to be the same plant, and the guard told me that it was the same.—R. MITCHEL BEAUCHAMP, Department of Botany, San Diego State College, San Diego, California 92115.

A FEN ON THE NORTHERN CALIFORNIA COAST

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Introduction

Sphagnum bogs are not common in California but are to be found in montane situations and, as a novelty, at elevations of less than 650 feet above sea level in drainage hollows on the sterile sands of the Blacklock soil series in the 'pygmy forest' area of Mendocino County. They have been unknown at sea level in this state. However, along the coast of the Pacific Ocean, in Oregon, Washington, British Columbia and Alaska, bogs among the sand-dunes are not uncommon. This paper reports the existence of a stand of sphagnum-containing aquatic and semi-aquatic vegetation six and a half miles north of Fort Bragg (Mendocino County), between Cleone and Inglenook (fig. 1). This appears to be the southernmost extant example of this kind of vegetation on the Pacific Coast and is better described as a fen than as a bog—and will be referred to in this paper as the Inglenook fen.

Fens have been studied most carefully in the British Isles (where they are especially extensive in eastern England) and it may, therefore, be most appropriate to turn to the late Sir Arthur Tansley's encyclopedic account of British vegetation for an explanation of the differences between marsh, fen and bog. Tansley (1939, p. 634) gives the title *marsh* to a soil vegetation type in which the soil is waterlogged, the summer water level being close to or conforming with, but not normally much above, the ground level, and in which the soil has an inorganic (mineral) basis. *Fen* is a corresponding type (whose vegetation is closely similar to that of a marsh) in which the soil is organic (peat) but may be alkaline, neutral or even somewhat acid in reaction. *Bog,* on the other hand, forms peat which is extremely acid and bears a radically different vegetation. Usually, the soil of a bog is very poor in exchangeable bases while a fen is relatively rich in them and, as a consequence, rather highly productive.

In fens, the soil may be pure peat or, if silting is a factor in the basin where the water accumulates, it may contain varying amounts of mineral matter. Often fens are clearly successional stages in hydroseres leading to a forest climax; the Inglenook fen appears to be of such a type and is surrounded by a woody *fen-carr* (cf. Tansley, 1939, p. 644).

For about ten miles along the coast north of Fort Bragg there are magnificent unstable sand-dunes. Sand which is brought to this stretch of the coast by ocean currents is carried onshore by tidal action and deposited. When dry, it is blown inland by the prevailing westerly winds. These sand-dunes are advancing over the lowest of a series of terraces (actually raised beaches) formed by a combination of ocean level changes and local tectonic movements. Gardner (1967) has described a series of these terraces at 100, 175, 300, 475 and 600 feet elevation. It is the lowest (and most seaward) of these which is presently being

Fig. 1. Fen–locations in California: shaded areas around and south of Fort Bragg are the "pygmy forests."

invaded by the sand-dunes. It is largely covered with coastal prairie (Munz and Keck, 1949–50). The coniferous forests of the area are developed on the older and higher dune and terrace systems and contain mostly *Pinus muricata* D. Don, *Sequoia sempervirens* (D. Don) Endl. and *Pseudotsuga menziesii* (Mirb.) Franco. Streams draining toward the coast from these forested hills are impeded by the sand-dunes and this is how Inglenook Fen is formed.

Slightly farther south are the "pygmy forests" of *Pinus contorta*
Dougl. var. *bolanderi* (Parl.) Vasey and *Cupressus pygmaea* (Lemmon)
Sarg. (fig. 1). The soils of all the coniferous forests are podsolized and
those of the pygmy forest represent an extreme in podsolization (Jenny,
Arkley and Schultz, 1969). Although the streams draining from the
forests into the Inglenook fen are too far north to carry drainage water
from the "pygmy forests" and their associated bogs, they are distinctly
acid in reaction. One such stream leads into the fen under State Route 1,
75 yards north of the junction with Little Valley Road, about 6 miles
north of Fort Bragg. The pH of its water measured on July 10, 1966
(Beckmann pH meter, model N) was 4.9. During and after the winter
rains the pH rises (e.g to 6.5 on April 12, 1969). On the other hand,
the sand-dunes into which the stream flows are rich in shell-fragments.
As a result, both the pH and the base status of the fen (which lies be-
tween the road and the dunes) may be expected to be raised by the
material which slips down or is blown from the dunes into the fen and
by the waters which drain from the dunes. A final barrier to the escape
of water from among the dunes is posed by the "Ten Mile River Logging
Road" of the Boise Cascade Company which runs from Fort Bragg to
the Ten Mile River along the margin of the ocean. Although there is
evidence of seepage and actual overflow beneath the road in one place,
the impediment is a real one and the area around the "outlet" receives
enough moisture to allow grass to grow and provide for limited cattle
grazing. As a consequence of these physical and chemical features of the
environment, a floristically rich and luxuriant vegetation (contrasting in
dramatic fashion with the floristic poverty and apparently very low
productivity of the true bogs of the "pygmy forest" are) is produced—
the Inglenook fen.

My attention was called to the existence of this remarkable piece of
vegetation by my interest in one angiosperm species which is an impor-
tant constituent of it. *Menyanthes trifoliata* L., the Bog Bean (or Buck
Bean), belongs to the family Menyanthaceae. It is of interest to students
of reproductive biology by reason of the heterostyly of its flowers (Dar-
win, 1877; Baker, 1959). The species has a circum-boreal distribution
and usually grows in acid waters; in northern Europe as well as in
eastern and northern North America it occurs at sea-level as well as in
the mountains, but passing southward in western North America the
lowland part of the elevational range is supposedly lost. In California, its
contemporary altitudinal range is given as 3,000 to 10,000 feet above
sea-level by Jepson (1939). According to Mason (1957) it is restricted
to the Sierra Nevada, while Munz (1959) reports its occurrence only
at elevations of 3,000 to 10,500 feet (in Yellow Pine Forest to Subalpine
Forest). Hewett (1964), in his account of the ecology of *M. trifoliata*
for the 'Biological Flora of the British Isles', draws conclusions as to
the limits for this species in western North America on the basis of the
distribution given in Munz (1959).

Consequently, I was excited when shown by Wayne Roderick a specimen of this species which he had collected at sea level in Mendocino County. I was introduced to the owner of the property, R. R. Ross, who graciously gave me permission to make a study of the plants and their habitat.

Both long-styled and short-styled plants of *M. trifoliata* occur in the Inglenook fen, so an artificial introduction of the species from one of its well-known high-altitude stations becomes an unlikely explanation for this apparently unique occurrenec at sea level in California. As will be seen later, the naturalness of its occurrence is backed up by the floristic constitution of the vegetation here—an association of species which naturally accompanies *Menyanthes* in a series of boggy sitautions northward along the Pacific coast to Alaska but is otherwise unknown from California at the present day. Hansen (1943) records *M. trifoliata* from what appears to be the next fen northwards, five miles south of Bandon, Coos County, Oregon. Here again, drainage from land covered by pine trees *(Pinus contorta)* is impeded by actively moving sand-dunes. *M. trifoliata* also occurs in other coastal bogs and fens as far north as British Columbia and Alaska (cf. Rigg, 1922, 1925; Jones, 1936; Hanson and Churchill, 1961, p. 182; etc.).

Although no lowland occurrence of *M. trifoliata* in California is mentioned by Mason (1957), there is, in the University of California Herbarium *(UC)*, in Berkeley, a specimen collected by him on 18 May, 1946 *(Mason 12771)*, at this very site.

The occurrence near sea level of a species which is otherwise of higher altitude distribution in California recalls two other instances. Along the South Fork of the Eel River, near Pesula Road, in Humboldt County, Ichiro Fukuda has found a triploid plant of *Achlys triphylla* (Sm.) DC. growing among the usual tetraploid plants under the shade of the Coast Redwood *(Sequoia sempervirens)*. A diploid form occurs at higher elevations, usually under Douglas Fir *(Pseutotsuga menziesii)* and the triploid is most reasonably explained as a relic hybrid from the days when the diploid grew at a lower altitude than that of its present stations (Fukuda, 1967). Similarly, A. P. Nelson (1962), investigating the genecology of *Prunella vulgaris* L. in California, concluded that some samples from the immediate vicinity of the South Fork of the Eel River (at Eagle Point, Humboldt County) also showed more affinity with montane races than is usually the case for plants growing at only 200 feet above sea level.

There is little doubt that there was a perceptible cooling of climate, during the glacial episodes of the Pleistocene epoch, far south of the limit of the ice sheets (Heusser, 1960; Axelrod, 1967). Unfortunately, the precise record for the northern California coast has still to be worked out. Thus, the pollen sequences in peat bogs studied by Heusser (1960), one of which was located two miles southeast of Fort Bragg in the pygmy

forest, begin only in the Late Postglacial, so that they show little diverg-
ence from contemporary pictures.

One conclusion of Heusser's, however, which may be important for
our consideration is that there was an extensive marine transgression
along the Pacific coast between 4,500 and 2,000 B.C., apparently due to
a eustatic rise in sea level resulting from the melting of polar ice during
the Hypsithermal (or Altithermal) period. According to H. Jenny (per-
sonal communication) the rise in sea level was probably of the order of
ca 13 feet. The altitude of the fen at present is less than 40 feet above
sea level and the open water (shown on the latest topographic map as
"Sandhill Lake") is 24 feet above sea-level, but no data are yet avail-
able to show whether this eustatic change would have caused marine
flooding in the fen because we know nothing of geologically recent iso-
static changes which may have occurred in the area. Even if the fen
did not exist in its present site, conditions for its occurrence may then
have been favorable farther inland.

The direct influence of the raised temperatures of the Hypsithermal
must also be taken into account. There is some evidence)Heusser, 1960;
Axelrod, 1967) that the Bishop Pine *(Pinus muricata)* extended its
range farther northward at this time (6,000–1,000 B.C.) and that Sitka
Spruce *(Picea sitchensis)* has migrated southward since that time in
response to a favorable increase in moisture. The present southernmost
stand of Sitka Spruce is located between Mendocino and Fort Bragg.
Consequently, it may be that the Inglenook fen is not more than 3 or 4
thousand years old, although, on the other hand, it (and its flora, in
particular) may also have a California coastal history which reaches
back to the Pleistocene.

If the *Menyanthes* population in the Inglenook fen should truly be a
relic from a cooler climatic period in the past (persisting in its present
locality because of the chill fogs which beset the Fort Bragg area, par-
ticularly during the summer months), it might be expected that traces
of the same plant association would be discovered elsewhere. In fact,
there is another lowland record of *M. trifoliata,* from San Francisco,
where it flourished in a "marsh" until it became extinct in 1859 (Behr,
1888). The circumstances of this occurrence will be referred to later.

Structure and Composition of the Inglenook Fen

The Inglenook fen shows a well-marked zonation which is indicated
roughly on the sketch-map (fig. 2). The following zones may be dis-
tinguished:

Open water   (a) with fringing emergent vegetation
Fen proper   (b) almost pure *Carex* and *Heleocharis* tussocks
             (c) *Calamgrostis*/Cyperaceae/*Menyanthes* fen with
                  Ledum, Sphagnum, etc.
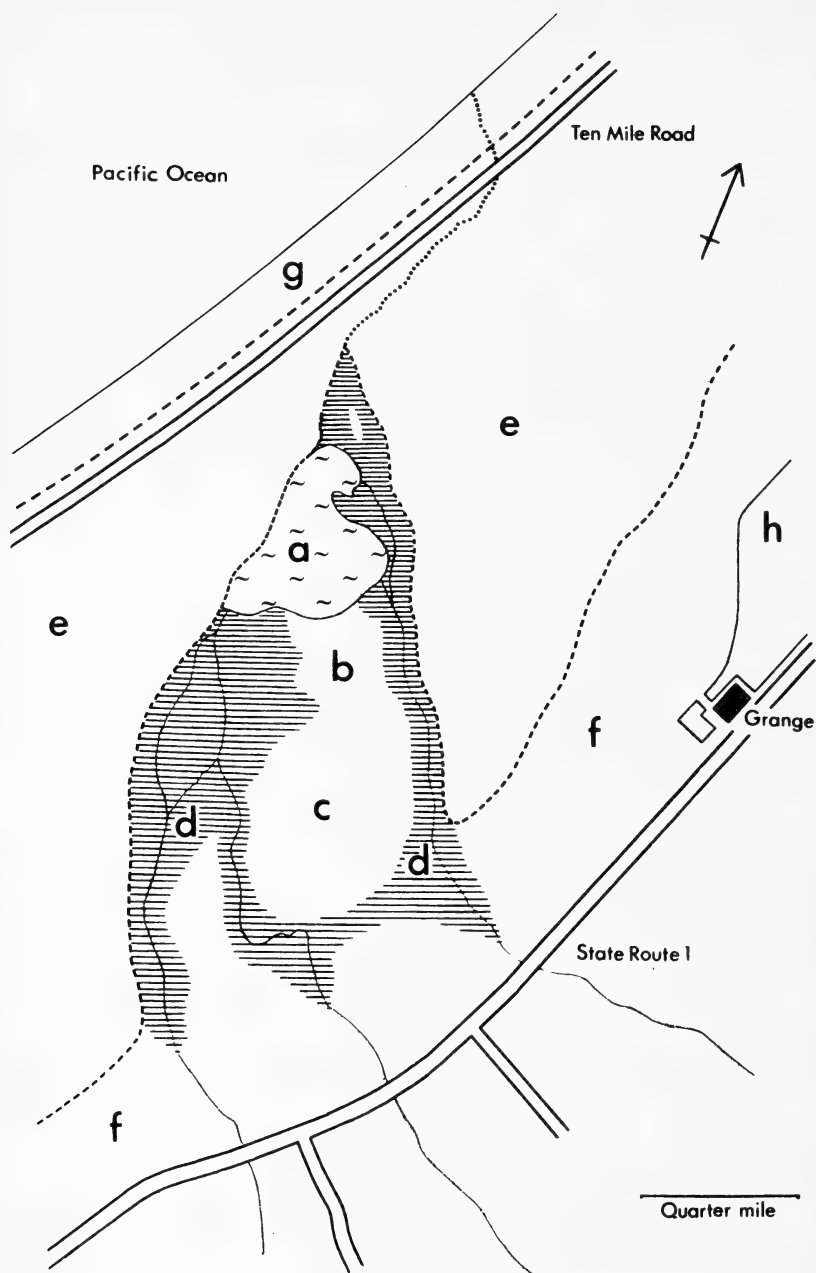   (d) Fen carr

Fig. 2. Sketch map of the Inglenook Fen and surroundings: a = open water; b = Cyperaceae dominated fen; c = Calamagrostis-Cyperaceae-Menyanthes fen; d = fen carr; e = sand dunes; f = coastal prairie; g = strand; h = Eucalyptus plantation.

The fen as a whole is bounded by the sand-dunes (e) which, of course, have a quite distinct flora and, at its inland limits, merges with the coastal prairie (f) of the 100 foot raised beach. The four major zones within the fen presumably represent successive stages in a hydrosere leading from fresh water which is too deep for rooted phanerogamic vegetation to a wet forest-type which is rather stable and might not give way to pine forest until some further raising of the land occurs.

Table 1A shows the results of analyses of water samples and, for comparison, a water extract of the sand-dune immediately adjacent to the fen. The influence of drainage and slippage from the dune in raising the pH of the pond is clear, as is the effect of peat formation in depressing it in the fen. The dunes are rich in calcium and contribute this to the fen while the sodium mostly comes from the inflow creek (and probably also from spray blown in from the sea). The calcium content of the water is high enough to supply plant needs and counteract unfavorable effects of high concentrations of sodium (H. Jenny, personal communication).

TABLE 1A. WATER SAMPLES AND WATER EXTRACTS (me/liter).

	pH	Na	K	Ca	Mg	Totals
Water from inflow creek	6.5	.66	.03	.40	.42	1.51
Water from auger hole (fen)	5.2	.97	.12	.20	.23	1.52
Water (surface) from Nuphar zone	5.6	.68	.02	.56	.25	1.51
Water from pond (west end)	7.0	.91	.03	.72	.27	1.93
Water extract of sand-dune						
(4 grms. in 250 ml.)	8.1	.10	.02	.93	.24	1.23

In Table 1B the acidity of the fen peat along with the relatively high base status of the samples is indicated. By comparison bog and sandy soil samples from the Blacklock soil series in the "pygmy forest" have even lower pH values and lower base status (A. E. Salem, unpub., and Jenny, et al., 1969).

TABLE 1B. SOIL SAMPLES—EXCHANGEABLE BASES (me/100 g. oven-dry material).

	pH	Na	K	Ca	Mg	Totals
Cyperaceae fen	4.5–4.8	6.6	5.1	18.2	13.6	43.5
Calam./Sphagnum fen	4.6	5.1	2.2	18.8	12.9	39.0
Fen carr (Menyanthes)	4.6–5.1	6.2	6.2	17.2	16.1	45.7
Fen carr	4.2	6.0	9.2	23.0	18.5	56.7

The floristic composition of the vegetational zones (table 2) is given without any claim that the lists are complete. All aspects of the ecology of this fen should be studied in appropriate detail in the future. When this is done, subdivision of the zones in the fen will certainly be possible. For example, the western part of the fen (toward the open water) consists of almost pure *Carex* and *Heleocharis* tussocks, while the greatest floristic diversity occurs in the central and eastern part of the fen. Topo-

TABLE 2. FLORISTIC COMPOSITION OF ZONES IN INGLENOOK FEN

	Zone 1 Open water	Zone 2 Fringing emergents	Zone 3 Fen	Zone 4 Fen Carr
Nuphar polysepalum Engelm.	+	+	+	
Equisetum hyemale L. var. robustum (A. Br.) A. A. Eat.		+		
Potentilla palustris (L.) Scop.		+	+	+
Cicuta douglasii (DC.) Coult. & Rose		+	+	
Oenanthe sarmentosa Presl		+	+	
Scirpus acutus Muhl.		+		
Typha latifolia L.		+	+	
Sphagnum sp.			+	
Calliergonella cuspidatum (L.) Loesk.			+	
Blechnum spicant (L.) Roth.			+	+
Hypericum anagalloides Cham. & Schlecht.			+	+
Nasturtium officinale R. Br.			+	
Ledum glandulosum Nutt. spp. columbianum (Piper) C. L. Hitchc.			+	
Gentiana sceptrum Griseb.			+	
Menyanthes trifoliata L.			+	+
Mimulus guttatus Fisch.			+	+
Myrica californica Cham. & Schlecht.			+	+
Epilobium adenocaulon Hausskn. var. parishii (Trel.) Munz			+	
E. watsonii Barb. var. franciscanum (Barb.) Jeps.			+	
Hydrocotyle ranunculoides L. f.			+	
Campanula californica (Kell.) Heller			+	
Veratrum fimbriatum Gray			+	
Lysichiton americanum Hult. & St. John.			+	+
Sisyrinchium californicum (Kerr) Dry.			+	
Habenaria dilatata (Pursh.) Hook. var. leucostachys (Lindl.) Ames			+	
Juncus effusus L. var. pacificus Fern. & Wieg.			+	+
J. effusus L. var. brunneus Engelm.			+	+
J. bolanderi Engelm.			+	
J. lesueurii Bol.			+	
J. phaeocephalus Engelm.			+	
J. ensifolius Wikstr.			+	+
Heleocharis acicularis (L.) R. & S.			+	
Carex vicaria Bailey			+	+
C. obnupta Bailey			+	+
Glyceria occidentalis (Piper) J. C. Nels.			+	
Calamagrostis nutkaensis (Presl.) Steud.			+	
Athyrium filix-foemina (L.) Roth. var. sitchense Rupr.				+
Scrophularia californica Cham. & Schlecht.				+
Collinsia corymbosa Herder				+
Veronica americana (Raf.) Schw.				+
Stachys stricta Greene				+
Potentilla egedei Worms. var. grandis (Rydb.) J. T. Howell				+
Rubus vitifolius Cham. & Schlecht.				+
Lotus aboriginum Jeps.				+

TABLE 2. *Continued.*

	Zone 1	Zone 2	Zone 3	Zone 4
Vicia americana Muhl.				
ssp. oregana (Nutt.) Abrams				+
V. gigantea Hook.				+
Alnus oregona Nutt.				+
Salix piperi Bebb.				+
S. sitchensis Sanson				+
S. coulteri Onderss.				+
Galium trifidum L. var.				
subbiflorum Wieg.				+
Lonicera involucrata (Rich.)				
Banks var. ledebourii (Esch.) Zabel				+
Baccharis douglasii DC.				+
Erechtites prenanthoides (A. Rich.) DC.				+
Smilacina stellata (L.)				
var. sessilifolia (Baker) Hend.				+
Polypogon monspeliensis (L.) Desf.				+

graphic diversity within the fen is provided by the tussocks of Cyperaceae and, especially, by the large tussocks of *Calamagrostis* and the build-up of material around the bases of the *Ledum* and *Myrica* bushes. Thus, *Menyanthes* and *Epilobium adenocaulon* can grow in the same zone in hollows and on tussocks, respectively.

The soils of the fen are by no means unrelieved peat; sand and mineral particles of smaller size occur in all zones. The mineral content predominates in the soil beneath the open water but decreases in proportion through the fen (where the loss on ignition averages about 50% of the dry weight of the soil) to the fen carr (where the loss on ignition reaches 77% in the surface litter and 78% in the subsurface peat). In the fen, *Sphagnum* peat appears to be accumulating patchily and much of the rest of the peat is derived from flowering plant remains.

Because the water and the peat in the fen have an acid reaction, the presence of such well-known "calcifuges" as *Sphagnum* spp., *Potentilla palustris*, *Blechnum spicant* and *Myrica californica* is not surprising. On the other hand, the reasonably high base status is indicated by the presence of such species as *Nasturtium officinale*, *Habenaria dilatata* and *Lysichiton americanum*. A notable absentee (present in the much shorter floristic lists from the acid, base-deficient bogs of the "pygmy forest" not far away) is the sundew, *Drosera rotundifolia*. Good descriptions of these "pygmy forest" bogs can be found in Rigg (1933) and McMillan (1956).

RELATION OF INGLENOOK FEN TO OTHER "BOGS" AND "MARSHES"

Table 3 shows species which are in common between the Inglenook fen and a number of coastal "bogs" ranging from Alaska southwards to

TABLE 3. SPECIES IN COMMON BETWEEN A NUMBER OF COASTAL "BOGS" AND "FENS" ON THE PACIFIC COAST OF NORTH AMERICA

	1	2	3	4	5	6	7
	Palmer, Alaska (incomplete)	Victoria, B.C.	Olympic Penin. Wash.	Bandon, Ore.	Inglenook, Calif.	Ledum Swamp (Point Reyes) Calif.	San Francisco, Calif. (incomplete)
Nuphar polysepalum	+	+	+	+	+		
Potentilla palustris	+	+	+	+	+		
Oenanthe sarmentosa		+	+		+	+	(+)
Sphagnum sp.	+	+		+	+		
Calliergonella cuspidatum		+	.		+		
Blechnum spicant					+	+	
Hypericum anagalloides					+	+	
Ledum spp.		+		+	+	+	
Gentiana sceptrum, etc.		+		+	+		
Menyanthes trifoliata	+	+	+	+	+		+
Mimulus guttatus					+	+	
Myrica spp.		+		+	+	+	
Lysichiton americanum				+	+		
Sisyrinchium californicum					+	+	
Habenaria dilatata var. leucostachys					+	+	+
Calamagrostis nutkaensis					+	+	
Athyrium filix-foemina					+	+	+
Alnus oregona		+		+	+		
Campanula californica					+	+	
Carex obnupta					+	+	
Heleocharis acicularis				+	+		

1. Hanson and Churchill (1961); 2. Rigg (1922, 1925); 3. Jones (1936); 4. Hansen (1943); 5. See Table 2; 6. Howell (1949); 7. Behr (1891), etc.

southern Oregon. In addition, the last column in the table indicates that some of these species were also present in the extensive "marsh" in San Francisco which Behr (1891) describes as having been destroyed by the growth in the city in the second half of the nineteenth century.

The San Francisco "marsh," which contained black, peaty soil according to Kellogg (cited by Brandegee, 1892), was adjacent to a pleasure resort called the Russ Gardens after the family who owned it. This was situated on the south corner of the intersection of Sixth and Harrison Streets (Eastwood, 1945). Behr (1891) describes the situation thus (Behr's punctuation is preserved): "Near the formerly well known Russ Gardens there were extensive marshes abounding especially about their borders in interesting plants. Here grew the large flowered dogwood *(Cornus Nuttallii),* the buckbean *(Menyanthes trifoliata), Epipactis gigantea,* the delightfully fragrant *Habenaria leucostachys,* and *Eriophorum gracile.* In the same vicinity I found in a single locality five

specimens of *Botrychium ternatum;* and the Lady-fern *(Asplenium filix-foemina),* grew luxuriantly, often forming root-stocks two feet high, simulating tree ferns." According to Eastwood (1945), Behr also found *Hippuris vulgaris* and Brandegee (1892) notes that Behr found *Cordylanthus maritimus* (under the name *Chloropyron palustre)* at this place.

No trace remains now of this, which must have been the southernmost representative of the coastal bog or fen formation along the Pacific Coast of North America. However, it is possible that an impoverished fragment of another example remains about 30 miles north of San Francisco, at the landward end of Point Reyes Peninsula. This is the well-known "Ledum Swamp" where acid waters draining from the quartz-diorite Inverness Ridge (covered with *Pinus muricata* and a podsolized soil) are impeded by nutrient-rich hills on the Peninsula. The next to last column in Table 2 contains a list of the species (from Howell, 1949) still occurring in Ledum Swamp which are also to be found in the Inglenook fen.

Only Inglenook fen now remains in California to represent this soil-vegetation type adequately, but it is a magnificent example. Because of its floristic richness and the completeness of its zonation and because it is the southernmost example of its kind, it is to be hoped that this fen can be preserved intact for study through the years to come. The area is also of anthropological interest, because it was here that the Coast Yuki Indians lived. This physically and linguistically isolated people and their artifacts are in need of further study (cf. Barrett, 1908; Thomsen and Heizer, 1964).

LITERATURE CITED

AXELROD, D. I. 1967. Geologic history of the California insular flora. In Proceedings of the Symposium on the Biology of the California Islands (ed. R. N. Philbrick). Santa Barbara Botanic Garden, Santa Barbara.

BAKER, H. G. 1959. The contributions of autecological and genecological studies to our knowledge of the past migrations of plants. Amer. Naturalist 93:255–272.

BARRETT, S. A. 1908. The ethno-geography of the Pomo and neighboring Indians. Univ. Calif. Publ. Amer. Archeol. and Ethnology 6(1):1–332.

BEHR, H. H. 1888. Flora of the Vicinity of San Francisco. San Francisco.

———. 1891. Botanical reminiscences. Zoe 2:2–6.

BRANDEGEE, K. 1892. Catalogue of the plants of San Francisco. Zoe 2:334–386.

DARWIN, C. R. 1877. The Different Forms of Flowers on Plants of the Same Species. John Murray. London.

EASTWOOD, A. 1945. The wild flower gardens of San Francisco in the 1890's. Leafl. W. Bot. 4:153–176.

FUKUDA, I. 1967. The biosystematics of Achlys. Taxon 16:308–316.

GARDNER, R. A. 1967. Sequence of podsolic soils along the coast of northern California. Ph.D. thesis, Univ. of California, Berkeley.

HANSEN, H. P. 1943. Paleoecology of two sand dune bogs on the southern Oregon coast. Amer. J. Bot. 30:335–340.

HANSON, H. C. and E. D. CHURCHILL. 1961. The Plant Community. Reinhold Publ. Co., New York.

HEUSSER, C. J. 1960. Late Pleistocene environments of North Pacific North America. Amer. Geog. Soc., Special Publ. no. 35, pp. 1–308.

HEWETT, D. G. 1964. Menyanthes trifoliata L. J. Ecol. 53:723–735.

HOWELL, J. T. 1949. Marin Flora. Univ. Calif. Press, Berkeley.

JENNY, H., R. J. ARKLEY, and A. M. SCHULZ. 1969. The pygmy forest-podsol ecosystem and its dune associates of the Mendocino coast. Madroño 20:60–74.

JEPSON, W. 1939. A Flora of California. vol. 3, part 1. A. S. U. C., Berkeley, California.

JONES, G. N. 1936. A Botanical Survey of the Olympic Peninsula, Washington. Univ. Wash. Publ. Bot. 5:5–286.

MASON, H. L. 1957. A Flora of the Marshes of California. Univ. Calif. Press, Berkeley.

MCMILLAN, C. 1956. The edaphic restriction of Cupressus and Pinus in the Coast Ranges of central California. Ecol. Monogr. 26:117–212.

MUNZ, P. A. 1959. A California Flora. Univ. Calif. Press, Berkeley.

———— and D. D. KECK. 1949–50. California plant communities. Aliso 2:87–105, and 2:199–202.

NELSON, A. P. 1962. A genecological study in Prunella vulgaris L. (Labiatae). Ph.D. thesis, Univ. Calif., Berkeley.

RIGG, G. B. 1922. A bog forest. Ecology 3:207–213.

————. 1925. Some sphagnum bogs of the north Pacific coast of America. Ecology 6:260–278.

————. 1933. Notes on a sphagnum bog at Fort Bragg, California. Science 77:535–536.

TANSLEY, A. G. 1939. The British Islands and their Vegetation. Cambridge Univ. Press, Cambridge.

THOMSEN, H. H. and R. F. HEIZER. 1964. The archaeological potential of Coast Yuki. Rep. Univ. Calif. Archaeol. Surv., no. 63, pp. 45–83.

NOTES AND NEWS

PLEUROPHYCUS GARDNERI SETCHELL & SAUNDERS, A NEW ALGA FOR NORTHERN CALIFORNIA.—The Laminariales have received considerable attention recently with Druehl's publications (Can. J. Bot. 46:539–547. 1968; Phycologia 9:237–247. 1970) on their distribution along the west coast of North America. In general, the Northern California Coast from Bodega Head to the Oregon border has received very little attention with the exception of Dawson's study (Marine Algae in the vicinity of Humboldt State College, Biology Department, Humboldt State College, Arcata, Ca., 1965). On 12 July 1971, collections of algae were made in the intertidal zone at Fort Bragg (39° 27′N, 123° 47′W) during —1.0 foot tide. One of the specimens has been deposited in the herbarium at Hopkins Marine Station. Other voucher specimens have been deposited in the Sonoma State College herbarium. At this locality, *Pleurophycus gardneri* Setchell & Saunders, heretofore known only north of Coos Bay, Oregon (43° 25′N, 124° 20′W) was collected from a large population on rocks at —1.5 foot tide level in a tide pool area. A single specimen was also collected by the author in October, 1970, from the drift at Salt Point (38° 36′N, 123° 21′W).—CHRIS K. KJELDSEN, Department of Biology, Sonoma State College, Rohnert Park, California 94928.

CHROMOSOME COUNTS IN SECTION SIMIOLUS OF THE GENUS MIMULUS (SCROPHULARIACEAE). IX. POLYPLOID AND ANEUPLOID PATTERNS OF EVOLUTION

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and R. K. Vickery, Jr.

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This cytological investigation clearly documents the presence of the unusual north to south polyploid-aneuploid-polyploid series in the *Mimulus glabratus* complex (table 1) adumbrated in our earlier reports (Mukherjee and Vickery, 1962; Mia, et al., 1964; Vickery, et al., 1968). The new chromosome counts—obtained by essentially the same aceto-carmine squash technique previously employed (Vickery, et al., 1968)— confirm the presence of diploid ($n = 15$), tetraploid ($n = 30$), aneuploid tetraploid ($n = 31$), and hexaploid ($n = 46$) members of the complex. The distribution of the 69 cytologically known populations (table 1 and Vickery, 1955; Mukherjee, et al., 1957; Mukherjee and Vickery, 1959, 1960; Mia, et al., 1964; Vickery, et al., 1968) reveals that the diploids occur in the Great Basin of the western United States, in the Great Plains region of the central United States, in southwestern Texas and New Mexico, and in the Sierra Madre Oriental of north-eastern Mexico. The tetraploids are found along the southern limit of the diploids, from west Texas to southeastern California. The aneuploid tetraploids occur further south in the highlands of western and central Mexico and in the mountains of Chiapas and Guatemala. The hexaploids are found in South America along both flanks of the Andean Cordillera from Columbia to southern Patagonia and in the Juan Fernandez Islands 500 km off the coast of Chile. Both the geographic extent and the north to south direction of this polyploid series appear to be exceptional, if not unique in the Western Hemisphere.

Several of the populations of the *M. glabratus* complex were observed to have one pair of chromosomes which was late condensing during prophase I, late in separating at anaphase I, and generally light staining (fig. 1). Aside from causing several errors in chromosome counts here corrected (table 1), this behavior suggests the interesting possibility that the genes controlling meiosis may be concentrated on that pair of chromosomes.

The new chromosome counts obtained in this investigation (table 1) for *M. guttatus* taken in conjunction with those previously reported (Calder and Taylor, 1968b; Vickery, 1955; Mukherjee, et al., 1957; Mukherjee and Vickery, 1959, 1960; Mia, et al., 1964; Vickery, et al., 1968) show that *M. guttatus* ($n = 14$) appears to be evolving tetraploid ($n = 28$) populations along the periphery of its range. Its range extends from the Aleutian Islands to Chihuahua and from the Pacific Coast to the Rocky Mountains. The tetraploid populations are found,
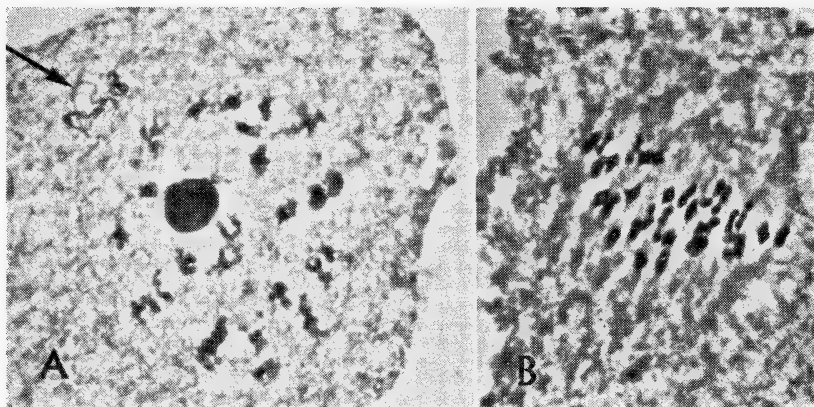
Fig. 1. Chromosomes of *Mimulus glabratus* var. *glabratus*. A. Late condensing bivalent, culture 7304, mag. ca. 1110×. B. First metaphase, culture 7299, 31 II, mag. ca 1345×.

typically at higher elevations, along the northwestern and southern edges of the range. The northern tetroploids are sufficiently morphologically distinct to suggest that they originated by alloploidy. In fact, the tetraploids of the Queen Charlotte Islands have been recognized as a separate subspecies, *M. guttatus* subsp. *haidensis,* by Calder and Taylor (1965, 1968a). Probably that name should be applied to all the northern tetraploids. The southern tetraploids are not distinct morphologically from the diploids and may have originated by autoploidy. For example, two populations consist of mixed diploid and tetraploid plants. No triploids were observed. The diploids show a consistent 14 II's, whereas the tetraploids exhibit an average of 6 IV's (range 3 IV to 9 IV) which suggests that these populations are now in the process of evolving auto-tetraploid forms.

The new counts for *M. nasutus* Greene and *M. tilingii* Regel confirm the presence of aneuploidy at the diploid level in both species (table 1). *Mimulus nasutus* has $n = 14$ and $n = 13$ populations (table 1; Mukherjee and Vickery, 1960; Mia, et al., 1964). *Mimulus tilingii* has $n = 14$ and $n = 15$ populations primarily (table 1; Vickery, 1955; Mukherjee and Vickery, 1959, 1960), with some $n = 24$ and $n = 28$ populations as well (Mukherjee and Vickery, 1959; Vickery, et al., 1968). However, for neither species are enough counts available to clarify its pattern of evolution.

In summary, this investigation indicates the presence of two distinctive patterns of evolution in section *Simiolus*. In the *M. glabratus* complex the pattern consists of a north to south series of increasing polyploid-aneploid-polyploid levels. In the common yellow monkey flower, *M. guttatus,* the pattern consists of an extensive, western North American area of diploid populations with occasional, apparently allo-tetra-

TABLE 1. CHROMOSOME COUNTS IN MIMULUS, SECTION SIMIOLUS.[1]

M. glabratus var. *externus* (Skottsb.) Skottsberg. **n** = **46**: Chile, Islas Juan Fernández, Isla Más-a-Tierra, 30 m, *7325* (*Meyer,* 1965).

M. glabratus var. *fremontii* (Benth.) Grant. **n** = **15**: U.S.A., Kan., Reno, Arlington, 472 m, *7648;* Neb., Custer, Victoria Sprs., 885 m, *7135;* Thomas, Middle Loup R., 930 m, *7136;* N. M., Catron, Allegros Pk. rd., 2135 m, *6610* so. of Reserve, 1770 m, *6612;* Grant, Gila R., 1340 m, *6616;* Rio Arriba, Abiquiu, 1770 m, *6621;* San Miguel, Tecolote Cr., 1800 m, *6620;* Socorro, Dripping Sprs., 1677 m, *6608;* Tex., Brewster, Calamity Cr., 1400 m, *6619;* Wis., Dane, Wingra Sprs., 262 m, *7701;* Mexico, Coahuila, Saltillo, 1677 m, *7308.* **n** = **30**: U.S.A., Tex., Culberson, near Van Horn, 1357 m, *6296, (McVaugh 8002);* Jeff Davis, Limpia Cr. Canyon, 1525 m, *6617;* and 1523 m, *6618;* Presidio, Fresno Cr., 823 m, *6294 (Johnson and Warnock 3682);* Gillespie, Enchanted Rock, 457 m, *6278.*

M. glabratus var. *glabratus.* **n** = **31**: Guatemala, Huehuetenango, El Tapon Canyon, 1982 m, *7299;* near Huehuetenango, 1951 m, *7300;* Quezaltenango, 35 km so. of Huehuetenango, 2440 m, *7301;* Totonicapán, near San Cristóbal, 2440 m, *7303;* near Totonicapán at km 104 no. of Guatemala City, 2287 m, *7304;* Mexico, Chiapas, near Santo Tomás, 2195 m, *7296;* near San Cristóbal de las Casas, 2165 m, *7297;* D. F., Miguel Hidalgo Nat. Park, 2744 m, *7305;* Durango, Papasquiaro, 2287 m, *6647*[2]; e. of El Salto, 2440 m, *7286;* Llano Grande, 2440 m, *7287;* Mex., Acambay, 2592 m, *7307.*

M. glabratus var. *michiganensis* (Pennell) Fassett. **n** = **15**: U.S.A., Mich., Cheboygan, Little Carp Lake R., 214 m, *7703;* Mackinac, Epoufette, 180 m, *6629.*

M. glabratus var. *parviflorus* (Lindl.) Grant. **n** = **46**: Argentina, Río Negro, Cerro Catedral, 1200 m, *9546;* Chile, Bío-Bío, Salta del Laja, 400 m, *6683;* Aconcagua, no. of La Laguna, 1 m, *7658;* Aisen, near Ibáñez, ca. 1220 m, *6327;* Bahia Jaras, 220 m, *6328;* Atacama, Quebrada, 1525 m, *9092;* Río Cholloy, 1400 m, *9093;* Coquimbo, near Illapel, 1300 m, *5041*[2]; U.S.D.A.P.I.S. *144534;* Concepción, Pen. de Tumbes, 1 m, *6317, (Moore 285);* Valparaiso, near Viña del Mar, 8 m, *9544;* Talco, Los Cipreces, 1050 m, *9098.*

M. glabratus subsp. *utahensis* Pennell. **n** = **15**: U.S.A., Calif., Mono, Mono Lake, 1964 m, *(Stebbins 714) 5048*[2]; Nev., Elko, Cherry Cr., 1982 m, *5972;* Mineral, Pilot Pk., 1677 m, *5747*[2]; White Pine, Ely, 1957 m, *7681;* Utah, Davis, Antelope Is., 1311 m, *5996;* Tooele, Wendover, 1311 m, *5852*[2].

M. guttatus Fischer ex DC. **n** = **14**: U.S.A., Ariz., Coconino, Oak Cr. Canyon, 1510 m, *7793;* Calif., Riverside, Hurkey Cr., 1326 m, *7561;* Calif., San Bernardino, Mill Cr., 915 m, *9109 (Mathews,* 1968) ; Utah, Salt Lake, west fork of Lambs Canyon, 1890 m, *7709;* Butterfield Cr., 1740 m, *9550;* Tooele, Middle Canyon, 2073 m, *9549;* Utah, Mt. Nebo, Salt Cr., 2317 m, *7711;* Loop Spr., 2561 m, *7712;* Mt. Timpanogas, 2256 m, *7713;* Washington, Blake Gubler Ranch, Pine Valley Mtns., 2135 m, *9548;* Sevier, in tributary of Fish Lake, 2881 m, *7625;* Utah, Summit, Lily Lake, 3065 m, *7495;* Beaver Cr. campground, 2256 m, *9653.***n** = **14, 28**: Ariz., Mohave, Moccasin, 1525 m, *7555;* Utah, Kane, Three Lakes, 1646 m, *9555.* **n** = **28**: Ariz., Cochise, Ramsey Canyon, 1646 m, *7558;* Colo., Grand, Rollins Pass, 3354 m, *7693 (Foreman,* 1967) ; Ore., Multnomah, at the base of Multnomah Falls, 85 m, *9562.*

M. nasutus Greene. **n** = **14**: U.S.A., Calif., Sonoma, near Stewarts Point, 15 m, *5865 (Holme,* 1951).

M. tilingii Regel. **n** = **14**: U.S.A., Calif., Mono, below Saddlebag Lake, 3018 m, *7684;* Utah, Duchesne, Lovenia Cirque, Uinta Mtns., 3,475 m, *7679 (Hall).* **n** = **15**: Utah, Mt. Timpanogas Trail, 1968, 2560 m, *7714* and 2745 m, *7717;* Emerald Lake, 3050 m, *7716.*

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[1] The taxonomic treatment is based on Fassett, 1939; Grant, 1924; Pennell, 1935; and Skottsberg, 1951. Collectors' names are not given for specimens collected by or for the authors and, hence, clearly identified by the culture number.

[2] Corrected counts.

ploid populations on the northern periphery and scattered, probably auto-tetraploid populations on the southern periphery of the range.

Literature Cited

Calder, J. A. and R. L. Taylor. 1965. New taxa and nomenclatural changes with respect to the flora of the Queen Charlotte Islands, British Columbia. Can. J. of Bot. 43:1387–1400.
————. 1968a. Flora of the Queen Charlotte Islands. Part 1. Systematics of the vascular plants. Queen's Printer, Ottawa.
————. 1968b. Flora of the Queen Charlotte Islands. Part 2. Cytological aspects of the vascular plants. Queen's Printer, Ottawa.
Fassett, N.C. 1939. Notes from the Herbarium of the University of Wisconsin. Rhodora 41:524–529.
Grant, A. L. 1924. A monograph of the genus Mimulus. Ann. Missouri Bot. Gard. 11:99–389.
Mia, M. M., B. B. Mukherjee, and R. K. Vickery, Jr. 1964. Chromosome counts in the section *Simiolus* of the genus *Mimulus* (Scrophulariaceae). VI. New numbers in *M. guttatus, M. tigrinus,* and *M. glabratus.* Madroño 17:156–160.
Mukherjee, B. B. and R. K. Vickery, Jr. 1959. Chromosome counts in the section *Simiolus* of the genus *Mimulus* (Scrophulariaceae). III. Madroño 15:57–62.
————. 1960. Chromosome counts in the section *Simiolus* of the genus *Mimulus* (Scrophulariaceae). IV. Madroño 15:239–245.
————. 1962. Chromosome counts in the section *Simiolus* of the genus *Mimulus* (Scrophulariaceae). V. The chromosomal homologies of *M. guttatus* and its allied species and varieties. Madroño 16:141–155.
Mukherjee, B. B., D. Wiens, and R. K. Vickery, Jr. 1957. Chromosome counts of the section *Simiolus* of the genus *Mimulus* (Scrophulariaceae). II. Madroño 14:128–131.
Pennell, F. W. 1935. The Scrophulariaceae of eastern temperate North America. Acad. Nat. Sci. Philadelphia Monogr. 1:115–123.
Skottsberg, C. 1951. The natural history of the Juan Fernandez and Easter Islands. Vol. Botany. Pt. 6, p. 784. Almquist and Wiksells, Uppsala.
Vickery, R. K., Jr. 1955. Chromosome counts in the section *Simiolus* of the genus *Mimulus* (Scrophulariaceae). Madroño 13:107–110.
————, K. W. Crook, D. W. Lindsay, M. M. Mia, and W. Tai. 1968. Chromosome counts in section *Simiolus* of the genus *Mimulus* (Scrophulariaceae). VII. New numbers for *M. guttatus, M. cupreus,* and *M. tilingii.* Madroño 19:211–218.

A NEW SPECIES OF DYSSODIA (COMPOSITAE)
FROM NORTH CENTRAL MEXICO

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It is with some embarrassment that I describe here a new species of the genus *Dyssodia*, since there appeared only a couple of years ago an excellent monograph of the genus by a former student of mine (Strother, 1969, Univ. Calif. Publ. Bot. 48: 1–88). But this merely reflects our poor knowledge of the flora of North Central Mexico, especially that found on gypseous soils. I. M. Johnston (1941, Jour. Arn. Arb. 22: 145–170) compiled a beginning list for several sites in this region, pointing to the significance of gypsum as a substrate factor for endemism. Gypsum sites in Mexico are clearly in need of much more intensive study and they will undoubtedly yield many new taxa as they are explored over a larger region.

Dyssodia gypsophila Turner, sp. nov.

Frutex diffusus divaricatus 30—60 cm altus. Caules veteres cortice dealbata demum decorticantes. Caules annotina glabrati hornotini puberuli pilis albis. Folia linearia plus minusve succulenta plerumque opposita vel prope capitula alterna (10—) 15—25 mm longa triquetra glabra sed margine ciliata glandibus marginalibus uniformiter dispersis tumidis in sicco badiis. Capitula radiata multiflora pedunculis unicapitulatis 1—4 mm longis dense pubentes. Involucra late turbinata-campanulata conspicuo albo-pubentia 7—9 mm alta 4—5 lata biseriata partibus calyculi 3—5 lineario-lanceolatis. Phyllaria ca 13 calyculo 2—3-plo longiora imbricata usque fereve ad apicem connata glandibus paucis grandibus uniformiter dispersis in sicco badiis apicibus scariosis acutis vel obtusis. Receptaculum planum nudum ca 2mm diametro. Radii flores saepe 8 corollis flavis tubulis 2—3 mm longis ligulis ellipticis 6—8 mm longis 2—4 mm latis retusis vel obtusis. Disci flores 25—30 corollis luteis 4—5 mm longis tubulosis lobulis brevissimis acutis. Styli rami appendiculati appendiculibus parvis acutis papillatis. Achenia a *D. acerosa* breviora crassioraque differunt distincte 4—5 angulata fuliginosa vel nigra omnino uniformiter conspicuoque pubentia pilis rectis albis mollis adpressis. Pappus squamiformis squamellis 15—20 debiliter evolutis sursum irregulariter dissectis setaceisque setis longioribus corollas disci superantibus achenia 1.5-plo longioribus.

Open, divaricately branched, shrubs, 30–60 cm high; stems very brittle, at first minutely white puberulent but becoming nearly glabrate with age and forming a white, sloughing bark; leaves linear, succulent, or nearly so, mostly opposite but becoming alternate just below the heads, (10)15—25 mm long, glabrous, except for the minutely, ciliate margins, triangular in cross section, the sides about 1 mm wide and

bearing relatively evenly-spaced, swollen, glands; heads borne on densely pubescent, peduncles, 1—4 mm long; calyculum of 3—5, linear lanceolate, pubescent bracts, $\frac{1}{3}$—$\frac{1}{2}$ times as long as the phyllaries; involucre broadly turbinate-campanulate, conspiculously white puberulent, 7—9 mm high, 4—5 mm through; phyllaries ca 13, biseriate, imbricately connate to the scarious, acute to obtuse tips, or nearly so, the bracts rather evenly dotted with relatively few, large glands; receptacle flat, naked, ca 2 mm across; ray florets mostly 8, corollas yellow, tube 2—3 mm long, lamina elliptic, 6—8 mm long, 2—4 mm wide, retuse or obtuse at the apex; disc florets 25—30, corollas light yellow, 4—5 mm long, tubular, lobes very short, acute; style branches with small, acute, papillate appendages; achene rather prominently 4—5 angled (short and thick as compared to *D. acerosa*), dark brown to black, evenly and conspicuously pubescent throughout with straight, white, soft, appressed hairs; pappus of 15—20 poorly developed squamellae, each dissected into 3—6 bristles of varying sizes, but the longer ones exceeding the disc corollas, being 1.5 times as long as the achene.

Holotype (TEX): MEXICO. Coahuila; 15 mi SW of Cuatro Cienegas, growing on gypsum dunes. 25 Sep 1970. *B. L. Turner 6172.* (Isotype UC).

Known only from the type locality where it is relatively uncommon on actively blowing dunes of gypsum.

The species has a very distinctive habit and is easily distinguished from its nearest relative, *D. acerosa,* which is a small, mostly suffruticose perennial possessing fasiculate foliage and much-shortened internodes, the leaves being very slender and decidedly acerose; the leaves of *D. gypsophila* are relatively evenly spaced along the stems at rather distant nodes, rarely if at all fasiculate and are decidedly thick and succulent.

In addition to features of the habit and foliage, *D. gypsophila* can be distinguished by its larger, more-or-less evenly punctuate, decidedly pubescent involucres, more numerous florets, smaller, more prominently pubescent achenes and longer pappus.

Dyssodia gypsophila is named for the remarkable habitat in which it grows and to which it is apparently restricted. The dune area is about 15—20 air line km SW of the village of Cuatro Cienegas. It is quite extensive, being comprised of perhaps 10—20 square kilometers of actively blowing dunes, 5—40 feet high, which are readily seen at a distance of some 10 km west of the highway leading SW from Cuatro Cienegas to San Pedro. *D. gypsophila* shares this habitat with several other prominent gypseous endemics, the more noteworthy being *Petalonyx crenatus, Coldenia hispidissima, Drymaria lyropetala, Selinocarpus purpusianus, Nerisyrenia castillonii* and *N. incana.*

MIMULUS GEMMIPARUS SP. NOV. FROM COLORADO

William A. Weber

University of Colorado Museum, Boulder 80302

Minulus gemmiparus W. A. Weber, sp. nov., Sect. *Simiolus*. Herba annua erecta, tota glabra, 1—10 cm alta, simplex, debilis, plus minusve succulenta. Folia internodiis breviora, ovata, petiolata, usque ad 10 mm longa et 7 mm lata, obscure triplinervia, apicibus obtusis vel rotundatis, basibus truncatis; petioli 2—3 mm longi, latero-compressi, profunde saccati, fere omnes propagulum lenticularem continentes. Flores solitarii, axillarii vel terminalii, brevipedicellati, bilabiati; calyx 3—4 mm longus, plicato-carinatus, subcampanulatus, emaculatus, laciniis subaequalibus, incurvatis; corolla calyce paullo longiora, 4—5 mm longa, cylindrica vel infundibuliformia, glabra, lutea, emaculata; faux brevis, aperta, intus parvicristata, non palatum formans; lobi subaequales, erecto-patentes, obtusi vel rotundati; stamina glabra, inclusa; lobi stigmatici rotundati. Capsula et semina ignota.

Annual herb; foliage and stem totally glabrous; stem 1—10 cm tall, simple, weak, somewhat succulent. Leaves shorter than the internodes, ovate, petiolate, up to 10 mm long and 7 mm wide, obscurely 3-nerved, the apices obtuse to rounded, the bases broad, truncate, the margins entire or remotely denticulate; petioles 2—3 mm long, laterally compressed, deeply saccate, almost every one containing a lenticular propagulum. Flowers solitary, axillary or terminal, short-pedicellate, bilabiate; calyx 3—4 mm long, plicate-keeled, subcampanulate, not spotted, the teeth subequal, incurved; corolla not much longer than the calyx, 4—5 mm long, cylindric to funnel-form, glabrous, yellow, not spotted; throat short, open, with two low parallel ridges within, not forming a prominent palate; lobes subequal, erect-spreading, obtuse or rounded; stamens glabrous, included; stigmatic lobes rounded. Capsule and seeds unknown. Chromosome number, $n = 16$ (*teste* R. K. Vickery in litt.). (Fig. 1.)

Holotype. U. S. A. Colorado. Rocky Mountain National Park; Old Fall River Road, east side of Continental Divide (Larimer County), 10,000 ft. alt.; on gently sloping seeping granite slopes, forming colonies in the protection of the overhanging rounded surfaces of erratic boulders, subalpine, open sites in *Picea-Abies-Populus tremuloides* association, 9,500—10,500 ft. alt.; associated with *Mimulus rubellus* A. Gray and *M. guttatus* DC. (*M. hallii* Greene), 8 July 1970, *W. A. Weber 10,462* (COLO).

Mimulus gemmiparus is characterized by a mode of vegetative reproduction unique in the genus (Grant, 1924) and perhaps unique in the Holarctic flora—the consistent production of saccate petioles that envelop a fleshy pair of rudimentary leaves, a rudimentary axis, and sometimes even the beginning of an adventitious root. The cotyledon-like leaves are laterally-oriented within the petiole, the entire structure
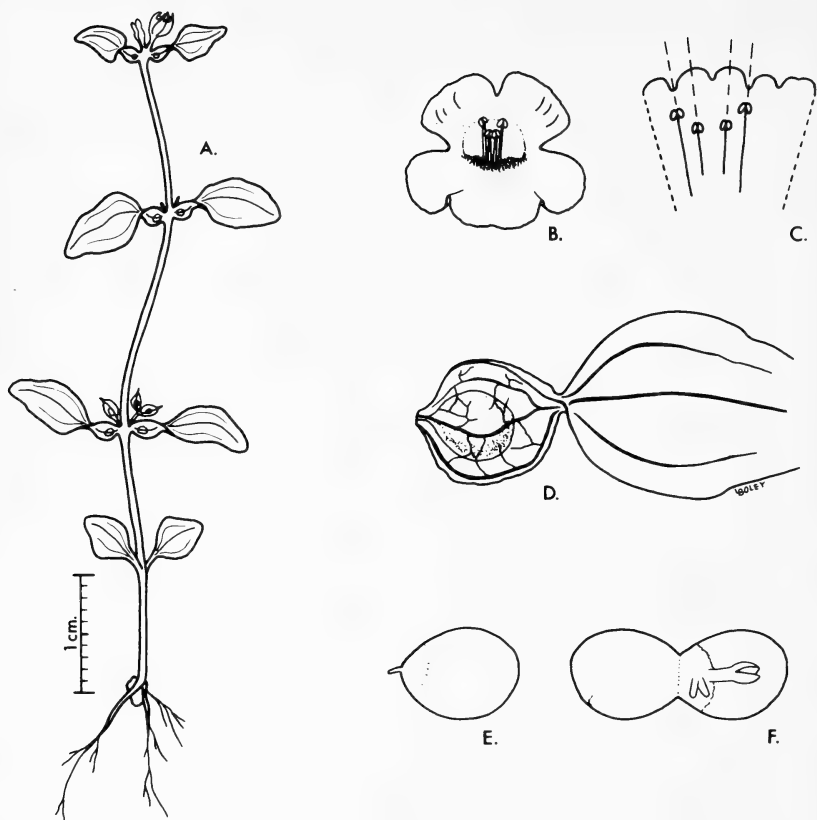
Fig. 1. Mimulus gemmiparus W. A. Weber: A, habit; B, face view of corolla; C, corolla, opened view showing staminal insertions; D, detail of saccate petiole with enclosed propagulum; E, F, propagulum, complete and dissected. Drawing by Linda Boley, Staff Artist, Univ. of Colorado Museum.

bearing an analogy to a small, one-seeded legume pod with the ventral suture open. The combined elements are released as a unit. When the plant reaches maturity, within a few weeks time, the leaf-lamina withers and falls away, and the propagulum dissociates from the drying stem. The flat, lenticular propagula, resembling large *Marchantia* gemmae, float down-slope in seepage water and tend to collect in drifts in sites suitable for germination.

A graded series of stages leading to the production of typical propagula may be observed on a single plant. The lowermost leaf pair is usually unmodified, with normal petioles and blades. Modification increases upward, with the leaves closest to the inflorescence bearing the

largest and plumpest propagula and most reduced leaf-blades. Even the abortive lateral shoots from the leaf-axils may bear minute leaves and saccate gemmiparous petioles.

Superposed buds evidently are produced at the nodes, for the production of a vegetative shoot in a leaf axil does not result in an empty petiolar sac. In almost all instances when a vegetative shoot diverges from a leaf axil, another, situated slightly below, grows into the petiolar sac, filling it with a propagular shoot.

R. K. Vickery (in litt.) feels that the relationships of the new species are with *M. guttatus* DC. although the shape of the corolla, with its very weakly-developed palate, more closely resembles that of *M. glabratus* H.B.K.

Mimulus gemmiparus has been known in the field and herbarium for over twenty years. It was first discovered by Ruth Ashton Nelson on the North Inlet Trail on the west side of the Continental Divide (Grand County). She experimentad with the propagula and was able to germinate them. Some years later, Mrs. Margaret Douglass became interested in the plant during her surveys of the vegetation of the Park. She forwarded living material to R. K. Vickery, who analyzed it cytologically. Although a great deal of field work has been done in the mountains of Colorado, this unique species has not yet been found outside Rocky Mountain National Park.

Flowers are very infrequently produced in *Mimulus gemmiparus* and the calyces that have been found lack mature capsules. Reproduction seems to be almost exclusively the function of the vegetative propagulum.

LITERATURE CITED

GRANT, A. L. 1924. A monograph of the genus *Mimulus*. Annals Missouri Bot. Garden 11: 99–388.

NOTES AND NEWS

AVAILABILITY OF SMILEY'S BOREAL FLORA OF THE SIERRA NEVADA.—A limited number of "A report upon the boreal flora of the Sierra Nevada of California" (Frank Jason Smiley, 1921. Univ. Calif. Publ. Bot. 9:1–423.) were recently uncovered from storage at Occidental College. Individuals interested in obtaining a copy for their institutional or herbarium library should address their request to Dieter Wilkin, Department of Biology, Occidental College, Los Angeles, California 90041.

NEW PUBLICATIONS

Systematics of the Onocleoid ferns. By ROBERT M. LLOYD. Univ. Calif. Publ. Bot. 61:1–86. 1971. A mongraphic study of Onoclea, Matteucia, and the monotypic Mexican-Guatemalan Onocleopsis hintonii.

A biosystematic study of the genus Brodiaea (Amaryllidaceae). By THEODORE F. NIEHAUS. Univ. Calif. Publ. Bot. 60:1–66. 1971. A comprehensive study of brodiaea, sensu stricto.

THE DIOECIOUS AMARANTHS: A NEW SPECIES NAME AND MAJOR RANGE EXTENSIONS

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The ten dioecious species of *Amaranthus* (Amaranthaceae) are native pioneers of North American stream banks, lake shores, tidal marshes, and sea beaches. Except for the southern water-hemp, *A. australis,* which has a widely disjunct Gulf-Caribbean range attributable to water-fowl dispersal, all were originally confined to coherent, scarcely over-lapping geographic ranges. During the last hundred years, several species have been expanding their ranges, mainly by gradual advances into adjacent territory as weeds of artificially modified habitats. Long-range seed dispersals have produced many isolated, ephemeral waifs but none of the species other than *A. australis* is known to have established suc-cessful disjunct colonies until very recently. This is in sharp contrast to the history of some monoecious species of *Amaranthus* that are no-toriously successful as weedy colonizers and agrees with Baker's (1967) general rule that self-incompatible taxa are at a disadvantage in estab-lishment after long-range dispersal.

A taxonomic revision of these species and a survey of their recent migrations were published about 15 years ago (Sauer, 1955, 1957). The present paper is intended as a supplement, presenting only information that is new or newly found since that time.

Rejection of Amaranthus tamariscinus Nutt.

This name and its synonyms, *Montelia tamariscina* (Nutt.) A. Gray and *Acnida tamariscina* (Nutt.) Wood, have long been applied to a species native to the southeastern Great Plains that has been gradually spreading northward and eastward since the mid 19th century. This species is clearly distinguished by the combination of dioecism, utricle dehiscence, and presence of a single well-developed tepal in the pistillate flowers. Unfortunately, as will be shown, Nuttall's name does not belong to this species, being based on a sterile hybrid between it and a monoe-cious species. It is obvious in retrospect that application of the name was based on habitat and geography rather than on diagnostic char-acters.

Nuttall (1835) published the name for plants he found in Arkansas Territory, in what is now Oklahoma:

> ". . . on the sand beaches of the Arkansas and Grand [Neosho] Rivers; abundant; possessing in some respect the aspect of *A. albus.* Stem 3–4 feet high and much branched, and as well as every other part of the plant per-fectly smooth; flowering branches very compound and destitute of leaves, so as almost to resemble branches of *Tamarix gallicus,* the bracts being green, minute, imbricated and spinulose."

The description of the inflorescence, including the comparison with a tamarisk, has always been puzzling, being quite inappropriate for the species in question. Nevertheless, when the first collections of this species began arriving at Harvard, Gray bestowed Nuttall's name on them. Among the earliest were Drummond's *no. 240* from Texas in 1835 (GH) and Fendler's *no. 737* from Texas in 1846 (GH). Specimens grown at Harvard from seed of the latter in 1848 were sent to Kew labelled *Amaranthus tamariscinus* Nutt. in Gray's hand. Also a note from Gray to Hooker in 1876 is attached to a specimen of the former collection (K): "I have found my own specimen of No. 240, Drummond, Texas, which I can now certify to be the true 'Montelia tamariscina' i.e. Nuttall's plant—with circumscissile utricle. Vale." Gray was guessing about the utricle of Nuttall's plant. In his published treatment of the dioecious amaranths, Gray (1876) wrote: "Nuttall's specimens of this are not even in flower, so that he was unaware that the plant was dioecious and the fertile flowers achlamydeous." Later Uline and Bray (1895) reported that a fragment of Nuttall's type, then in the herbarium of Columbia College, was "very immature, but the locality, the slender, acuminate spikes, and the spinulose bracts enable us to determine its place with reasonable certainty." Like Gray, they identified it with the eastern Great Plains dioecious species and I made the same mistake (1955, 1957) until encountering a Nuttall specimen that I am convinced belongs to the type collection of *A. tamariscinus*.

This specimen is in the British Museum of Natural History and is labelled "Amaranthus *tamariscinus, Arkansas, Herb. T. Nuttall." The asterisk is Nuttall's standard indication of a new species. The inflorescence is in fact very compound and leafless and does strongly resemble a tamarisk. The plant is not at all immature but completely sterile and lacks even rudiments of flowers in the bract axils. It is an example of what Murray (1940) designated as neuter plants, bearing abundant bracts without flower primordia, which he produced in abundance in the course of an experimental investigation of sex determination among amaranths. These comprised a large proportion of the F_1 progeny of crosses between *"Acnida tamariscina"* and certain monoecious *Amaranthus* species. (For corrected determinations of some of Murray's experimental lines, see: Sauer, 1953.) Murray's voucher specimens (CU, F) of artificial hybrids between the eastern Great Plains dioecious species and *A. hybridus* L. are an excellent match for Nuttall's specimen. The native range of *A. hybridus* is mainly eastward of Oklahoma in moister parts of North America and southward into tropical America. It is interesting that it was already hybridizing with the local dioecious species before white settlement of the region. Later collections of these sterile hybrids are mostly from weed populations of artificially disturbed places rather than from river banks.

Nuttall also collected, perhaps at the same place, a normal specimen of the dioecious species; it has the typical simple inflorescence, unbranched

above the upper leaves. He labelled it "Amaranthus *virgatus, Arkansas" (BM) but unaccountably neglected to publish the name. Since the species has never been named, the following name is given.

Amaranthus rudis sp. nov.

Plantae annuae, dioeciae, caulibus erectis multiramosis, foliis oblongis. Inflorescentiae cymosae axillares et thyrsum longum terminale formantes. Bracteae 1½–2 mm longae, subulatae. Flores staminati pentameri, tepalis exterioribus circa 3 mm longis, acuminatis, tepalis interioribus circa 2½ mm longis, obtusis vel retusis. Flores pistillati tepalo evoluto unico circa 2 mm longo, acuminato; utriculus circumscisse dehiscens. Semen circa 1 mm diametro, nigrum.

TYPE: *J. B. Norton 428*, common weed, Riley County, Kansas, August 6, 1895. Holotype: Missouri Botanical Garden (MO 1740436). Isotypes: GH, KSC, NMC, RM, US.

Recent Dispersals of A. rudis

Isolated colonies of this species have continued to appear outside its coherent range, as they have since the late 19th century. However, the most recent finds are far more widespread than formerly and some of the isolated colonies are beginning to reproduce themselves.

The species was collected in 1970 at two places along the railroad near Charleston, West Virginia, the first records from the state. One was an unpollinated female (*O. L. Eye s.n.*, WVA) but the other included both sexes and was producing seed (*M. E. Denison s.n.*, WVA).

An old collection from the state of Washington was the sole record of the species west of the Rockies until 1957, when male and female plants were found ten miles apart along the railroad in Santa Barbara County, California (*H. M. Pollard s.n.*, CAS, LA). In 1969, a solitary male was found near the highway in a salt flat in Douglas County, Nevada (*J. T. Howell 46183*, CAS).

The first known record of any dioecious amaranth in Asia was a collection of both sexes of *A. rudis* on Okinawa in 1951 (*S. Sonohara s.n.*, KAG). The colony may be reproducing, since the species was collected on Okinawa again in 1955 (*T. Amano 7523*, KAG) and on nearby Toku no Shima in 1962 (*G. Ikeda 530*, KAG).

The first European record of the species (as *"A. tamariscinus"*), apart from a doubtful report from Hamburg in 1908, was from the Netherlands in 1953 (Aellen, 1961). A persistent colony has evidently been established near the harbor at Wageningen, where both males and seed-bearing females were collected in 1961 and subsequent years (*M. J. Jansen s.n.*, L, WIS). The same collections include sterile hybrids with *A. hybridus*, which preceded *A. rudis* to Europe by over a century. The two species have thus resumed in a Dutch urban habitat the miscegenation begun in the wilds of Oklahoma.

In England, male plants of this species are reported from the Avon-
mouth docks, Gloucestershire, in 1957 to 1959 (Brenan, 1961). In
Czechoslovakia, the species was collected in 1967 and 1968 at three differ-
ent railway yards and a river port, all in Northern Bohemia (*V. Jehlík
4052–4056*, WIS). Both sexes were represented but no seed was borne
on the specimens examined.

Adventive A. Arenicola in California

Amaranthus arenicola I. M. Johnston is native to the High Plains and
was not recorded west of the Rockies until 1963, when it was reported
at two places in California (Howell, 1966). Collections consist of an
immature female found by the railroad at Santa Barbara (*H. M. Pol-
lard s.n.*, CAS) and part of a large, isolated female bearing a few pre-
sumably hybrid seeds that was found near the highway at King City,
Monterey County (*J. T. Howell 4066*, CAS). Although an annual at
home, the species can live longer in California. Howell found the same
Monterey County plant flourishing over a year later, but it has since
disappeared. In 1965 *A. arenicola* was collected along the highway near
Santa Ynez in Santa Barbara County, about 25 miles from the previous
Santa Barbara record; the colony extended for some distance along both
sides of the road and included both sexes (*C. F. Smith 9065*, CAS). By
1971 the same colony numbered thousands of plants, mostly right at
the edge of the road shoulder (*J. Sauer 4871*, LA, WIS); the plants
face immediate bulldozing in a massive highway reconstruction project
but this may cause further dissemination.

Recent Dispersals of A. palmeri

Amaranthus palmeri S. Wats. has been by far the most successful field
weed of all the dioecious amaranths. Native to Mexico and the south-
western United States, it has been expanding its range on various bor-
ders since 1900. It has been found in five additional states since 1960,
all north and east of its former range. In 1962 in the first Arkansas
record, it was found in cotton fields around Newport as a conspicuous
weed that was producing abundant seed (*J. Sauer & D. Gade 3358*, B,
F, DAV, WIS). Another colony was found in 1963 near Malvern, Ar-
kansas, on a site disturbed by road work (*D. Demaree 48940*, WIS).
In Nebraska in 1963, a troublesome new weed, 10 to 12 feet tall, was
reported interfering with mechanical corn pickers near Trenton; subse-
quently a mass collection (*J. Furrier s.n.*, WIS) showed these giants to
be sterile hybrids in mixed populations of *A. rudis* and newly immigrated
A. palmeri. In the first South Carolina record, seed-bearing *A. palmeri*
was collected in a cornfield near Sumter in 1966 (*T. Bradley & R. S.
Blaisdell 3443*, U, WIS). The species first appeared in Florida in 1967,
already producing seed, near Immokalee (*D. B. Ward s.n.*, WIS). The

species was first found in West Virgnia in 1970 along the railroad near Charleston; the specimen is an immature female (*M. E. Denison s.n.,* WVA). The first known Canadian record, also pistillate and seedless, was a garden weed at Lambton, Ontario, in 1963 (*L. Gaiser s.n.,* WIS).

The earliest European collections of *A. palmeri* were from cotton mill waste in Bohemia in 1908 (*V. V. Cypers s.n.,* W) and Switzerland in 1921 (*R. Probst s.n.,* L); only staminate plants were included. There were few more finds until the 1950's, when they began to multiply. The total is now over 25, almost all from cotton mill waste or other dumps or dock areas. These will not be cited in detail because they do not represent established colonies. Both sexes occur but no seed-bearing specimens are known. However, it is remarkable how widely the species has been found: Sweden (W), England (L, WIS), Netherlands (L, U, WIS), Luxembourg (WIS), Germany (K, M, W, WIS), and Austria (W). Aellen (1961) and Brenan (1961) cite additional collections that I have not seen. Seed of *A. palmeri* must be arriving continually in cotton bales from the United States, maybe more frequently since picking was mechanized. The rate may also have increased with the recent immigration of the species into cotton fields of the southeastern states and perhaps even more with expansion of cotton growing in the western states where it is a native. Twisselmann (1963) noted that *A. palmeri* had become a common and widespread weed in San Joaquin valley cotton fields.

EUROPEAN COLONIES OF OTHER SPECIES

Although native to the Midwestern United States, *Amaranthus tuberculatus* (Moq.) Sauer was originally described in 1849 from living plants in the Geneva Botanical Garden; both sexes were present and producing seed. The species was also being grown at the Munich Botanical Garden between 1849 and 1853 (*Anonymous s.n.,* M). A hundred year gap in the record ensues before the species reappears as a weed. Since 1949, both sexes have been found repeatedly along railroads and on dumps near Graz, Austria (*H. Melzer s.n.,* WIS; other citations by Aellen, 1961). In 1958 and 1959, individual female plants were found on the Avonmouth docks where *A. rudis* and *A. palmeri* were also found (Brenan, 1961).

Another dioecious amaranth, *A. watsonii Standl.,* was also collected on the Avonmouth docks in 1959, both sexes being present (Brenan, 1961). This species is native to arroyos and beaches of Baja California but may have arrived via southern California, where it has been spreading as a weed since about 1900.

RANGE EXTENSIONS OF A. AUSTRALIS

Amaranthus australis (A. Gray) Sauer, the southern water hemp, has extensive populations in the Everglades and the Gulf coast of the south-

ern United States. Widely scattered colonies have long been known from a few places in Mexico, the West Indies, and Venezuela. Some additional disjunct colonies, none of which appear to be new, can now be reported.

In 1962, a large population of *A. australis* was found near Chenkán, Campeche, Mexico, growing with sedges and cattails in a marsh behind the coastal beach ridges (*J. Sauer & D. Gade 3183*, F, WIS). The nearest previously known colonies lie 150 miles to the southwest in Tabasco and 250 miles to the northeast in Quintana Roo.

Until recently, I was unaware that the species ranged into the Guianas. European herbaria have many specimens from Surinam, the earliest collected in 1920 at the mouth of the Corantijne River (*A. Pulle 376*, U; *378*, BM, K). Twelve other Surinam collections were made between 1927 and 1969 in the districts of Nickerie, Coronie, Saramacca, Suriname, and Marowijne (K, U). Notations on these show that the plant is common in coastal marshes, both fresh and brackish, and on margins of mangrove swamps. As in the Everglades, the plants reach giant size; notes on Surinam specimens (U) give plant heights up to 5 m, stem diameters to 25 cm. The species is also reported as common in coastal sedge-cattail marshes in western French Guiana; a synonymous name is used: *Acnida cuspidata* (Vann, 1969).

From Brazil, I have seen only one collection, a seed-bearing female found near Porto Alegre, Rio Grande do Sul, in 1899 (*E. M. Reineck s.n.*, E). This is some 2,500 miles from the nearest Guiana collections, but unknown colonies may exist in the intervening swamps and marshes.

There is some new evidence that migratory birds may disperse amaranth seeds over long distances, although it does not derive specifically from *A. australis*. DeVlaming and Proctor (1968) reported that *Amaranthus* and *Polygonum* seeds, unidentified as to species, often constitute the bulk of the seeds in the digestive tracts of killdeer shot in Texas. They fed *A. palmeri* seeds to captive killdeer and mallard ducks and found that they were passed in viable condition after many hours retention within the bird, long enough for killdeer to fly over 1,000 miles and mallards over 500.

DISTRIBUTION OF A. GREGGII CLARIFIED

Amaranthus greggi S. Wats. appeared in my revision (1955) as a rare species, known from only 3 Texas and 6 Mexican localities. The distribution is now much better known (fig. 1). The following citations, located by municipio, parish, or county within each state, should be added to those given previously. The additional citations all date from between 1958 and 1965 except Wawra's. Heinrich Wawra, Ritter von Fernsee, was chief surgeon on the Austrian frigate "Novara" on which Maximilian and Carlotta sailed to claim their Mexican empire in 1864.

The ship is known to have made a brief excursion around the Gulf while stationed at Vera Cruz the following year and Wawra's collections were probably made then.

Abbreviations: *J. S(auer); D. G(ade)*.

Mexico

CAMPECHE. CAMPECHE: *J. S. 2412*, B, BM, F, GH, MICH, MO, UC, WIS. CARMEN: *J. S. 2446*, F, WIS; *J. S. & D. G. 3148*, WIS; *3352*, WIS; *H. Wawra 235*, W. TABASCO. FRONTERA: *J. S. & D. G. 3117*, DAV, WIS, *3142*, WIS. PARAISO: *F. Barlow 12/6*, WIS. TAMAULIPAS. VILLA CECILIA: *J. S. & D. G.*
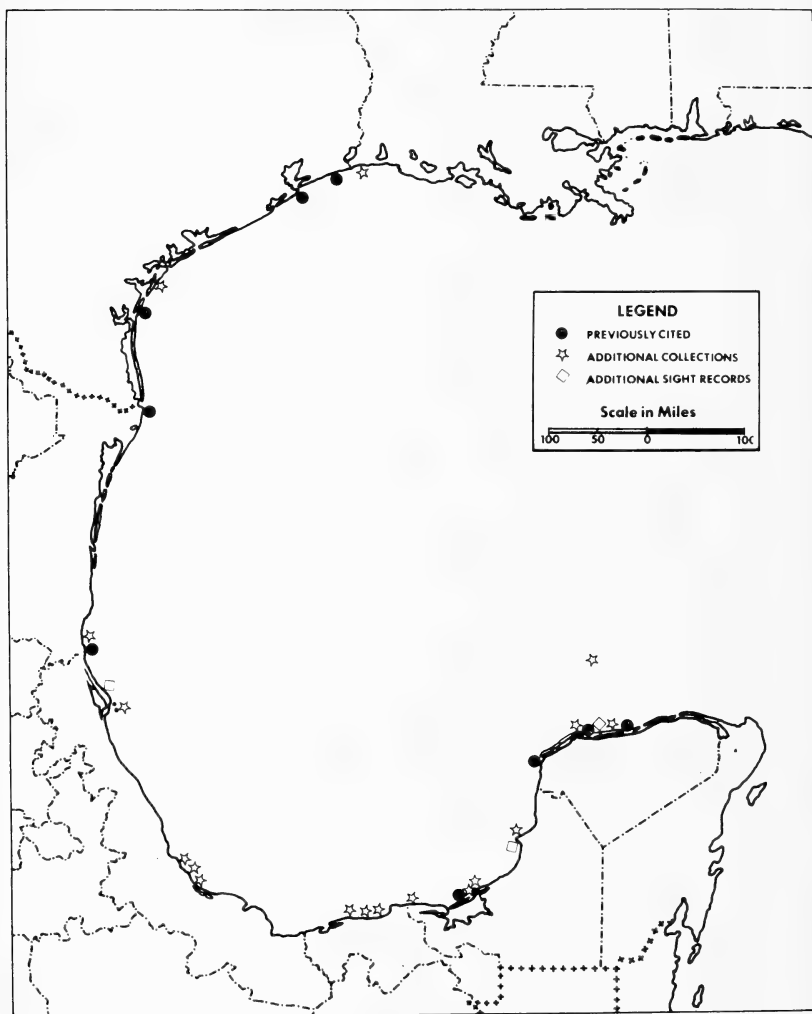

FIG. 1. *Amaranthus greggii:* revised distribution map.

2960, F, WIS. VERA CRUZ. ALVARADO: *J. S. & —D. G. 3102,* WIS; *H. Wawra 431,* W. BOCA DEL RIO: *J. S. 2465,* F, WIS: *J. S. & D. G. 3085,* WIS. TAMIA-HUA: *W. G. McIntire s.n.,* WIS. YUCATAN. ARRECIFE ALACRAN: *H. Wawra 106,* W. DZILAM: *J. S. & D. G. 3225,* WIS. PROGRESO: *J. S. 2360,* BM, DH, F, GH, MICH, MO, UC, WIS.

United States

LOUISIANA. CAMERON: *J. W. Thieret & W. D. Reese 10028,* WIS. TEXAS. ARANSAS: *J. S. 2572,* WIS, *2607,* TEX.

Sight records (fig. 1) are from published vegetational transects (Poggie, 1962; Sauer, 1967).

Amaranthus greggii has an extraordinarily predictable distribution pattern. Its niche is a linear zone at the outer fringe of pioneer beach vegetation; it commonly grows closer to the sea than any other species. It is relatively indifferent to grand regional rainfall gradients. It does not grow on limestone shores or other stable substrates but only on loose sand. The sand may be light or dark, calcareous, quartz, or of heavy minerals. It makes little difference whether the beach is wild and remote or inhabited and heavily trodden. The species is particularly abundant at the head of the Bay of Campeche and along the northern Yucatan barrier islands; in both sectors it is a summer colonizer of beaches swept clean by northerly winter storm winds, the famous Gulf *nortes.* Its frequency decreases northward along the Vera Cruz coast. On the Tamaulipas and Texas barrier islands there seems to be no regular niche for it between the bare beach and the grassy foredunes. In this sector, sporadic occurrences may increase after hurricanes. For example, in 1959 near Port Aransas, Texas, I found only a few isolated individuals of the species on St. Joseph and Mustang Island beaches, none at all in rather extensive transects of the dunes. In the same area in 1962, nine months after hurricane Carla, *A. greggii* was conspicuous and locally abundant in the devastated dunes. Thieret and Reese's outlying Louisiana record was also made the year after Carla and was probably ephemeral.

Presumably seeds are continually floating up the Tamaulipas and Texas coast in the predominantly clockwise longshore currents from the tropical stronghold of the species. The seeds alone are not buoyant but the indehiscent, inflated utricles are and I have found they float in an occasionally agitated Petri dish for over a week before waterlogging.

It seems likely that *A. greggii* evolved into a distinct species along the tropical Gulf coast beyond the range of *A. arenicola,* its closest relative. Evolutionary changes required to derive *A. greggii* from the latter consist of little more than suppression of utricle dehiscence and increasing coriacous texture of the foliage. Although its main populations are in the High Plains, *A. arenicola* approaches the Gulf in southern Texas and Tamaulipas. At the mouth of the Rio Panuco, it grows on active dunes (*J. S. & D. G. 2959,* F, WIS) within sight of storm beach colonies of *A. greggii.* Apparent hybrids occur, including the types of *A. myrian-*

thus Standl., collected at the mouth of the Rio Panuco in 1910 (*E. Palmer 266, 511,* CAS, GH, K, MO, US, WIS).

The peculiarly regular winter storm regime of the Gulf evidently offered an evolutionary opportunity for an annual pioneer from a temperate zone background. *Amaranthus greggii* and a few of its associates, e.g. species of *Cakile,* are anomalous in this respect among the mass of tropical beach pioneers, which are typically perennials adapted to nonperiodic storm regimes.

LITERATURE CITED

AELLEN, P. 1961. Die Amaranthaceen Mitteleuropas. *In* G. Hegi, Illustrierte Flora von Mitteleuropa, 2d, ed., 3(2):461–535.

BAKER, H. G. 1967. Support for Baker's Law—as a rule. Evolution 21:853–856.

BRENAN, J. P. M. 1961. *Amaranthus* in Britain. Watsonia 4:261–280.

DE VLAMING, V. and V. W. PROCTOR. 1968. Dispersal of aquatic organisms: Viability of seeds recovered from the droppings of captive killdeer and mallard ducks. Amer. J. Bot. 55:20–26.

GRAY, A. 1876. Notes on *Acnida*. Amer. Nat. 10:487–489.

HOWELL, J. T. 1966. *Amaranthus arenicola* in Monterey County, California. Leafl. W. Bot. 10:256.

MURRAY, M. J. 1940. The genetics of sex determination in the family Amaranthaceae. Genetics 25:409–431.

NUTTALL, T. 1835. Collections towards a flora of the Territory of Arkansas. Trans. Amer. Philos. Soc., n. ser., 5:139–203.

POGGIE, J. J. 1962. Coastal pioneer plants and habitat in the Tampico region, Mexico. Louisiana State University, Coastal Studies Institute, Technical Report 17A:1–62.

SAUER, J. D. 1953. Herbarium specimens as records of genetic research. Amer. Nat. 87:155–156.

————. 1955. Revision of the dioecious amaranths. Madroño 13:5–46.

————. 1957. Recent migration and evolution of the dioecious amaranths. Evolution 11:11–31.

————. 1967. Geographic reconnaissance of seashore vegetation along the Mexican Gulf coast. Louisiana State University, Coastal Studies Series Number 21:1–59.

TWISSELMANN, E. C. 1963. Plant records in Kern County, California. Leafl. W. Bot. 10:46–64.

ULINE, E. B. and W. L. BRAY. 1895. Synopsis of North American Amaranthaceae. Bot. Gaz. 20:155–161.

VANN, J. H. 1969. Landforms, vegetation, and sea level change along the Guiana coast of South America. State University College, Buffalo, N. Y., Technical Report No. 3:1–128.

THE MOSSES OF THE CHANNEL ISLANDS, CALIFORNIA

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Off the coast of Southern California is a group of eight islands, the Channel Islands, or the Southern Californian Islands. These along with eight others off the coast of Baja California (Baja California Islands), make up the California Islands (Philbrick, 1967).

The Santa Barbara Botanic Gardens has had a continuing program of study of the flora of these islands for some time. A listing of vascular plants of Santa Barbara Island will soon appear in this journal (Philbrick, in press). Numerous trips have been made to these islands by various staff members. E. R. Blakley collected bryophytes and sent them to the author for identification.

Bryophyte collections from the Channel Islands are not plentiful. Sayre (1940) listed the reports given prior to that date naming 39 species. According to her, all islands were represented except Anacapa and Santa Rosa. However, her list did not include Santa Barbara Island. Steere (1954) reported 47 species of mosses which he found on Santa Catalina Island during a foray of the California Botanical Society, thereby doubling the previously known number.

Now that additional collecting has been carried out on each of these islands it seems appropriate to bring the information on these taxa up to date. Eleven new records are reported. Voucher specimens of these have been deposited at SBBG and DEK.

LIST OF NEWLY RECORDED SPECIES

Brachythecium albicans (Hedw.) B. S. G. Dirt bank, north slope, elevation 100 ft. Cherry Canyon at junction with Windmill Canyon, Santa Rosa Island.

Claopodium whippleanum (Sull.) Ren. & Card. var. *leuconeuron* (Sull. & Lesq.) Grout. Santa Catalina and Santa Cruz Islands.

Didymodon mexicanus Besch. var. *subulatus* Ther. & Bartr. *ex* Bartr. Halfway between the mouth of Willow Canyon and Cardwell Point at Triangulation Point, San Miguel Island. Elevation 125 ft.

    Rocky north slope; scattered. Elevation 350 ft. Head of Middle Canyon, Santa Barbara Island. Soil bank on north slope with grass. Elevation 100 ft. Rocky cliff on canyon side, halfway between Eel Point and Seal Cave. San Clemente Island, Los Angeles Co.

Eurynchium praelongum (Hedw.) B. S. G. var. *stokesii* (Turn.) Habk. From trunk of *Quercus tomentella*. Elevation 1500 ft. Air Force Radar Station. Santa Rosa Island.

    Shady rock under *Quercus*. Elevation 400 ft. Hill east of Coches Prietas anchorage. Santa Cruz Island.

Gimmia apocarpa Hedw. var. *atrofusca* (Schimp.) Husn. On wood, north slope. Trunk of Island Oak, *Quercus tomentella*. Air Force Radar Station. Santa Rosa Island.

Grimmia involucrata Card. Scattered on silt deposits over rocks. Elevation 400 ft. First large canyon west of Profile Point. Santa Cruz Island. Santa Barbara Co., California.

Grimmia ovalis (Hedw.) Lindb. On rock in shade of Island Ironwood trees. Eleva-
tion 400 ft. Hill on west side of Coches Prietas Canyon. Santa Cruz Island.
Santa Barbara Co.

Orthotricum tenellum Bruch *ex* Brid. var. *coulteri* (Mitt.) Grout Bark of *Quercus*
agrifolia. Elevation 150 ft. Cherry Canyon, Santa Rosa Island.

Branch of *Quercus agrifolia*. Elevation 500 ft. Canyon south of Santon Ranch
headquarters, Santa Barbara Island.

On bark of *Quercus agrifolia* in shade. Elevation 400 ft. Hill on west side of
Coches Prietas Canyon, Santa Cruz Island. (Identified by S. Flowers as *O.
cylindrocarpum* Lesq.)

Scleropodium apocladum (Mitt.) Grout Shady rock under *Quercus* and *Heteromeles*.
Elevation 700 ft. Oak Grove Canyon on north side of highest peak. Anacapa
Island, Ventura Co.

Rocky beach cliff under *Eucalyptus* trees. Elevation 20 ft. 100 yards west of
Prisoner's Harbor. Santa Cruz Island.

On rock in shade. Torrey Pine grove at Beeches Bay. Santa Rosa Island.
(Identified by Harold Robinson.)

Tortula obtusissima (C. Mull.) Mitt. Shady rock under *Quercus*. Elevation 400 ft.
Hill east of Coches Prietas anchorage. Santa Cruz Island.

Tortula princeps De Not. Common on the bark of *Quercus*. Elevation 800 ft. One
fourth mile below the lower reservoir in Bullrush Canyon. Santa Catalina Island.
Bark of *Quercus agrifolia*. Elevation 150 ft. Cherry Canyon, Santa Rosa Island.

COMPARISON OF AREA WITH NUMBER OF SPECIES OF PLANTS

An interesting comparison between the area of each island and the
number of vascular plants (Raven, 1967) and moss species can be made.

	Area in Sq. Miles	Vascular Plant Species	Moss Species
Santa Cruz	96	420	20
Santa Rosa	84	340	18
Santa Catalina	75	375	59
San Clemente	56	233	12
San Nicolas	22	120	7
San Miguel	14	190	6
Anacapa	1.1	70	6
Santa Barbara	1.0	40	5

Raven makes the suggestion that "all of the islands, with the possible
exception of San Nicolas, are approximately 'saturated' with species of
vascular plants in the sense of MacArthur and Wilson." If one assumes
that the same relationship holds for bryophytes (and there is no evi-
dence one way or another for this), and extrapolating from these figures,
additional numbers of species can be expected on all islands except
Anacapa. It is also evident that 60 is over twice the number one would
expect on Santa Catalina. On the other hand, if the 60 mosses on Santa
Catalina can be said to "saturate" that island in the same manner as
the vascular plants, then more species can be expected to be found on
all other islands. It is doubtful that this condition exists since topog-
raphy and microclimate play a greater role in the distribution of mosses
due to their smaller size and their ability to exist in small crevices, etc.
Goats have grazed these islands for many years. It is likely that they
have exterminated many species of both vascular and non-vascular

plants. The accessibility of Santa Catalina by both ship and plane means that more collecting can be easily carried out there. Since other islands are either privately owned or have military installations on them, collecting will continue to be limited.

Table 1 gives the complete list of 76 species and their distribution among the islands according to all reports. Nomenclature has been adjusted to conform to Crum, Steere, and Anderson (1965). Abbreviations for these islands are as follows: Anacapa, A; San Clemente, SCl; San Miguel, SMi; San Nicolas, SN; Santa Barbara, SBa; Santa Catalina, SCa; Santa Cruz, SCr; and Santa Rosa, SR.

TABLE 1. MOSSES RECORDED FROM THE CHANNEL ISLANDS AS DERIVED FROM ALL KNOWN SOURCES

	SMi	SR	SCr	A	SBa	SN	SCa	SCl
Aloina aloides var. ambigua							X	
A. pilifera							X	
Alsia californica		X	X				X	
Anacolia menziesii var. baueri							X	X
Anoectangium obtusifolium							X	
Antitrichia californica							X	
Barbula brachyphylla	X	X				X	X	
B. convoluta							X	
B. cylindrica							X	
B. vinealis	X	X	X	X	X	X	X	X
Bartramia stricta		X	X	X			X	X
Bestia brevipes							X	
Bestia vancouverensis			X	X				
Brachythecium albicans		X						
Bryoerythrophyllum recurvirostrum		X						
Bryum argenteum var. lanatum							X	
B. bicolor							X	
B. canariense							X	
B. capillare							X	
B. creberrimum							X	
Ceratodon purpureus	X					X	X	X
Claopodium whippleanum							X	
C. whippleanum var. leuconeuron			X				X	
Crossidium desertorum						X		
Desmatodon convolutus		X					X	
D. guepinii							X	
D. hendersonii							X	
Dicranella varia							X	
Didymodon mexicanus var. subulatus	X				X			X
D. tophaceus						X	X	
Encalyta vulgaris var. mutica							X	
Entosthodon bolanderi		X						X
Eucladium verticillatum			X			X	X	
E. praelongum var. stokesii		X	X					
Eurynchium pulchellum		X					X	
Fissidens limbatus							X	
Funaria hygrometrica							X	

TABLE 1. *Continued.*

	SMi	SR	SCr	A	SBa	SN	SCa	SCl
F. muehlenbergii							X	
Grimmia apocarpa var. atrofusca		X						
G. decipiens								X
G. involucrata			X					
G. laevigata								X
G. ovalis			X					
G. pulvinata							X	
G. trichophylla							X	
Haplocladium microphyllum							X	
Homalothecium aeneum							X	
H. arenarium			X	X	X		X	X
H. nuttallii							X	
H. pinnatifidum							X	
Isothecium cristatum							X	
Orthotrichum lyellii		X	X				X	
O. speciosum								X
O. tenellum		X	X				X	
O. tenellum var. coulteri		X	X		X			
Phascum hyalinotrichum							X	
Pottia arizonica							X	
P. bryoides							X	
Pterogonium gracile			X				X	
Rhynchostegiella compacta							X	
Scleropodium apocladum		X	X	X				
S. californicum	X	X	X	X		X	X	X
S. cespitans							X	
S. tourettei							X	
Timmiella anomala							X	
Tortula bolanderi							X	
T. brevipes	X	X					X	
T. californica							X	
T. intermedia			X				X	
T. laevipila			X				X	
T. obtusissima			X					
T. princeps		X					X	
T. ruralis			X		X			X
Trichostomopsis brevifolia							X	
T. fayae							X	
Weissia controversa							X	
Totals	6	18	20	6	5	7	59	12

LITERATURE CITED

CRUM, H., W. C. STEERE, and L. E. ANDERSON. 1965. A list of the mosses of North America. Bryologist 68:377–432.

PHILBRICK, R. N., ed. 1967. Proceedings of the symposium on the biology of the California Islands. Published by Santa Barbara Botanic Gardens, Santa Barbara, California.. In press. The plants of Santa Barbara Island, California. Madroño.

RAVEN, P. H. 1967. The floristics of the California Islands *in* R. N. Philbrick, ed. Proceedings of the symposium on the biology of the California Islands, pp. 57–67.

SAYRE, G. 1940. Mosses of the Santa Barbara Islands. Bryologist 43:32–35.

STEERE, W. C. 1954. Bryophyta of Santa Catalina Island, California. Madroño 12:180–189.

THE VEGETATIONAL GRADIENT ON THE LOWER SLOPES OF THE SIERRA SAN PEDRO MARTIR IN NORTHWEST BAJA CALIFORNIA

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The coastal plains of northwestern Baja Califorina are covered with a unique vegetation which has interested botanists through the years. Shreve (1936) considered this vegetation, which covers a 100 mile extent roughly between Ensenada and Rosario, as a distinctive transitional type between the desert scrub of the south and the chaparral (the dense evergreen sclerophyllous scrub characteristic of Mediterranean type climates) of the north. He viewed the vegetation as transitional primarily in the sense that it has ecological features, in terms of cover, life form, and leaf types, intermediate between desert scrub and chaparral. Floristically, however, he stated that the vegetation was distinctive because of the large number of prominent endemics including, for example, *Aesculus parryi, Adolphia californica, Bergerocactus emoryi,* and *Rosa minutifolia.*

Epling and Lewis (1947) briefly discussed this vegetation in their comprehensive floristic view of the chaparral and coastal sage (a shrubby vegetation type which is lower in stature than the chaparral, and which is composed of primarily drought-deciduous elements) vegetation types. They state that the coastal sage vegetation, which is confined primarily to the California coastal regions at elevations below the chaparral, extends from the San Francisco Bay Region of central California southward to Rosario in Baja California. This would then include the transitional type of Shreve. Epling and Lewis (1947) noted that many of the transition zone endemics, particularly the woody elements, ". . . do not seem to form an integral part either of the coastal sage or the chaparral—but seem to hold themselves somewhat apart. . . ." They felt that Shreve's interpretation of the transitional type was somewhat confused because of his failure to recognize the identity of the coastal sage vegetation and its ecological position relative to the chaparral.

Neither Shreve nor Epling and Lewis visited the vegetation lying inland from the coastal plains on the slopes of the Sierra San Pedro Martir although they felt this region might be critical to an understanding of the so-called transition vegetation.

The present study examines some of the ecological characteristics of the coastal lowland vegetation as it compares with the vegetation on the lower slopes of the Sierra San Pedro Martir, including the chaparral.

The Study Area and Sampling Methods

The vegetation was examined in a west-to-east transect in the foothill

region between San Telmo and Valladares Rancho. This region of the
Sierra San Pedro Martir is located at approximately 31°S. The highest
elevation encountered, near the eastern end of the transect, was 800 m.
Near the base and presumably the driest portion of the transect at San
Telmo, which is located at 175 m elevation, average annual precipita-
tion is 160 mm (Hastings, 1964).

Observations of the general vegetational trends were made throughout
the transect with quantitative samples at three points: 100, 430, and
800 meters elevation. At the sampling stations three 20-meter line inter-
cepts were utilized. The height and projected cover of each individual on
the line were recorded. The cover values given in the results are aver-
ages for all sample lines at each station. Presence of species in the general
area that were not encountered on the lines was also noted.

RESULTS

The leaf type (evergreen, drought-deciduous, or stem-succulent) and
the percentage cover of each species encountered at the three sample
stations are given in Table 1. The number of species decreases with
elevation, whereas the total vegetation cover increases. A few species
were found at all stations, such as *Rhus laurina, Ephedra californica,*
and *Eriogonum fasciculatum.* The first two, however, were only occa-
sional individuals at each site. The low- and mid-elevation sites shared
about 20% of their species; the mid- and high-elevation sites somewhat
more.

One of the most striking aspects of the vegetational gradient is the
shift in leaf type with elevation (fig. 1). Over 35% of the species at
the lowest site were succulents, whereas no succulents were present at
the highest elevations. Further, the percentage of evergreen species in-
creases greatly with elevation. Eighty per cent of the species are ever-
green at the highest elevation site, whereas there are only 20% ever-
greens at the lowest site. The results are generally similar when con-
sidered on the percentage cover of the various leaf types at each site
(table 1), rather than the percentage of species present of a given leaf
type as is shown in Figure 1. For example, evergreen species constitute
72% of the cover at the 800 m site, and only 7% at the 100 m site.
Drought-deciduous species are most prevalent at the mid-elevation site
where they constitute over 71% of the species (fig. 1) and 73% of the
cover (table 1).

The assessment of leaf type (deciduous vs. evergreen) was made at
the end of the drought season in mid-December, 1968. In all cases,
except for *Eriogonum fasciculatum,* the leaf type was constant for a
given species at all stations. *Erigonum* plants at the lowest sites had only
a few terminal green leaves present, whereas at the highest sites they
held a large number of apparently functional leaves.

Another vegetational trend with elevation is the increasing stature
(and woodiness) of the plants (fig. 2). At the 800 m site most of the

TABLE 1. LEAF TYPE AND PER CENT COVER OF THE PERENNIAL PLANTS ENCOUNTERED IN TRANSECT.*

	100	400	800
Agave shawii Engelm.	7.90(S)		
Machaerocereus gummosus (Engelm.) Britt. & Rose	4.00(S)		
Echinocereus maritimus (M. E. Jones) K. Schum.	0.25(S)		
Mammillaria dioica K. Brandegee	0.33(S)		
Bergerocactus emoryi (Engelm.) Britt. & Rose	1.16(S)		
Dudleya ingens Rose in Britt. & Rose	0.83(S)		
Myrtillocactus cochal (Orcutt) Britt. & Rose	P　(S)		
Opuntia rosarica G. Lindsay	P　(S)		
Franseria chenopodifolia Benth.	17.63(D)		
Euphorbia misera Benth.	0.41(D)		
Harfordia macroptera (Benth.) Greene & Parry	1.91(D)		
Lycium californicum Nutt. ex A. Gray	P　(D)		
Unknown shrub	P　(D)		
Galvezia juncea (Benth.) Ball	P　(D)		
Rhus integrifolia (Nutt.) Benth. & Hook.	P　(E)		
Rosa minutifolia Engelm.	15.73(D)	2.91(D)	
Viguiera laciniata A. Gray	P　(D)	15.46(D)	
Simmondsia chinensis (Link) Schneider	7.25(E)	P　(E)	
Eriogonum fasciculatum Benth.	0.83(D)	8.95(D)	1.66(E)
Ephedra californica Wats.	P　(E)	1.45(E)	P　(E)
Rhus laurina Nutt. in T. & G.	P　(E)	P　(E)	P　(E)
Acalypha californica Benth.		0.16(D)	
Eriogonum sp.		0.21(D)	
Artemisia californica Less.		2.49(D)	
Encelia californica Nutt.		P　(D)	
Aesculus parryi A. Gray		P　(D)	
Salvia munzii Epl.		15.83(D)	
Lotus scoparius (Nutt. in T. & G.) Ottley		27.69(D)	26.66(D)
Cneoridium dumosum (Nutt.) Hook.		P　(E)	0.41(E)
Adenostoma fasciculatum H. & A.			49.41(E)
Arctostaphylos oppositifolia Parry			20.66(E)
Trichostema parishii Vasey			0.83(E)
Fraxinus trifoliata (Torr.) Lewis & Epling			5.00(D)
Xylococcus bicolor Nutt.			P　(E)
Juniperus california Carr.			P　(E)
Total % plant cover	58.23	75.15	104.63
Per cent cover by plant leaf types			
Stem succulents	14.47	0	0
Drought-deciduous	36.51	73.70	31.66
Evergreen	7.25	1.45	72.97

* Numbers refer to percentage plant cover; P notes presence of species. Letters in parentheses refer to plant leaf types: E, evergreen; D, drought-deciduous; and S, stem succulent.

species are greater than 1.5 m tall. In contrast, the lowest site had species of many different size classes, but most were less than 1.5 meters tall.

All of the sites showed some evidence of light grazing. This may explain the importance of such subshrubs as *Lotus scoparius* at the high-elevation chaparral site where it probably is successional and indicates evidence of disturbance. As is often the case to the north, coastal sage
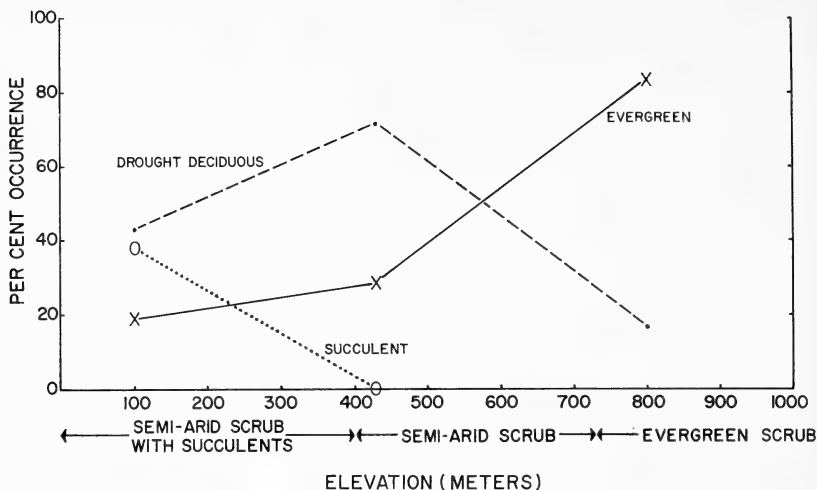
FIG. 1. Percentage of the species occurring at each sample site which are drought deciduous, evergreen, or stem succulent. In order to compare the vegetation types encountered in this study with those found in other Mediterranean climatic regions generalized descriptive terms are used in this figure. Evergreen scrub would correspond to chaparral of the text, semi-arid scrub to coastal sage, and semi-arid scrub with succulents to the "transitional vegetation." The elevational limits of the vegetation types are generalized and apply only to the immediate transect route.

elements may occur as successional species within disturbed areas of the chaparral (Harrison et al., 1971).

DISCUSSION

The lowest elevation vegetation within the study area is distinctive from the coastal sage vegetation to the north in two regards: 1) the number of endemic species it contains, and 2) the large number of succulents present. More closely allied to the northern coastal sage, both ecologically and floristically, is the vegetation which occurs in the study area between elevations of 400 and 730 m. Here, as in the north, the predominant growth form is a drought-deciduous shrub less than a meter in height. *Artemisia californica, Salvia munzii, Viguiera lacinata, Encelia californica, Eriogonum fasciculatum,* and *Lotus scoparius,* all characteristic of the coastal sage according to Epling and Lewis, are present at mid-elevations. A few of these species also occurred at the other sampling stations but it appears that this southern version of coastal sage vegetation reaches its lower limit near 400 m elevation. Floristically, the picture is difficult to assess in detail because only the dominantts have been considered. More detailed study of the distribution of all floristic elements within this region and in adjacent areas would be useful, but must be analyzed in relation to the complex microhabitat variation of the region. For example, *Heteromeles arbutifolia,* a charac-
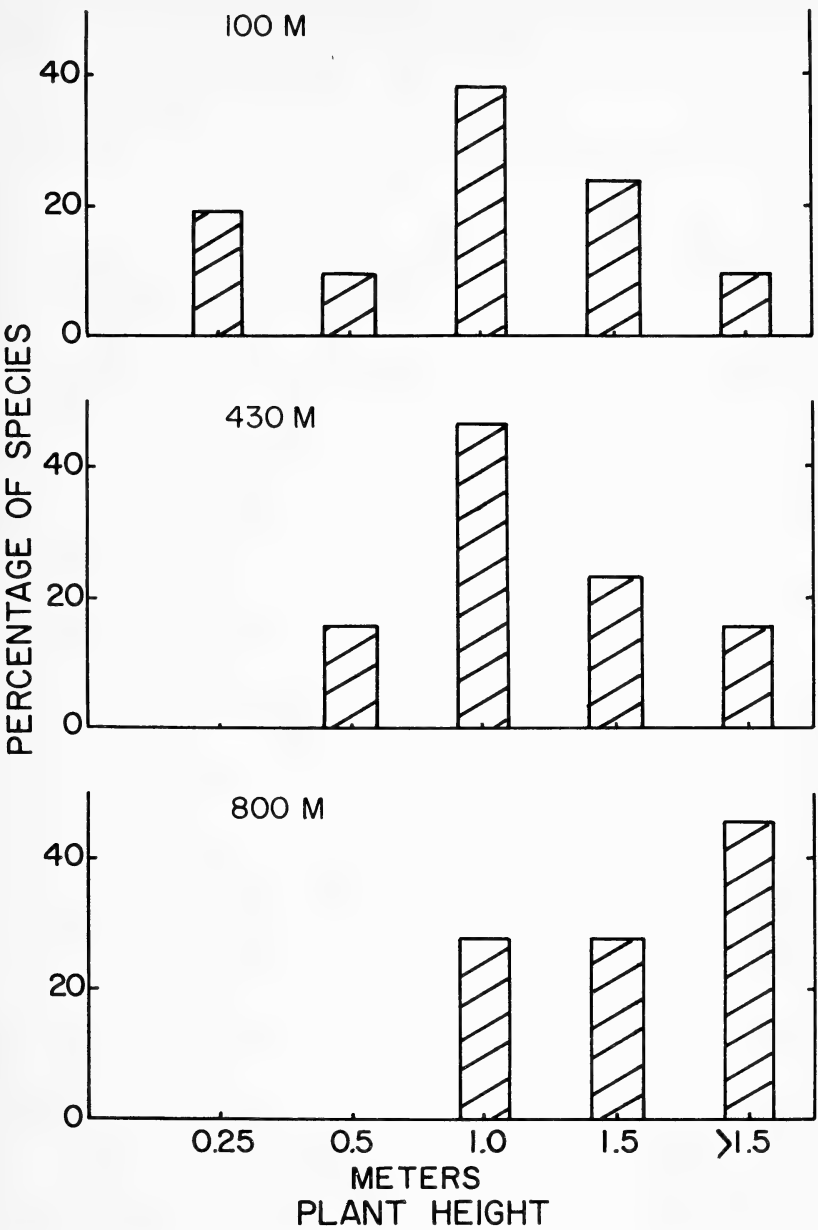
Fig. 2. Frequency distribution of plant heights of all species occurring at sample sites at 100, 430, and 800 meters elevation.

teristic chaparral plant is often found in favorable microsites within a matrix of the more xeric coastal sage elements in this area.

Certain ecological trends are, however, quite clear. Shreve noted a number of tendencies which were apparent going from the desert vegetation at the southern end of the transition type to the chaparral to the north, or in other words, along a gradient of increasing available moisture and decreasing temperatures. These are: 1) an increasing density of the vegetation, 2) an increasing uniformity in the heights of the dominants, and 4) an increasing loss of the drought-deciduous elements and an increase in the evergreens. All of these trends apply in the gradient from the coastal vegetation in the transition area through chaparral vegetation on the mid-elevation slopes of the Sierra San Pedro Martir. Similar ecological changes have also been noted along an altitudinal gradient in the Santa Catalina Mountains of Arizona by Whittaker and Niering (1965).

These altitudinal trends are the same that prevail latitudinally in California and even along comparable climatic gradients in Chile (Mooney *et al.*, 1970). The basis for certain of these trends, particularly growth form and leaf type, has been discussed by Mooney and Dunn (1970), in relation to the photosynthetic economy of the various plant types (evergreen, drought-deciduous, and succulent) and habitat water availability. Such compact gradients encompassing such a wide diversity offer an excellent opportunity for the study of problems relating to ecological variability and adaptation.

The coastal vegetation with its large number of unique and beautiful succulents is unfortunately being rapidly decimated, as is the related coastal sage to the north, due to rapid development in these favorable building and agricultural sites. Hopefully, representative areas can be saved for future study. These areas are particularly rich in the variability of ecological types which they contain. Only limited studies have been made of them at the present.

LITERATURE CITED

EPLING, C. and H. LEWIS. 1947. The centers of distribution of the chaparral and coastal sage associations. Amer. Midl. Naturalist 27:445–462.

HARRISON, A. T., E. SMALL, and H. A. MOONEY. 1970. The drought relationships and distribution of two Mediterranean-climate California plant communities. Ecology 52:869–875.

HASTINGS, J. 1964. Climatological data for Baja California. Univ. Arizona Institute of Atmospheric Physics. Tech. Dept. 14. 132 pp.

MOONEY, H. A., E. L. DUNN, F. SHROPSHIRE, and L. SONG, JR. 1970. Vegetation comparisons between the Mediterranean climatic areas of California and Chile. Flora 159:480–496.

———, and E. L. DUNN. 1970. Photosynthetic systems of Meditteranean-climate shrubs and trees of California and Chile. Amer. Naturalist 104:447–453.

SHREVE, F. 1936. The transition from desert to chaparral in Baja California. Madroño 3:257–264.

WHITTAKER, R. H., and W. A. NIERING. 1965. Vegetation of the Santa Catalina Mountains, Arizona. A gradient analysis of the south slope. Ecology 46:429–452.

REVIEW

The Savory Wild Mushroom. By Margaret McKinney. Revised and enlarged by Daniel E. Stuntz. XXI + 242 pp., illustrated. University of Washington Press, Seattle, Wash. 98105. 1971. $8.95 cloth; $4.95 paperback.

The first edition of this popularly written handbook on the more common species of west coast mushrooms proved so useful and attractive that it soon became out of print. This newly revised edition will undoubtedly prove even more popular since it is considerably enlarged, and the species descriptions are somewhat more detailed. As in the first edition the book is divided into three sections with the first and largest part being devoted to a treatment of approximately 150 species of fleshy fungi followed by a chapter devoted to mushroom poisoning and concluding with two chapters devoted to mycophagy. The format is similar to that of the first edition with each species receiving a short description along with pertinent comments on its distinctive features and edibility. Since it is designed primarily as a field manual all microscopic data are omitted, and no taxonomic keys are included. In the new edition all species of a given group are placed together rather than being artificially divided on the basis of edibility with the result that it is much easier to use. Representatives of most of the major groups of fleshy fungi are included, but the gill fungi receive the most space. A photograph of each species is included many of which are in color. Since Professor Stuntz is the dean of agaricologists on the West Coast, it is not surprising that the species determinations are highly accurate and carefully presented. So far as is known this publication represents the most complete compilation of west coast fungi available.

The most disappointing feature is the generally poor reproduction of the color plates. The colors, particularly the red shades, are badly reproduced as shown in *Amanita muscaria,* for example, which appears dark brown rather than bright red. The black and white photographs are much better but in some the composition and lighting could have been improved. From a taxonomic point of view only a few minor criticisms might be made. At least one new combination has been made without following the International Code. It is now apparent that *Boletus olivaceobrunneus* is not at all related to *Boletus edulis* as indicated in the text but is perhaps synonymous with *Tylopilus pseudoscaber.* Also the photograph of *Boletus eastwoodeae* is somewhat misleading since the more typical variety has a much shorter and darker colored stipe.

The chapter on mushroom poisoning, written by Professor Tyler, is excellent. It is well written, authoritative and should be required reading for all those interested in mycophagy. In a considerably lighter vein is a chapter on edibility and mushroom cookery written by A. M. Pellegrini. It is lively and thoroughly enjoyable and provides a good commentary on the present practices in preparing these fungi for the table. The recipes in the final chapter are essentially the same as in the first edition.—HARRY D. THIERS, Department of Ecology & Systematic Biology, San Francisco State College, San Francisco, California 94132.

ADDITIONS AND CORRECTIONS TO THE FLORA
OF BODEGA HEAD, CALIFORNIA

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The vascular plants and major plant communities of Bodega Head on the California coast (38°20'N, 123°4'W) have recently been described (Barbour, 1970). Subsequently, 28 additional species have been noted. This paper lists those additions as well as some corrections to the first report. Voucher collections have been deposited at DAV.

At present the Bodega Head area is known to support 60 families of vascular plants, 172 genera, and 243 species. About two thirds of the species are native. Additional species are to be expected in the near future on the Head, for it appears that the grassland community is undergoing succession to northern coastal scrub. Comparison of aerial photographs taken in 1954 and 1970 demonstrates a three-fold increase in the grassland area dominated by lupine shrubs *(Lupinus arboreus)*. Grazing and heavy human use of the grassland have been stopped since 1962; possibly, then, shrub invasion had been held back by disturbance of various sorts. *Lupinus variicolor, Delphinium coccineum, Poa unilateralis,* and *Bromus carinatus,* all native perennials, have also dramatically increased in the past 2—3 years. Annuals, however, and many of them introduced, still dominate the grassland.

Check List
Calamophyta
Equisetaceae

Equisetum hyemale L. var. *robustum* A. A. Eat. Giant scouring rush. Perennial, native. Occasional on shaded, wet banks.

Pterophyta
Salviniaceae

Azolla filiculoides Lam. Water fern. Native, Occasional in still water in the fresh water marsh. Only vegetative plants seen.

Anthophyta—Dicotyledoneae
Caryophyllaceae

Cerastium arvense L. Mouse-ear chickweed. Perennial, native. Rare in the grassland and in drier areas of the fresh water marsh. May–June.

Sagina crassicaulis Wats. Pearlwort. Perrennial, native. Rare in the dunes. April–May.

Compositae
Gnaphalium luteo-album L. Cudweed. Perrennial, introduced. Rare in seasonally wet depressions. November.

Malacothrix californica DC. Annual, native. Rare in dunes. April–May.

Senecio vulgaris L. Common groundsel. Annual, introduced. Rare to occasional in dunes. April–May.

Geraniaceae
Geranium dissectum L. Annual, introduced. Occasional in grassland. April–May.

Labiatae
Marrubium vulgare L. Horehound. Perennial, introduced. Rare along roads. November.

Monardella villosa Benth. var. *franciscana* (Elmer) Jeps. Coyote mint. Perennial, native. Occasional on grassland hilltops. July.

Leguminosae
Lupinus chamissonis Esch. Lupine. Perennial, native. Localized (less than 50 shrubs) on established dune ridge tops, not intermixed with *L. arboreus*. April–May.

L. densiflorus Benth. var. *palustris* (Kell.) C. P. Sm. Lupine. Annual, native. Rare to occasional on rodacuts. June.

L. variicolor Steud. Lupine. Perennial, native. Occasional along roadsides. April–June.

Trifolium gracilentum T.&G. Clover. Annual, native. Occasional in the grassland and in disturbed areas. April–May.

T. macraei H.&A. Clover. Annual, native. Occasional on rocky grassland hilltops. April–May.

Onagraceae
Camissonia strigulosa (Fisch. & Mey.) Raven. Annual, native. Rare to occasional on established dunes. April–May.

Plantaginaceae
Plantago hookeriana F.&M. var. *californica* (Greene) Poe. Annual, native. Occasional in disturbed parts of the grassland. April–May.

Polemoniaceae
Linanthus androsaceus (Benth.) Greene. Annual, native. Rare on established dunes. April–May.

Polygonaceae
Polygonum coccineum Muhl. Perennial, native. Rare in the fresh water marsh. Only vegetative plants seen.

Ranunculaceae
Delphinium decorum F.&M. Perennial, native. Rare on rocky grassland hilltops. April–May.

Rubiaceae

Galium aparine L. Bedstraw. Annual, introduced. Occasional in wet, shaded microhabitats in established dunes, also scattered in drier parts of the fresh water marsh. April–June.

NOTE: *G. asperrimum* voucher is missing, and identification may be in error. This plant has not been found again; rare in grassland.

G. nuttallii Gray. Bedstraw. Perennial, native. Occasional in seasonally wet depressions. October.

Scrophulariaceae

Linaria canadensis (L.) Dum.-Cours. Annual, native. Rare to occasional in established dunes. April.

Orthocarpus pusillus Benth. Annual, native. Occasional in grassland. April.

Umbelliferae

Berula erecta (Huds.) Cov. Perennial, introduced. Common in the wetter parts of the fresh water marsh. Only vegetative plants seen.

Hydrocotyle ranunculoides L. Marsh pennywort. Perennial, native. Abundant in the wettest part of the fresh water marsh. Only vegetative plants seen.

Anthophyta—Monocotyledoneae

Cyperaceae

Carex obnupta Bailey. Sedge. Perennial, native. Rare in fresh water marsh. April–June.

Gramineae

Agrostis alba L. Redtop. Perennial, introduced. Occasional, in dense swards, on grassland hilltop. July.

Festuca megalura Nutt. Foxtail fescue. Annual, native. Rare along sandy roadsides. May,

Poa unilateralis Scrib. Perennial, native. Occasional to common in the grassland. May.

Lemnaceae

Lemna valdiviana Phil. Duckweed. Native. Abundant to common in quiet, fresh water. Only vegetative plants seen.

Typhaceae

NOTE: —*Typha angustifolia* misidentified; should be *T. domingenses* Pers. Rare to occasional.

Zosteraceae

Zostera marina L. Eel grass. Perennial, native. Common in Bodega Harbor; rarely exposed. Only vegetative plants seen.

LITERATURE CITED

BARBOUR, M. G. 1970. The flora and plant communities of Bodega Head, California. Madroño 20:289–313.

BARBOUR, M. G., R. CRAIG, F. DRYSDALE, and M. GHISELIN, in press. Bodega Head: coastal ecology. Univ. Calif. Press, Berkeley.

A record from the Klamath Mountains for the Sierran endemic, monotypic genus, Whitneya (Compositae).—*Whitneya dealbata* Gray is recorded in floras and recent papers concerning California botany as an uncommon upland endemic in the Sierra-Nevada, ranging from Shasta Co. to Fresno Co. Stebbins and Major (Ecol. Monogr. 35:1–35. 1965) consider it to be a relict species which occurs only in the Sierra and the Cascade—north Sierra subdivisions of the California floristic province (*ibid.*, fig. 1). It is at least of passing interest then that a population of *Whitneya* was recently discovered in the North Coast subdivision of the floristic province on the southern flank of the Klamath Mountains in Trinity Co., on Weaver Bally at 6970 feet elevation, 9 miles NW of Weaverville by road. The plants are the dominant herb on a ridge-top just east of the U. S. F. S. lookout, covering an opening among *Abies magnifica* A. Murr., and also growing under *Prunus emarginata* (Dougl.) Walp. and *Arctostaphylos patula* Greene. The population is about 75 m long and 20 m broad. Other species in the immediate area, in approximate order of decreasing commonness are: *Castanopsis sempervirens* (Kell.) Dudl., *Ceanothus velutinus* Dougl. ex Hook., *Happlopappus greenei* Gray, *Pinus lambertiana* Dougl., *P. ponderosa* Dougl. ex B. C. Lawson, *Penstemon anguineus* Eastw., and *Eriogonum umbellatum* Torr. Plants in the most exposed parts of the population were just beginning to flower on July 21, 1970 (*Spellenberg 2249*, NY) and only a few shaded plants were still flowering on the following August 24 (*Spellenberg 2510*, DS).—Richard Spellenberg, Department of Biology, New Mexico State University, Las Cruces 88001.

Geranium potentilloides in California.—As indicated by Bergseng (Madroño 18:213, 1966), this taxon was first reported from Marin County as *G. sibiricum* L. by Eastwood (Erythea 6:117. 1898). Howell (Marin Flora. p. 181. 1949) regarded the collections to represent a shade form of *G. pilosum* Forst. f. Bergseng (*loc. cit.*) applied the name *G. microphyllum* Hook. f. to these and more recent collections, Howell (Marin Flora, ed. 2. p. 345. 1970) indicated that the Hooker name was a synonym of "*G. potentilloides* L'Hér." The full citation for the Marin County plant is *Geranium potentilloides* L'Hér. ex DC., Prodr. 1:639. 1824. The plants appear to represent the typical variety. According to Carolin (Proc. Linn. Soc. N. S. Wales 89:337–340. 1964), var. *potentilloides* is native to Australia (Australian Capital Territory, New South Wales, South Australia, Victoria), Tasmania, New Zealand, and New Guinea, where it is usually found in mesic forests or woodlands. This species is a member of section *Australiensia* Knuth, and appears to be most closely related to *G. magellanicum* Hook. f. of Chile and Argentina.

All of the California collections cited by the above authors appear to have been made in the same locality near Olema, now within the boundaries of Pt. Reyes National Seashore. Two further collections may be added to the list: *Porter 1573*, 8 Oct. 1967 (DS) and *Porter & Porter 1579*, 11 Nov. 1967 (CAS, MO). Both were made in a grassy picnic area near the Park Headquarters. Plants of *G. potentilloides* were common here in the trampled ground under large specimens of *Pseudotsuga menziesii* (Mirb.) Franco and *Quercus* sp. They were spreading horizontally and rooting at the nodes, and were rarely over three inches high. It is surprising that this species, so common in this spot, has not spread further in the over 70 years that it has been known from the State.—Duncan M. Porter, Missouri Botanical Garden, St. Louis 63110.

REVIEW

Flora of New Zealand. By L. B. Moore and E. Edgar. Vol. 2. x1 + 354 pp., illustrated. Indigenous Tracheophyta: Monocotyledones except Gramineae. Government Printer, Wellington. 1970. $4.50(NZ).

It has been nine years since the publication of the first volume of the Flora of New Zealand (see Madroño 17:66–67). The present volume, devoted to the non-poaceous native monocots of New Zealand, continues in the tradition of excellence established by the first volume. It is dedicated to H. H. Allan, who completed most of the text of volume 1, but who died in 1957 before its publication. The contents of the book cover a broader scope than indicated by its title. The text is preceded by a useful "Annals" section which lists important systematic contributions to New Zealand botany published between 1959 and 1968, as well as some earlier publications omitted from a similar section in volume 1. At the end of the text there are a glossary, a list of chromosome numbers of New Zealand seed plants extracted from the published literature, and corrigenda for volume 1.

In volume 2, 22 monocot families are included, encompassing 75 genera and 339 species. The largest monocot families in New Zealand (excluding Gramineae) are the Cyperaceae (167 spp.), Orchidaceae (72 spp.), and Juncaceae (29 spp.). The circumscription of the families has been influenced strongly by the classification system of John Hutchinson, e.g., *Phormium* and *Cordyline* are placed in the Agavaceae, and the Philesiaceae, Hypoxidaceae, and Smilacaceae are retained as distinct families. The generic classification of the orchids follows that of Dressler and Dodson. The text is accompanied by excellent illustrations executed by Nancy Adams and J. B. Irwin (orchids only). As in the first volue, discussions of such topics as affinities, natural hybridism, taxonomic problems, and variation patterns make this book interesting browsing for phytogeographers and systematists who are concerned with the remarkable flora of New Zealand.—Robert Ornduff, Department of Botany, University of California, Berkeley, 94720.

A WEST AMERICAN JOURNAL OF BOTANY

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Contents

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

TWO NEW SPECIES OF TRIFOLIUM (LEGUMINOSAE) FROM CALIFORNIA AND NEVADA

JOHN M. GILLETT

Research Branch, Canada Department of Agriculture, Ottawa, Ontario
Contribution No. 856, Plant Research Institute

In the course of present taxonomic studies of *Trifolium* L. section
Lupinaster (Adans.) Ser., two new species were found that I am describ-
ing in this paper. I take pleasure in dedicating these two new species to
the collectors who have kindly supplemented their collection data with
additional information through correspondence.

Trifolium dedeckerae Gillett, sp. nov.

Trifolium perenne caespitosum, caulibus brevibus, stipulis ovatis per-
sistentibus, foliolis lanceolatis-linearibus serratis, capitulis semiglobosis,
pedunculis longis, pedicellis deflexis, lobis calycis 4–6 mm longis, subu-
latis, vexillo late oblongo, purpureo, ovario glabro. Affinis *T. producto*
Greene sed differt haec species a foliolis lanceolatis-linearibus, serratis,
calycis lobis tenuis et vexillo lato.

Type in the herbarium of Rancho Santa Ana Botanic Garden (RSA
202326) collected in the Sierra Nevada at 7500 ft. along Horseshoe
Meadows Road on a ridge south of Carroll Creek, Inyo County, Cali-
fornia. Growing with *Erysimum capitatum* (Dougl.) Greene and scat-
tered pinyon, on steep exposed slope of decomposed granite, May 30,
1968, *DeDecker 1899*.

Glabrous cespitose perennial with few to numerous short stems form-
ing a crown from a thickened woody taproot. Stems clothed in persistent
whitened stipules. Leaves with three leaflets, petioles 0.5–1.5 dm long
often overtopping the heads, leaflets sessile, 2–4 cm long, 0.1–0.6 cm
wide, lanceolate to linear, margins remotely serrate, abaxial face with
prominent veins terminating in the serrations, leaflets of extreme basal
leaves occasionally ovate-elliptic and smaller. Stipules pale green, ovate,
persistent and later chartaceous. Inflorescence initially somewhat elon-
gate, pedicels soon reflexed, the head then broader than long, hemi-
spherical, of 10–18 flowers in 2–4 whorls, the rachis extending beyond
the head, the upper peduncle slightly curved below the rachis, the head
then slightly tilted. Flowers curved saccate at the base, tubular, pink to
purple, about 1.5 cm long. Calyx glabrous, 10-veined, tube 2.5 mm long,
the lobes subequal, 4–6 mm long, triangular subulate, the sinuses rounded.
Standard 1.4 cm long, 0.6 cm wide when flattened, the terminal portion
0.7 cm long flared upwards. Wing petals about 1 mm longer than those
of the keel, blades 6.5 mm long. Staminal filaments fused about $\frac{1}{3}$ their

length to the claws of the lateral petals, anthers 0.5 mm long, pointed. Ovary glabrous, slender, 6.0 mm long, 2-ovuled, style slender. Legume not seen. Figure 1.

FIG. 1. Type specimen of *Trifolium dedeckerae* Gillett.

Other specimens seen: Wyman Cañon, White Mountains, Inyo N.F., June 13, 1919, *Tidestrom 9901* (NY, US); White Mountains, Inyo County, California, in rock crevices, uncommon; flowers pink. About 3 miles below Roberts Ranch, Wyman Creek, altitude ca 7000 to 7500 feet, Inyo County, California, 20 May 1931, *Duran 3026* (NY, UC, UTC).

Trifolium dedeckerae is allied to *T. productum* Greene but differs by the strkingly lanceolate-linear leaflets, the larger calyx with slender lobes and by the broad standard. Geographically, too, the known range is far to the south of that of *T. productum* which is known only as far south as Sonora Pass in the Sierra Nevada. This species is associated with *Pinus monophylla* Torr. & Frem. in the type locality. Climatic and ecological conditions in the mountains west of Owens Lake in Inyo County would be similar to those found in the White Mountains.

Trifolium rollinsii Gillett, sp. nov.

Trifolium perenne caespitosum, caulibus brevibus, stipulis ovatis persistentibus chartaceis, foliolis ovatis-rhombeis, dentatis, capitulis semiglobosis, pedunculis longis, pedicellis deflexis, lobis calycis 1 mm longis subulatis purpureis, vexillo angustato, purpureo, ovario glabro. Affinis *T. producto* Greene sed differt haec species a foliis basalibus et foliolis ovatis-rhombiformibus.

Type in the Dudley Herbarium (DS 275618), collected in Nevada, Nye County, flowers reflexed, pink, rocky eastern slope of Toiyabe Dome, Toiyabe Mountains, altitude 10,500 ft., July 13, 1938, *Rollins & Chambers 2526.*

Glabrous cespitose perennial with a somewhat scaly vertical, horizontal, or ascending rhizome (no true root available) bearing persistent stipules. Leaves with three leaflets, nearly all basal, petioles to 6 cm long, petiolules 0.5 mm long, leaflets obovate to rhombic, cuneate, the apex rounded to acute mucronate, dentate, dark green above; pale below with prominent veins terminating in the teeth. Stipules blunt ovate, chartaceous with reticulate veins. Inflorescence hemispherical, the flowers soon reflexed, of up to 15 flowers in 3–4 whorls, the upper flowers reduced or aborted, the rachis extending beyond the head, the upper peduncle slightly curved below the rachis, the head then turned to one side. Flowers curved saccate at the base, tubular, the standard only slightly curved upward near the tip, pink to purple, about 1.3 cm long, calyx glabrous, purpled, 10-veined, tube 3.5 mm long, lobes subulate, 2 mm long, sinuses rounded. Standard 1.4 cm long, 0.6 cm wide, oblong-ovate, the terminal portion flared upwards. Wing petals about 1 mm longer than those of the keel, blades 6.5 mm long. Ovary glabrous, slender, about 6 mm long, style about 4 mm long, 2–ovuled. Legume not seen. Figure 2.

Other specimen seen: Nevada, Nye County, Toiyabe Forest, Head of Crane Creek, altitude 10,000 ft. steep west talus slope, rocky clay soil, fairly common, *Crane,* July 30, 1941 (NY).

The discovery of this species is of interest because in the same area

FIG. 2. Type specimen of *Trifolium rollinsii* Gillett.

Rollins also collected a new species of *Draba,* later named *D. arida* Hitchcock (Hitchcock, 1941). Not far from this locality but further down the slope, he also found a new *Arabis* that subsequently he named *A. fernaldiana* Rollins (Rollins, 1941). Apparently the Toiyabe Range is in

need of more intensive scrutiny and further new items of interest might yet be found. This mountain range is physically somewhat isolated and the mesic upper slopes have become ecologically separated by arid habitats from the related flora of the Sierra Nevada.

Trifolium rollinsii is morphologically closely related to *T. productum* and is spatially close to the margin of its range. But the basal position of the leaves and distinctive shape of the leaflets of *T. rollinsii* are attributes which resemble those of *T. macilentum* Greene of southwestern Utah. On the other hand, the calyx of *T. rollinsii* is similar to that of *T. productum* but that of *T. macilentum* is like that of *T. kingii* Watson of central and eastern Utah.

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LITERATURE CITED

HITCHCOCK, C. L. 1941. A revision of the Drabas of western North America. Univ. Wash. Pub. Biol. 11:52.

ROLLINS, R. C. 1941. Monographic study of *Arabis* in western North America. Rhodora 43:430 (Contrib. Gray Herb. 138).

NOTES AND NEWS

A NEW NAME IN LICEA (MYXOMYCETES).—*Licea deplanata* nom. nov. ≡ *Licea applanata* Kowalski, Mycologia 62:1058, 1970. Not *Licea applanata* Berk., Lond. J. Bot. 4:67, 1945. = *Dictydiaethalium applanatum* (Berk.) Rost., in Fuckel, Jahrb. Nassauischen Vereins Naturk. 27–28:69, 1873. = *Dictydiaethalium plumbeum* (Schum) Rost., in A. Lister, Mycetozoa p. 157, 1894. Because of its flattened sporocarp, I applied the specific epithet *applanata* to this species, but because the combination is a later homonym of *L. applanata* Berk., it is illegitimate. The epithet *deplanata* is equally descriptive and has not, so far as I can discover, been used in *Licea*.—DONALD T. KOWALSKI, Department of Biological Sciences, Chico State College, Chico, Ca. 95926.

NEW SPECIES OF PERITYLE AND AMAURIA (COMPOSITAE)

A. Michael Powell

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Recent systematic studies of *Perityle* sect. *Perityle* and *Amauria* have disclosed two undescribed Mexican species. Taxonomic treatments of both genera are nearing completion, and it is convenient to publish the novelties at this time in order to facilitate later reference to the taxa.

Perityle turneri Powell, sp. nov. Plantae perennes herbaceae vel sufruticosae diffusae vel decumbentes vel pendulae vel semi-erectae; caules 20–45 cm longi saepe purpurascentes inferiores saepe ad nodos radicantes superiores puberuli vel subtomentosi; folia plerumque opposita ovata vel deltoidea 3–4.5 (–8.5) cm longa 1.5–3 (–4) cm lata puberula vel subtomentosa saepe purpurascentia apice acuta vel attenuata basi interdum subcordatis margine serrato vel serrato-crenato vel serrato-laciniato vel duplicato-serrato-laciniato; petioli 1–1.5 (–3) cm longi; capitula radiata 5–7 mm alta 7–14 mm lata solitaria vel in catervas 2–3 (–4) capitulatas aggregata; pedunculi (1–) 2–6 cm longi; involucrum hemisphaericum vel late campanulatum; receptaculum conicum; radii flores 12–18 ligulis oblongis (3–) 6–9 mm longis albis; disci corollae (1.8–) 2–2.8 (–3) mm longae flavae; achenia compressa 1.5–2 mm longa obovata vel oblongo-ovata superficiebus ad centrum puberulis marginibus ciliatis crassiuscule vel tenuiter callosis; pappus prominens coroniformis; pappi squamellae plures; pappi setae 2 raro solitariae inaequales seta longiore 0.6–1.5 longa; chromosomatum numerus **n = 17.**

TYPE. MEXICO: Durango: 3.4 mi E of El Palmito, 2 Apr 1970, *A. M. Powell 1858* (Holotype, TEX; Isotype, SRSC and to be distributed).

Specimens examined. MEXICO: Chihuahua: 4 mi SW of Villa Matamoros, *D. S. Correll & H. S. Gentry 22819* (LL); near La Rocha, NE slope of Sierra Mohinova, *Correll & Gentry 23109* (LL); Burro Canyon near Parral, *C. G. Pringle 13650* (ARIZ, CAS, GH, SMU, TEX, UC, US). Durango: Quebrada San Juan, ca 50 mi W of Durango and 23 mi NW of Los Coyotes Railroad, *A. Cronquist 9568* (NY, SMU, TEX, US); 6 mi W of La Ciudad, *D. Flyr 273* (TEX); ca 35 mi W of El Salto, *Gentry & J. Arguelles 18210* (US); San Ramon, *E. Palmer 60* (GH, NY, UC, US); 2.2 mi E of El Palmito, *Powell 1857* (SRSC, TEX); 12 mi W of La Ciudad, *S. Sikes & C. Babcock 380* (SRSC, TEX). Sinaloa: 0.9 mi W of El Palmito, ca 47 mi E of Concordia, *D. Breedlove 1721* (DS).

Perityle turneri belongs with a white-rayed alliance (8 spp.) of sect. *Perityle* (Powell, 1968) that is distributed mainly in mountain habitats from Durango, Mexico, to central Arizona. The species is related to *P. microcephala* A. Gray, *P. microglossa* Benth., and probably *P. lineari-loba* Rydb., of the Sierra Madre Occidental in Durango and Chihuahua.

The distinguishing features of *P. turneri* include its decumbent to prostrate habit with lower stems often rooting at the nodes, leaf characters, capitulescence of 1–3(4) relatively large heads on peduncles (1.0–)2–6 cm long, ligules (3–)6–9 mm long, conical receptacles, and high-altitude habitat (7000–9500 ft.). The above four species are similar in characters of the disc corollas, achenes, and pappus.

All the specimens of *P. turneri* known to me were collected at relatively high altitudes in three general localities: (1) west of Ciudad Durango in the vicinity of El Salto and the Sinaloa border, (2) near San Ramon in west-central Durango, (3) and near Parral in southern Chihuahua. The plants from each of the three localities differ slightly in vegetative characteristics and head size, suggesting that the species as presently understood is polymorphic. I suspect that the taxon is actually widespread in suitable habitats of the Sierra Madre, but that isolated populations have been evolving independently for some time. Furthermore, distributional and morphological considerations suggest that *P. turneri* is primitive in the white-rayed alliance referred to above, and perhaps gave rise to its related species. The supposedly primitive characteristics of *P. turneri* include its large heads, long ligules, conical receptacles, perennial habit, and high-elevation distribution. The related species, indicated above, have small heads, short ligules (excepting *P. lineariloba*), and flattened receptacles. Both *P. microcephala* and *P. lineariloba* are bluff-dwelling perennials at intermediate elevations, while *P. microglossa* is an annual at lower altitudes. It is notable that specimens of the *Palmer 60* collection are somewhat intermediate morphologically between *P. microcephela* and other morphotypes of *P. turneri*.

The species is named for B. L. Turner who has made significant contributions to the systematics of Compositae, and who originally suggested *Perityle* to me as an interesting study. I am grateful to M. C. Johnston, of the University of Texas, Austin, for providing the Latin translation.

Amauria carterae Powell, sp. nov. Plantae humiles perennes, fasciculos 10 cm alt., 20 cm lat. efficientes; caules superiores dense minuteque glandiferi-puberuli; folia succulentia, basaliter dense aggregata, minute glandiferi-puberula, 1–2 cm long., 0.5–0.8 cm lat., subcruciformia, 3(5) segmenta maiora habentia, marginibus segmentorum lobos non profundos habentibus aut indentatis crispatisque; petioli 0.7–1.1 mf long.; capitulescentia e capitulis singulis in pedunculis 1–2 cm long. portatis admodum constantia; capitula 5–6 mm alt., ca 5 mm lat.; involucra campanulata; bracteae 5–6 mm long., 1.0–1.3 mm lat., oblanceolatae, non carinatae, admodum glabrae aut minute puberulae; flores radii ca 18, ligules oblongis ad subspathulatas 5.5–7.5 mm long., 2.0–2.5 mm lat.; discocorollae 3.0–3.5 mm long., faucibus tubulari-infundibuliformibus, ca 1.5 mm long., styli tenues, ca 1.6 mm long., in cacumen tenue angustati; achenia ca 1.5 mm long., linearia, faciebus glabris, marginibus pilis satis longis, parce ciliatis, pilis plerumque tortis crispatisve, aut satis antrorse

appressis; pappus carens; antherae ca 1.5 mm long., chromosomatum numerus $n = $ ca 20.

TYPE: MEXICO: Baja California Sur: Sierra de la Giganta, Cerro Mechudo, 600 m, ca Lat. 24° 55′ N, Long. 110° 45′ W, 21 Feb. 1970, *A. Carter 5439* (Holotype, UC).

Amauria carterae is the third species to be recognized for this Baja Californian genus, the others being *A. rotundifolia* Benth. and *A. brandegeana* (Rose) Rydb. The new species is known only from the type collection, but it is clearly distinct from the other Amaurias and from its closest relative, *A. rotundifolia*. Its most salient features include: low perennial habit; subcruciform leaves; achenes ca 1.5 mm long, with rather long, twisting or curling hairs on the margins, faces glabrous; bracts oblanceolate, thin, not keeled, essentially glabrous; capitulescence essentially of solitary heads; styles tapering to a fine point; leaves and young stems glandular-puberulent. I have grown seed progeny of *A. carterae* and the distinguishing characteristics are maintained in greenhouse plants.

I take pleasure in naming this species after Annetta Carter who found the plants while collecting for her proposed Sierra de la Giganta Flora, recognized the taxon as undescribed, and called it to my attention. I thank Hannah Croasdale for the Latin translation.

LITERATURE CITED

POWELL, A. M. 1968. Additional discussions pertaining to the congeneric status of *Perityle* and *Laphamia* (Compositae). Sida 3:270–278.

NOTES AND NEWS

STELLATE EPIDERMAL HAIRS, SOME 10,000 YEARS OLD.—The palaeontologists who worked in the Pleistocene of the Rancho La Brea pits naturally devoted their attention to the fossils of the gigantic animals entombed in the tar (Stock, Chester. 1930. Rancho La Brea, a record of the Pleistocene in California. Los Angeles County Museum of Natural History in California. Science Series 20; Palaeontology 11.). Recently, a new dig (28 x 28 x 10 ft deep) in the general area reveals abundant plant remains. Samples of tree trunks and branches, after detarring, were identified by the Forest Products Laboratory, Madison, Wisconsin, as juniper, cypress, redwood, and willow. In fragments of reticulate-veined leaves the epidermis consists of thick-walled cells with numerous guard cells, glands, and stellate hairs. The tapering cells of the hairs, six to ten in number and from twenty to fifty microns in length, are cutinised and thick-walled. The lumen is partially filled with the clear remains of protoplasm. In general form they resemble the epidermal hairs of a *Fremontodendron* or of a chinquapin *(Castanopsis)*. The underlying cylindrical palisade and the lobed spongy mesophyll cells are thin-walled and protoplasm is also evident in the lumen of these cells. The results of these preliminary observations indicate the significance of the Pleistocene plant remains in the current Rancho La Brea dig. This vegetation differs markedly from that of the region today. The astounding structural preservation of the stellate epidermal hairs and of the leaf tissue in general present significant problems to palaeobotanists.—FLORA MURRAY SCOTT, University of California, Los Angeles 90024.

TAXONOMY OF CHAETADELPHA
(COMPOSITAE: CICHORIEAE)

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Chaetadelpha is a monotypic genus endemic to the western edge of the Great Basin region of the western United States. Stebbins (1953) included the genus in his subtribe Stephanomerinae. Although *Chaetadelpha* has been merged with *Stephanomeria* (Macbride, 1922), it appears to be more closely related to *Lygodesmia* than to other members of subtribe Stephanomerinae. More specifically *Chaetadelpha* resembles *Lygodesmia juncea* in habit and characters of the involucre and florets. In fact, *C. wheeleri* is frequently misidentified as *Lygodesmia juncea*. (*L. juncea*, primarily a Great Plains species, is rare west of the continental divide.)

Only one chromosome count ($2n = 18$) has been reported for *Chaetadelpha* (Stebbins et al., 1953). The perennial species of *Lygodesmia* also have $2n = 18$ (Tomb, 1970), whereas all species of *Stephanomeria* counted to date have $2n = 16$ or $2n = 32$ (Stebbins et al., 1953; Tomb, 1970; Gottlieb, personal communication).

The pollen grains of *Stephanomeria* and *Chaetadelpha* are similar, being echinate and tricolporate. *Lygodesmia* pollen is echinolophate and tricolporate. The fine structure of pollen in these genera and other members of subtribe Stephanomerinae will be discussed in detail in another publication (Tomb, Larson, and Skvarla, in preparation).

Table 1 and the following description are intended to clarify the generic limits of these genera and to aid in the identification of *Chaetadelpha wheeleri*.

CHAETADELPHA WHEELERI Gray ex Watson, Am. Naturalist 7:301. 1873.
  Stephanomeria wheeleri Nelson & Macbride, Contrib.
      Gray Herb. 2.65:45–46. 1922.
      Illustration: Rothrock, J. T. 1878. U.S. Geographical Surveys West
      of the 100th Meridian. VI Botany. Plate XV. Government Printing
      Office, Washington.

Herbaceous, rhizomatous perennials, 18–40 cm high; from deep seated rootstocks; stems ascending to sub-erect, intricately branched, striate, glabrous; leaves 0.3–5.0 cm long, 2–4 mm wide, linear to linear–lanceolate or reduced to scales, lacking a prominent midrib, often deciduous; heads terminal, 5-flowered; involucre cylindrical, 1.1–1.4 cm long, 3–4 mm wide; principal bracts 5, margins hyaline, apices ciliate; outer bracts in about 2 series 2–4 mm long, forming a calyculum; ligules 6–9 mm long, ca 3 mm wide, before drying, sordid pink to white, exserted from

TABLE 1. A COMPARISON OF THE PRINCIPAL DIFFERENCES
BETWEEN CHAETADELPHA, LYGODESMIA AND STEPHANOMERIA

Lygodesmia (8 species)	*Chaetadelpha* (1 species)	*Stephanomeria* (ca 18 species)
perennial*	perennial	10 perennials, ca 8 annuals
pappus of numerous fine, capillary bristles	pappus of two types of bristles; many fine, capillary bristles and 5 rigid, thick, tapering bristles	pappus usually of few to numerous plumose bristles (capillary in two species)
achenes sub-cylindrical; basal ⅔ usually expanded abaxially, surface either striate or smooth or rugose on the adaxial surface; 1.0–1.8 cm long	achenes columnar with 4 or 5 prominent ridges; 0.9–1.2 cm long	achenes columnar, or prismatic; striate, and/or rugose; abaxial and adaxial surfaces not differentiated; 0.5–0.8 cm long
pollen grains echinolophate, tricolporate	pollen grains echinate, tricolporate	pollen grains echinate, tricolporate
cotyledons elongate, filiform after germination often elongating to over 7 cm	cotyledons elongate, filiform after germination (Gottlieb, personal communication)	cotyledons after germination short and spatulate, rarely over 2.5 cm in length
chromosome base number, $x = 9$	chromosome base number, $x = 9$	chromosome base number, $x = 8$

* *Lygodesmia exigua* and *L. rostrata* are considered distinct from *Lygodesmia*. *L. exigua* is placed in the monotypic genus *Prenanthella* Rydb. (Tomb, 1970), and *L. rostrata* appears to be closer to the genus *Crepis* than to any taxon in subtribe Stephanomerinae.

the involucre ca 7 mm, apparently persistent for several days; corolla tube 7–9 mm long; anthers 5–9 mm long, exserted 2–4 mm out of the corolla tube; style branches 3–4 mm long; achenes 9–12 mm long, ca 1 mm wide, columnar, glabrous, with 5 prominent ridges, truncate at each end; pappus 9–12 mm long, of two types of bristles, the 5 bristles above the ridges of the achene thicker and more rigid than the numerous fine capillary bristles (at least some of the latter fused to each of the rigid bristles); pollen grains echinate, tricolporate, mean equatorial diameter 52 μ; chromosome number **2n = 18.**

Lectotype: Southern Nevada. Lt. Wheeler's expedition. 1872. *Wheeler s.n.* GH! Isotype US! The type locality is given as "southern Nevada on the borders of Arizona" by Gray (1874).

Distribution: Western edge of the Great Basin, southeastern Oregon, western Nevada and adjacent eastern California (Mono and Inyo counties); sand dunes and sandy soils with *Atriplex confertifolia,* ca 3,000 to 6,000 ft. Figure 1.
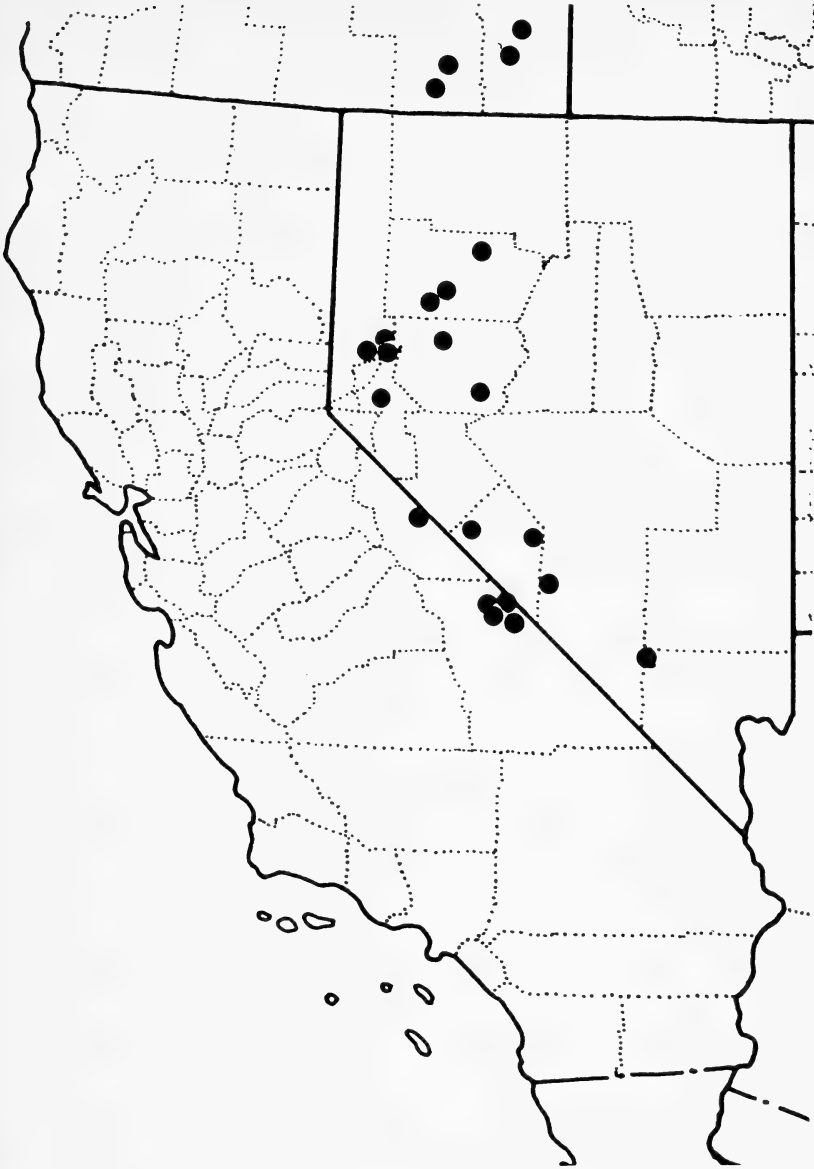
Fig. 1. Distribution of *Chaetadelpha wheeleri*.

Representative specimens: CALIFORNIA: Inyo County: W side of Eureka Valley at mouth of Marble Canyon, 13 May 1955, *Roos 6364* (CAS,DS,NY,US); Shealy, 16 June 1933, *Duran 3486* (ARIZ,CAS,DS,GH,NY,UC,US,UT).
NEVADA: county unknown: Unionville Valley, Jun 1864, *Watson 706* (NY). Churchill Co.: Carson Sink Region, Oct 1907, *Kennedy 1704* (ARIZ,DS,NY,UC,US). Esmeralda Co.: SW of Columbus Salt Marsh, 15 May 1941, *Eastwood & Howell*

9509 (CAS). Candelaria, Jun 1888, *Shockley s.n.* (DS,NY,UC). Lyon Co.: Pine Grove Hills, 25 Jun 1947, *Alexander & Kellogg 5322* (DS,SMU,UC,UTC). Mineral Co.; Rhodes, 23 Jun 1882, *Jones 3951* (CAS,DS,NY,UC,US). Nye Co.: 30 mi S of Goldfield, 24 May 1945, *Maguire & Holmgren 25172* (ARIZ,CAS,DS,NY,PH,SMU, TEX,US,UTC). Pershing Co.: Lovelock, 1 Jun 1933, *Train 55* (US) ; 25 mi SW of Winnemucca, 22 Jun 1959, *Cronquist 8537* (CAS,DS,KANU,NY,TEX,UC,UT). Washoe Co.: 7 m N of Wadsworth, 29 Jun 1938, *Archer 6194* (ARIZ,DS,NY,PH,UC).

OREGON: Harney Co.: Alvord Desert, 30 Jun 1896, *Leiberg 2429* (GH,NY,UC, US). Malheur Co.: 4 mi W of Rome, 8 Jun 1944, *Ripley & Barneby 6161* (CAS,NY).

Literature Cited

Gray, A. 1874. Notes on Compositae and characteristics of certain genera and species. Proc. Amer. Acad. 9:218.

Macbride, J. F. 1922. Various North American spermatophytes, new or transferred. Contrib. Gray Herb. Ser. 2, 65:45–46.

Stebbins, G. L., Jr. 1953. A new classification of the tribe Cichorieae, family Compositae. Madroño. 12:65-81.

————, J. A. Jenkins, and M. S. Walters. 1953. Chromosomes and phylogeny in the Compositae, tribe Cichorieae. Univ. Calif. Publ. Bot. 26:401–430.

Tomb, A. S. 1970. A cytotaxonomic study of the genus *Lygodesmia* (Compositae: Cichorieae). Ph.D. Dissertation. Univ. Texas, Austin.

NOTES AND NEWS

Fasciation in Redwood.—The Centralized Title Service provided by the Commonwealth Forestry Bureau, Oxford, England, has cited a recent note in Madroño (Becking, R. W., Madroño 20:382–383. 1970) which discussed fasciation in redwood [*Sequoia sempervirens* (D. Don) Endl.]. The card incorrectly states that "only two occurrences (of fasciation) on this species are so far known".

For this reason I want to correct errors promulgated by Becking's note. First, Becking wrote that "fasciation has not yet been reported on coastal redwood". Yet a cursory review of literature shows that this phenomenon was described more than 70 years ago (Peirce, G. J., Proc. Calif. Acad. Sci. 3rd Ser. Bot. 2:85–105. 1901). Second, although not common, fasciation in redwood is not, as Becking called it, "very rare". In 1910, W. L. Jepson (The silva of California. Mem. Univ. Calif. 2, 1910) reported that "fasciation of stump sprouts in redwood has also been observed a number of times". The first time I saw fasciation in redwood was in 1932 at Cazadero, California. Third, the statement that "fasciation is sometimes only of annual duration" is misleading. J. S. Boyce (Forest pathology. New York and London: McGraw-Hill Book Co., Inc. 1938) reported that this kind of "malformation is usually confined to the growth of one season; perennial fasciation is rare".

Furthermore, some of Becking's speculations on the causes of fasciation seem to be without scientific bases. His contention that fasciation "is considered to be genetically controlled by a mutation, which can be propagated vegetatively and which may come true from seed" is not supported by any evidence. His statement should be documented if he has evidence. That fasciation in redwood is caused by "wound stimulation", and specifically by insect attack, is remote. Fasciation in sweet peas is known to be induced by bacteria (Tilford, P. E., Jour. Agr. Res. 383–394. 1936), and in some cases its occurrence in other plants has been attributed to local over-nutrition (Boyce, J. S., Forest pathology. New York and London: McGraw-Hill Book Co., Inc. 1938). Since examples of fasciation have been found on redwood sprouts that are nurtured by well-developed root systems of logged parent trees, over-nutrition seems a likely cause of fasciation in redwood sprouts. However, the causes of most fasciations are unknown. Since only occasional stems are affected, the subject is academic only.—Douglass F. Roy, Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Berkeley, Calif., stationed at Redding, California 96001.

A PROPOSAL FOR CLASSIFICATION OF THE ANNUAL SPECIES OF STEPHANOMERIA (COMPOSITAE)

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Among the most common and conspicuous plants of the late-summer flora in many regions of California and adjacent areas are the annual species of *Stephanomeria* (Cichorieae, Compositae). These plants, some of which tower more than eight feet high, are readily identifiable to genus, even when observed from a car zooming along at 60 m.p.h., but their morphological intergradation has vexed many collectors who have attempted to key them to species.

Recent extensive field study and experimental analysis, however, have elucidated the characteristics of the individual species and have clarified their relationships. As a group, the annual Stephanomerias comprise both a polyploid complex and a homogamic complex (Grant, 1953) in which both tetraploid and diploid taxa are morphologically intermediate between two divergent diploid species, *Stephanomeria exigua* and *S. virgata*, both of which are polytypic. Experimental evidence regarding the evolutionary relationships of *S. exigua*, *S. virgata*, and *S. diegensis*, a morphologically intermediate diploid species, has been presented elsewhere (Gottlieb, 1971). The purpose of this paper is to propose a taxonomic arrangement of all the annual species and to present a key for their identification. *Stephanomeria* also includes about nine or ten herbaceous perennial species, some of which are widely distributed in western North America, that are clearly distinct from the annual species in habit and morphology. Their relationships have not been investigated and they are not discussed in this report.

The taxonomic difficulties in the annual Stephanomerias result from their substantial morphological similarities. Thus, Ferris (1960) noted, "Different strains are sometimes locally recognizable but intergrading forms are constantly to be found even in the same region." With the exception of absence of grooves on the achenes, which is now known to distinguish *S. virgata*, no single morphological key character is restricted to a single taxon. Species identification is further complicated by the overlap in geographical ranges, particularly in central and southern California. In addition, what has proven to be one of the most serviceable characters for identification, the state of the calyculate involucral bracts (reflexed or appressed to the involucre), is not easy to ascertain on pressed herbarium specimens. Many of the characters that have been utilized in various recent keys for *Stephanomeria* such as pappus color, achene shape and surface condition, and stem width are misleading because of their genetic variability and phenotypic plasticity. In this group of plants, the species and their morphological limits became apparent only following cytological examination of numerous populations and the

results of experimental hybridizations. These studies (Gottlieb, 1969, 1971) revealed the widespread occurrence of tetraploid populations, the karyotypic differences among the diploid species, and the type and strength of reproductive isolating barriers among the species.

The most divergent species are the widespread diploids, *S. exigua* and *S. virgata,* that differ in many morphological features, karyotype, and chromosomal structural arrangement resulting in strong reduction of the fertility of hybrids between them. Although the differences between the species apparently mark a fundamental phylogenetic divergence, their features are combined in several other species, in slightly different combinations in each case. These morphologically intermediate taxa plus the occurrence of hybrid swarms or hybrid individuals where different Stephanomerias grow together in nature effectively blur the morphological distinctions between *S. exigua* and *S. virgata,* and are responsible for the taxonomic complexities of the entire group.

For example, all the morphological features of the diploid *Stephanomeria diegensis,* with the exception of high floret number and long lateral pinnae along the pappus bristles, are an amalgam of those found in *S. exigua* and *S. virgata* ssp. *virgata.* Similarly, the allotetraploid *Stephanomeria elata* is morphologically intermediate between *S. exigua* and *S. virgata* but with a different combination of characters. To a lesser extent, both *S. exigua* ssp. *carotifera* and *S. exigua* ssp. *macrocarpa* have morphological features (reflexed calyculate bracts and certain features of the pappus in subspecies *carotifera*) that are also found in *S. virgata* ssp. *virgata.* A reasonable hypothesis to explain the morphological intermediacy of these taxa that has not been overthrown by the available evidence is that they have resulted from independent interspecific hybridizations between *S. exigua* and *S. virgata* followed by selection for genotypes with a new balance of adaptation (Gottlieb, 1971, unpublished).

In order to deal with this complex situation, the species concept adopted in *Stephanomeria* utilizes both experimental results and convenience. The decision to recognize *S. exigua* and *S. virgata* as polytypic species rather than recognizing a number of separate species is based on relative degrees of reproductive isolation as well as morphological and chromosomal differentiation. The differences between any pair of subspecies of *S. exigua,* or between the two subspecies of *S. virgata,* are substantially less well developed than are the differences between the two species or between either of them and *S. diegensis.* Biologically, the taxa recognized within each species have reached the level of divergence designated semispecies, and their biological relationships seem best depicted by treating them taxonomically as subspecies rather than species.

Stephanomeria paniculata is diploid, self-compatible, and highly self-pollinating in the greenhouse (Gottlieb, 1969). It has the same karyotype as *S. exigua,* and its morphological features also ally it to that species, particularly subspecies *coronaria.* Substantial reproductive isolation is present since experimental hybrids between *S. paniculata* and subspecies

coronaria are difficult to obtain and when they are produced average less than 25% pollen stainability (Gottlieb, 1969). Since the subspecies that comprise *S. exigua* are moderately to strongly divergent and, since on the basis of its morphological features, *S. paniculata* is most likely derived from the self-incompatible *S. exigua* ssp. *coronaria,* one could argue that it too should be treated taxonomically as another subspecies of *S. exigua.* Although this would not be inconsistent with what is known of the biology of these organisms, nothing would be gained by such a taxonomy. In a complex group of plants like *Stephanomeria* that is actively differentiating, and in which morphological distinctions are few and bridged by intermediate taxa, the designation of taxonomic rank is arbitrary. *Stephanomeria paniculata* has been recognized as a species for more than 100 years and, probably, because of its northern distribution (fig. 1), has not been confused with the other taxa of *Stephanomeria.* To reduce it to subspecific rank does not further clarify its relationships. Therefore, I propose that it is not necessary to change the taxonomic rank of *S. paniculata.*

Stephanomeria diegensis is more sharply isolated reproductively from both *S. exigua* and *S. virgata* than they are from each other, yet its morphological characteristics are a composite of their features. These three species can be considered a homogamic complex. The particular combination of features that distinguish *S. diegensis* is present in all its populations and, together with its striking reproductive isolation, warrant its recognition as a species.

Stephanomeria elata comprises all the annual tetraploid populations of *Stephanomeria.* These are a highly variable group of populations that cytogenetical analyses reveal have an allotetraploid origin between *S. exigua* and *S. virgata* (Gottlieb, 1969). The three species together are a classic example of a polyploid complex. The tetraploid populations exhibit substantial interpopulation morphological variability, but the pattern of their features together with geographical distribution generally permits their identification without counting chromosomes. Triploid hybrids between *S. elata* and *S. virgata* are known in nature, but no evidence is available that such individuals serve to transfer genes between ploidy levels. The tetraploid plants are self-compatible and, since they are highly self-pollinated (at least in the greenhouse), it has not been possible to make hybrids among them. Since the tetraploid populations are considered to have a common origin and in the absence of positive evidence of any reproductive isolation among them, it is convenient to treat them as a single species. However, the present treatment may have to be modified when additional information is amassed.

Taxonomy

The morphological descriptions presented below emphasize characters that are useful in differentiating the taxa and ignore certain features that are alike in all of them. All have taproots and form basal leaf rosettes

before the single erect stem is produced. All have leaves or leafy bracts on the stem and branches; the leaves vary from entire to pinnatifid and are oblanceolate to spatulate in shape. The involucres are cylindrical or oblong with a series of equal-sized phyllaries equivalent in number to the number of florets and subtended by fewer calyculate bracts. The ligules are generally similar in length (9–15 mm) and width (2.8–4.7 mm) except that those of the self-compatible *S. exigua* ssp. *macrocarpa, S. paniculata,* and *S. elata* are smaller. The achenes are light tan to dark brown, oblong, sometimes curved, truncate at the apex, five-ribbed, with the surface between the ribs either smooth or rugose-tuberculate. Measurements presented in the key and in the descriptions below are averages for populations. Representative specimens from my collections will be distributed to UC, RSA, SBBG, MICH, DAV, and NY. Only some of the specimens examined are cited below. Included are collections that document distributions and some that are widely distributed in herbaria for reference purposes. Collection numbers prefixed by *G* are my own.

Key to the Annual Taxa of Stephanomeria

Achenes grooved longitudinally.
　Heads in small panicles along branches; peduncles 10–40 mm long.
　　Calyculate bracts strongly reflexed; South Coast Ranges of California . . . . . 1c. *S. exigua* ssp. *carotifera*
　　Calyculate bracts appressed.
　　　Peduncles and involucres glabrous or sparsely glandular; Mojave Desert and east to Texas.
　　　　　　　　　　　　1a. *S. exigua* ssp. *exigua*
　　　Peduncles and involucres conspicuously glandular; coastal mountains and valleys from Los Angeles to northern Baja California.
　　　　　　　　　　　　1b. *S. exigua* ssp. *deanei*
　Heads solitary or clustered on short divaricate peduncles < 10 mm long.
　　Pappus bristles not thickened at base, free, breaking off cleanly from achene.
　　　Pappus bristles plumose on upper 80–85% of length; pubescence on involucres glandular; coastal southern California to northern Baja California.
　　　　　　　　　　　　3. *S. diegensis*
　　　Pappus bristles plumose throughout; pubescence glandular or not; widely distributed, southwestern Oregon south to Santa Barbara and western slope Sierra Nevada . . . . 4. *S. elata*
　　Pappus bristles at least slightly thickened, often connate in groups of 2–4 at bases, breaking off above bases which remain adnate to achene.

Achenes averaging > 5.5 mm long; western slope Sierra
    Nevada . . . 1d. *S. exigua* ssp. *macrocarpa*
Achenes < 4.5 mm long.
    Calyculate bracts appressed.
        Pappus bristles plumose throughout with heavily
            thickened, setulose bases; achenes av-
            eraging > 3.5 mm long; northern Cali-
            fornia and Great Basin.
                    2. *S. paniculata*
        Pappus bristles plumose on upper 60–85% of
            length, connate or not; achenes averag-
            ing < 3.5 mm long; widely distributed
            California and north in Great Basin.
                1e. *S. exigua* ssp. *coronaria*
    Calyculate bracts reflexed . . . . . 4. *S. elata*
Achenes not grooved.
    Calyculate bracts reflexed; 8–9 florets per head; southern California.
                5a. *S. virgata* ssp. *virgata*
    Calyculate bracts appressed; 5–6 florets per head; widely distrib-
    uted from southwestern Oregon in both Coast Ranges and
    Sierra Nevada to northern Baja California.
              5b. *S. virgata* ssp. *pleurocarpa*

1a. STEPHANOMERIA EXIGUA Nutt. ssp. EXIGUA, Trans. Amer. Phil. Soc.
    2:7:428. 1841.
    Stephanomeria pentachaeta D.C. Eaton, Bot. King Expl. 199.
        1871.
    (Type from "Truckee and Humboldt Valleys", Nevada, illus-
        trated in above)
    Ptiloria exigua Greene, Pittonia 2:132. 1890.
    Ptiloria pentachaeta Greene, Pittonia 2:133. 1890.
    Stephanomeria exigua var. *pentachaeta* Hall, Univ. Calif. Publ.
        Bot. 3:260. 1907.
Peduncles and involucres glabrous or sparsely glandular–pubescent;
heads paniculate, peduncles 10–40 mm long (fig. 2); heads average 5–8
florets; involucres subtended by appressed calyculate bracts; ligules
various shades of pink on upper surface, purple-tinged on back; achenes
averaging 2.6–3.2 mm long, five-sided with a narrow longitudinal groove
on each side (fig. 3); pappus bristles averaging 5–13 in number, plumose
on the upper 45–55% of their length, thickened and often connate in
groups of 2–4 at the bases which generally remain adnate to the achene
(when only 5 bristles are present, these break off cleanly). $n = 8$.
    Type. "Colorado of the west, 1834–35", T. Nuttall. (Holotype: GH!)
    Distribution. Widely distributed (fig. 1) from Mojave and Colorado
Deserts in California across the southwest to western Colorado and west-
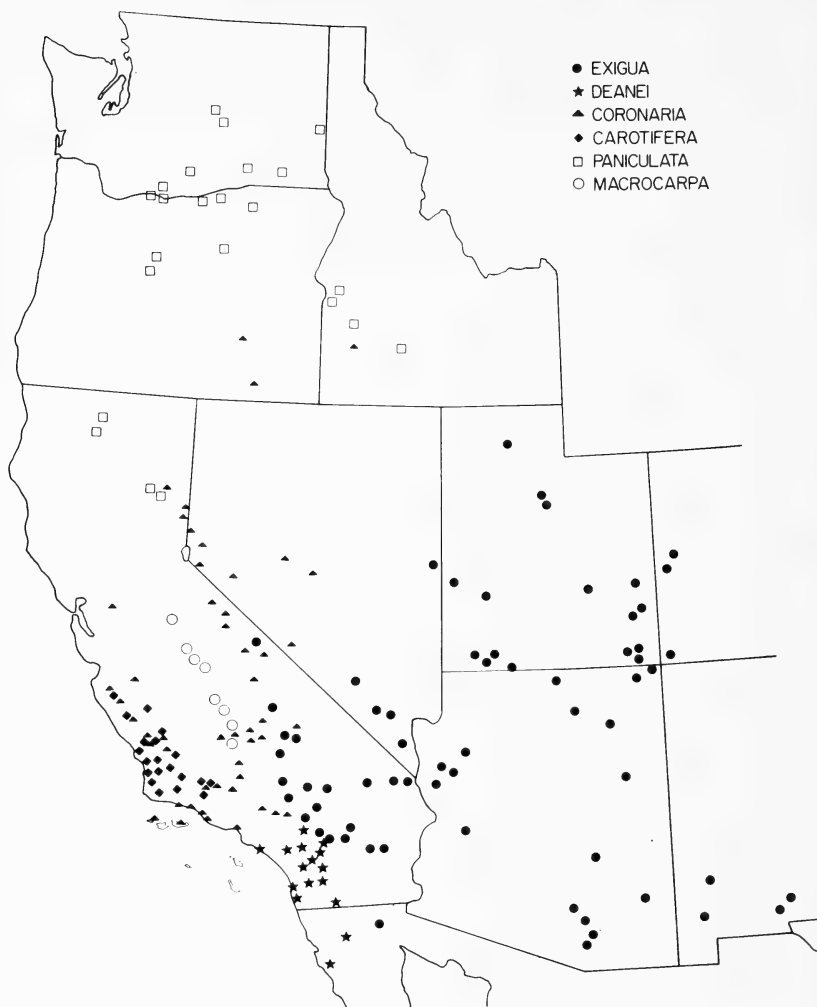
Fig. 1. Distribution of the five subspecies of *Stephanomeria exigua* and of *S. paniculata*.

ern Texas. In sandy soil in sagebrush, creosote bush, and *Coleogyne* shrub communities. Flowers May to July.

Representative specimens. TEXAS. El Paso Co.: lower slopes of Franklin Mt., east side, bajada at end of mountain road, *Correll and Correll 38619*. NEW MEXI-CO. Dona Ana Co.: 1 mile west of Organ on U.S. 70 and south ½ mile on Blair Canyon Road. *G-684*. Hidalgo Co.: Lordsburg, *Eastwood 8545*. Luna Co.: 1 mile west of Road 81 on U.S. 10, *G-686*. ARIZONA. Apache Co.: Canyon de Chelly National Monument, south rim, across from Antelope Point, *Bailey 375;* Junction to Petrified Forest, east of Holbrook, *Raven 13020*. Coconino Co.: 14 miles north-
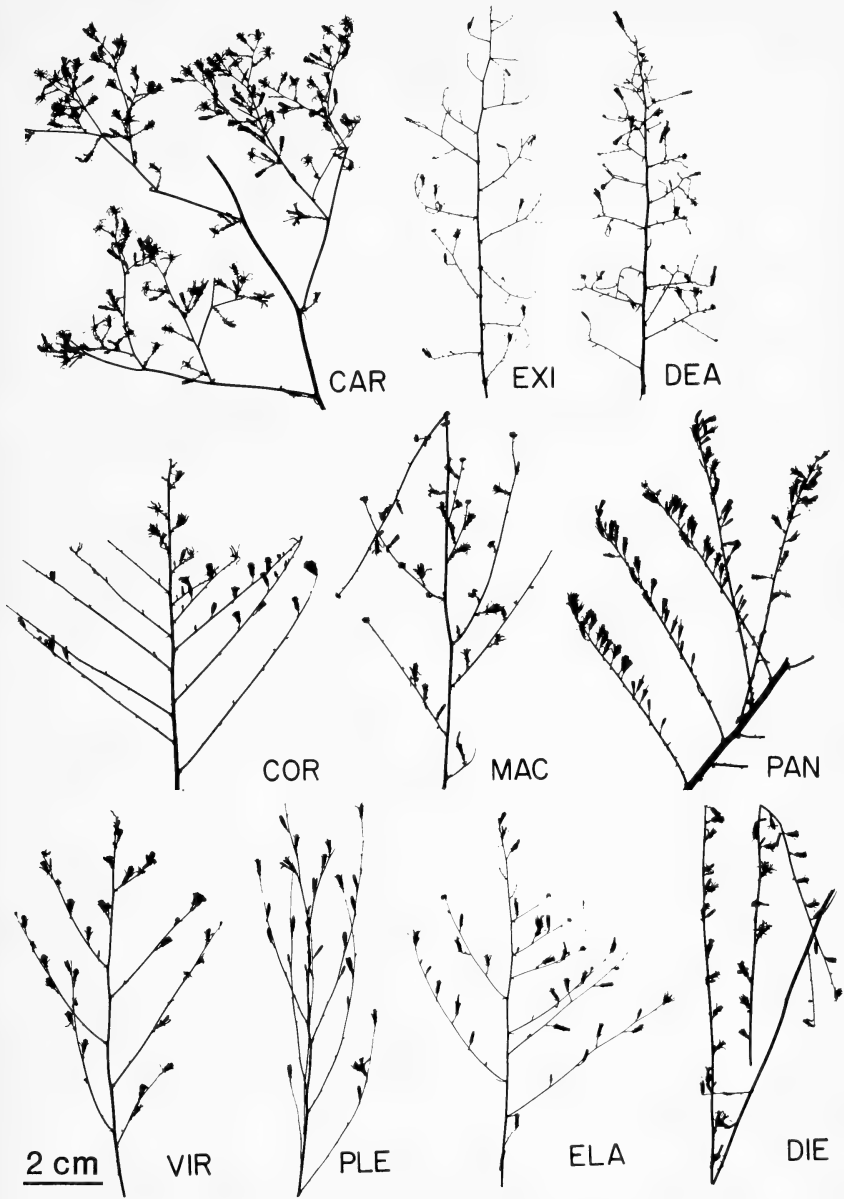
FIG. 2. Silhouettes of the branches of the annual taxa of *Stephanomeria* (modified with additions after Gottlieb, 1971, fig. 5).

east of Tuba City, *Cronquist 9140;* Middle Mesa, *Gould and Phillips 4738.* Mohave Co.: Vulcan's Throne, Toroweap, *Cottam 13357;* between Hualpai Wash and junction of Pierce's Ferry Road with U.S. 466, *Ferris 9889;* Yucca, *Jones 3931.* Navajo

Co.: Monument Valley, *Eastwood and Howell 6654.* Pima Co.: Santa Rita Experimental Range, Study Area 199B, *G-6811.* Yuma Co.: Harcuvar Mountains, *Peebles 13876.* COLORADO. Mesa Co.: Grand Junction, *Eastwood 7218.* UTAH. Milford, *Jones 1798.* Grand Co.: ½ mile north of Arches National Monument on U.S. 160, *G-691.* Kane Co.: East entrance Zion National Park, *Kamb 633;* 1 mile east of Kanab, *Maguire 18902.* San Juan Co.: Rainbow Bridge Trail, *J. T. Howell 24653.* Utah Co.: Springville, *Jones 5618.* NEVADA. Clark Co.: Kyle Canyon, *Clokey 7764;* 12 miles north of Searchlight at Marshall's Wash, *Gullion 323.* Lander Co.: Toiyabe Range, *Eastwood and Howell 7354.* Nye Co.: 4–6 miles north of Tonopah on road to Cloverdale, *Henning 185.* White Pine Co.: 2 miles south of Baker, Snake Range, *Maguire 20850.* CALIFORNIA. Inyo Co.: Olancha, *Hall and Chandler 7344.* Kern Co.: Red Rock Canyon, *Twisselmann 15411.* Mono Co.: Chalfant Flats, Shealy, *Duran 3487.* Riverside Co.: Hot Springs, 8 miles north of Garnet, *Rose 35675.* San Bernardino Co.: Palm Springs, *Eastwood 2961;* Adelanto, *Parish 11814;* Deadman's Point, *J. T. Howell 2504;* 21 miles east of Lucerne Valley on Old Womman Springs Road, *G-6650.*

Pappus bristle number is variable in *Stephanomeria exigua.* Those plants with a pappus of five bristles, *Stephanomeria pentachaeta,* are not distinct from subspecies *exigua;* individuals with five bristles appear occasionally in populations throughout the distribution and are fully interfertile with plants having higher bristle numbers.

1b. **Stephanomeria exigua** ssp. **deanei** (MacBride) n. comb.

> *Stephanomeria exigua* var. *deanei* MacBride, Contrib. Gray Herb., n.s., 53:22. 1918.
>
> *Ptiloria exigua* var. *deanei* MacBride ex. Davids. & Moxley. Fl. S. Calif. 355. 1923.

Peduncles and involucres conspicuously glandular-pubescent; heads paniculate, peduncles 10–40 mm long (fig. 2); heads averaging 7–9 florets; involucres subtended by appressed calyculate bracts; ligules various shades of pink or white on upper surface, purple-tinged on back; achenes averaging 2.1–2.4 mm long, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 9-14 in number, plumose on the upper 55–60% of their length, thickened and generally connate in groups of 2–4 at the bases which usually remain adnate to the achene when the bristles break off. **n = 8.**

Type. "California, San Diego Co., Sweetwater Valley, Las Paderas Ranch, 23 July 1888, G. C. Deane." (Holotype: GH!)

Distribution. Sandy fields and chaparral in coastal mountains and valleys from Los Angeles County south to northern Baja California (fig. 1). Flowers June to October.

Representative specimens. CALIFORNIA. Riverside Co.: Chalk Hill, San Jacinto Mountains, *Hall 7.* San Diego Co.: Julian, Oct. 16, 1894, *T. S. Brandegee;* Lakeside, *Hall 7439;* 1.8 miles from Ballena on road to Ramona, *Raven and Snow 9585;* 1 mile west of Manzanita, at Tierra del Sol turnoff from U.S. 80, *G-6635;* between Anza and Cahuilla on Rt. 71, *G-6658;* Rincon Springs, *G-66160.* MEXICO. Baja California: Cardon Grande, April 23, 1889, *T. S. Brandegee;* El Llano de Santana, May 10, 1889, *T. S. Brandegee;* San Carlos River, *Eastwood 12422;* Las Animas
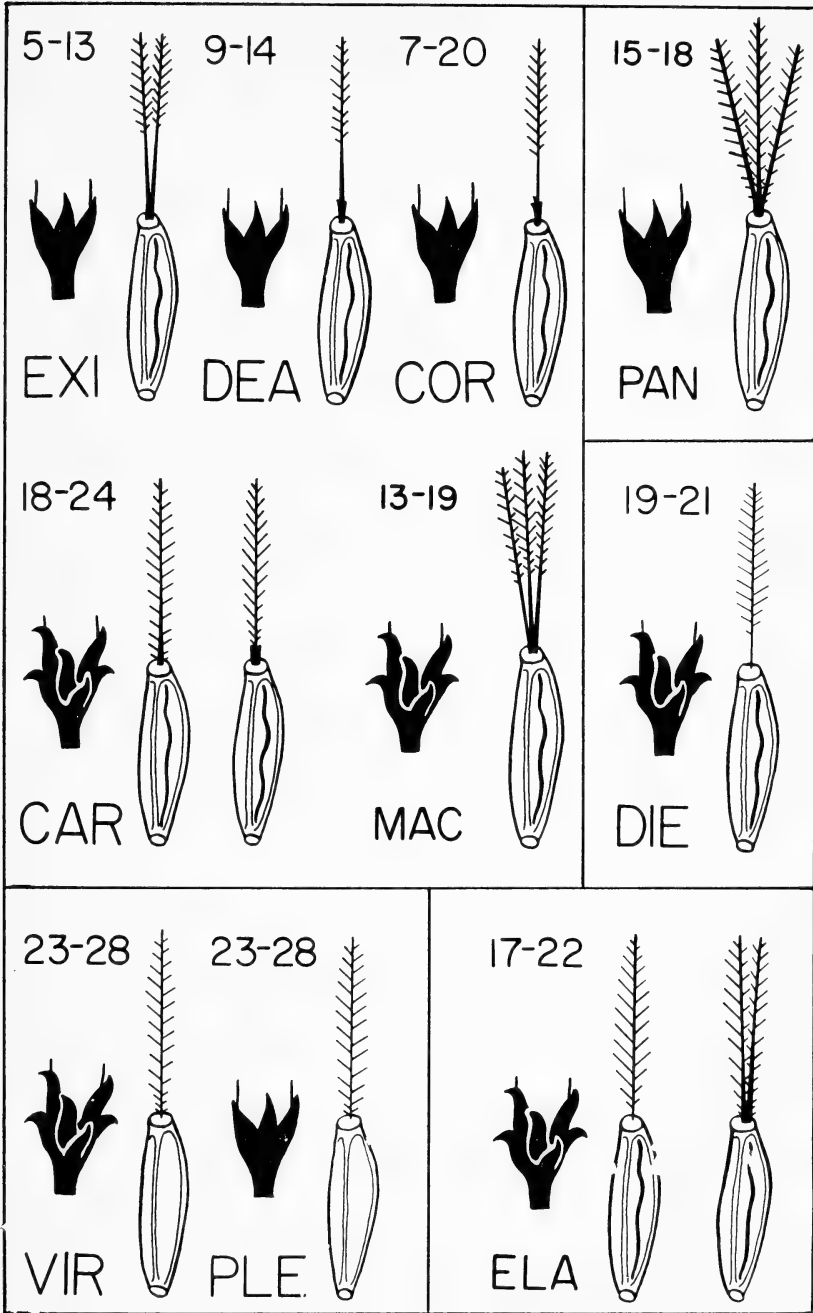
Fig. 3. Diagram of the morphological characteristics of the achenes, pappus bristles including number per achene, and involucres of the annual taxa of *Stephanomeria* (modified with additions after Gottlieb, 1971, fig. 4).

Canyon, 23 miles south of Ensenada, *Wiggins and Demaree 4712;* Yellow Pine Belt between Ojos Negros and Neji Ranch, *Wiggins and Gillespie 4136.*

Subspecies *deanei* is most closely allied to subspecies *exigua.* The two are separated on the basis of a few constant morphological characters, their allopatric distribution, and a reduction in fertility of hybrids between them.

1c. **Stephanomeria exigua** ssp. **carotifera** (Hoover) n. comb.

Stephanomeria carotifera Hoover, Leafl. W. Bot. 10:252. 1966.

Herbage glabrous or tomentose on stems and involucres; heads paniculate, peduncles averaging greater than 12 mm long (fig. 2); heads averaging 7–9 florets; involucres subtended by strongly reflexed calyculate bracts; ligules various shades of pink or white on upper surface, purple-tinged on back; achenes averaging 3.2–4.3 mm long, five-sided with a narrow longitudinal groove on each side; pappus bristles either thickened or not (fig. 3), when thickened, often connate at the bases in groups of 2–4, bristles plumose to the top of the thickening, and breaking off above the bases that remain adnate to the achene, when not thickened, distinct at the base, bristles plumose their entire length, and breaking off completely or nearly so; in both types, bristles average 18–24 in number. $n = 8.$

Type. "Open south-facing hill near San Bernardo Creek east of Morro Bay, in clay among serpentine rock, July 11, 1964, Hoover 9191." (Holotype: CAS 453,631!)

Distribution. Inland populations in open, sandy and shale soils in inner South Coast Ranges (fig. 1) such as the Temblor and Diablo Ranges and north into various creeks draining into the Salinas and San Antonio Valleys, or coastal populations on sand dunes and shale and serpentine from the vicinity of San Luis Obispo to Surf, Santa Barbara County, and on Figueroa Mountain, Santa Barbara County, Hi Mountain, San Luis Obispo County, and Sespe Creek, Ventura County. Flowers August to October.

Representative specimens. CALIFORNIA. Kern Co.: Santos Canyon, 10 miles south of Blackwell's Corner, *Twisselmann 832;* Mt. Abel Road, 5.1 miles north of Maricopa Highway, *Twisselmann 3135;* ½ mile east of Temblor Mountain summit on Route 58, *G-6845.* Monterey Co.: 15 miles west of Greenfield on Jamesburg Road, *J. T. Howell 27477;* Mustang Grade, between Mustang summit and San Lorenzo Creek, *J. T. Howell 40073;* 1 mile south of Jolon on Jolon-Lockwood Road, *G-66127.* San Luis Obispo Co.: Palo Prieta Canyon near summit, *Twisselmann 3108;* Twisselmann Ranch, summit of Choice Valley, *Twisselmann 5564;* Carrisa Plains School, *Twisselmann 7915;* Bellevue-Santa Fe School, *Hoover 9977;* Grover City, *Hoover 10092;* Oso Flaco Lake, *Hoover 10865;* 3 miles northeast of Tepusquest Road on Colson Canyon Road, *G-7072;* near summit of Hi Mountain, south of Pozo, *G-7076;* 6.5 miles west of Shandon on Route 41, *G-7080.* Santa Barbara Co.: dunes at Surf, *Pollard, July 22, 1954;* 7 miles west of Buellton on Route 150, *Pollard, September 13, 1956;* Union Oil Refinery, Route 1, west of Santa Maria, *G-7074;* immediately east of Figueroa Mountain Campground on Cachuma Saddle Road, *G-7134.* Ventura Co.: Quatal Canyon, *Twisselmann 2319;* 2–3 miles south of Sandstone Campground, Sespe Creek, *G-7064.*

Subspecies *carotifera* was originally described as a species because it was thought to be perennial and morphologically distinct from other perennial Stephanomerias. However, field and greenhouse studies show that it is an obligate annual. When it was first described, the morphological characteristics of the annual Stephanomerias were not known and, consequently, its relationships were obscured. It is now clear, however, that in morphological features, karyotype, and reproductive compatibilities, subspecies *carotifera* is closely allied to the other subspecies of *S. exigua*. For some of the characters that distinguish it from these subspecies, it varies toward *S. virgata* ssp. *virgata,* a situation that suggests the possible effects of past hybridization (Gottlieb, 1971).

The coastal and inland populations are alike in most of their morphological features but they can be separated by several characteristics of their pappus bristles. Inland populations have strongly thickened bristle bases whereas the bristles of the coastal populations are not or only very slightly thickened as described above. Reproductively, both are fully crossable, and their hybrids are highly fertile. The minor morphological differences and the full reproductive compatibility mean that there is neither taxonomic nor biological reason for distinguishing them. Populations of subspecies *carotifera* hybridize with both subspecies of *S. virgata* in northern Ventura County. A hybrid swarm is present where subspecies *carotifera* and subspecies *coronaria* meet at the junction of Roads G16 and G17 at the Arroyo Seco Bridge in Monterey County.

1d. **Stephanomeria exigua** ssp. **macrocarpa** n.ssp. Differt ab aliis subspeciebus capitulis in ramulis abbreviatis et tegulis valde reflexis, acheniis longioribus (5.5-6.8 mm longis).

Herbage glabrous or tomentose on stems and involucres; heads solitary or clustered on short (5–10 mm) peduncles (fig. 2); heads averaging 6–8 florets; involucres subtended by strongly reflexed calyculate bracts; ligules various shades of pink or white on upper surface, occasionally purple-tinged on back; achenes averaging 5.5–6.8 mm long, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 13–19 in number, often connate in five groups of 2–4 each, 6.2–7.5 mm long, plumose on the upper 60–70% of their length, strongly thickened and tawny at the base, remaining on the achene. $n = 8$.

Type. On Route 168, ½ mile east of Tollhouse on road to Pineridge, Fresno County, California, September 4, 1970, *Gottlieb 7048.* (Holotype: UC).

Distribution. On western slope of Sierra Nevada from 1000 to about 4000 feet from Kern County to Stanislaus County (fig. 1). Flowers August and September.

Representative specimens. CALIFORNIA. Kern Co.: 3–4 miles east of Glennville on Rt. 155, *G-7028.* Mariposa Co.: 8 miles southwest of Mariposa on Merced Road, *Stebbins 2653;* 1 mile south of east fork Chowchilla Bridge on Rt. 49, *G-6954.* Stanislaus Co.: Knights Ferry, *Eastwood July 25, 1923.* Tulare Co.: near Eleven

Range View Point, Sequoia National Park, *J. T. Howell 28901;* 12 miles south of Fountain Springs and approximately 7 miles north of California Hot Springs, *G-7042;* between Lemon Cove and Badger on J21, *G-7044.* Tuolumne Co.: 1½ miles northeast of Riverside Station on North Fork, Tuolumne River, *G-7052.*

Specimens of subspecies *macrocarpa* have rarely been collected although it is common within its limited range of distribution. The achenes of this subspecies are the largest of any of the annual Stephanomerias. Reproductively, it is close to subspecies *coronaria* and the two hybridize where they come together in Kern County. The strongly reflexed calyculate bracts of subspecies *macrocarpa* also relate it to subspecies *carotifera;* experimental hybrids between them have not yet been grown. Subspecies *macrocarpa* is self-compatible and it is highly self-pollinating in the greenhouse.

1e. **Stephanomeria exigua** ssp. **coronaria** (Greene) n. comb.

> *Stephanomeria coronaria* Greene, Bull. Calif. Acad. 1:194. 1885.
> *Ptiloria coronaria* Greene, Pittonia 2:132. 1885.
> *Stephanomeria exigua* var. *coronaria* Jepson, Man. Fl. Pl. Calif. 998. 1925.

Herbage glabrous or sparsely pubescent on stems and involucres; head solitary or clustered on short (3–5 mm) peduncles (fig. 2); heads averaging 5–11 florets; involucres subtended by appressed calyculate bracts; ligules various shades of pink or white on upper surface, generally purple-tinged on back; achenes averaging 2.3–3.1 mm long, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 7–20 in number, plumose on the upper 60–85% of their length, thickened (at least slightly) and occasionally connate in groups of 2–4 at the bases, which often remain adnate to the achene. **n = 8.**

Type. "California, Santa Lucia Mountains, August, 1885. T. S. Brandegee." (Holotype: GH!)

Distribution (fig. 1). In California, widespread in many diverse habitats: equable maritime sites on off-shore islands and along coast from Goleta to Ventura; arid sandy soils in inner South Coast Ranges; raisin vineyards south of Fresno; openings in yellow pine forest to 6500 feet in Greenhorn and San Gabriel Mountains; volcanic soils in eastern Sierra Nevada to 9300 feet. In Oregon and Idaho on sandy or limestone or volcanic soils in sagebrush desert. Flowers July to October.

Representative specimens. CALIFORNIA. Contra Costa Co.: sand dunes at Antioch, near Kaiser plant, *G-6959.* Kern Co.: Tejon Pass, *J. T. Howell 27490;* Edison, *J. T. Howell 32702;* Castaic Valley, 1 mile south of Lebec on Frazier Park Road, *Twisselmann 8004;* entrance to Tehachapi Mountain Park, *G-7036;* 2.1 miles north of Greenhorn Summit on Tobias Pass Road, *G-7116;* ½ mile east of Woody on Route 155, *G-7117.* Inyo Co.: south side Wonoga Peak, *J. T. Howell, 26288;* Onion Valley Road, *J. T. Howell 27439;* 13.5 miles west of Bishop on Sabrina Lake Road, *G-6667.* Los Angeles Co.: Prairie Fork, San Gabriel River, *Johnston 1654;* ridge

southwest of Swartout Valley, San Gabriel Mountains, *Munz 7671;* Sepulveda Canyon, Santa Monica Mountains, *Raven and Thompson 14515;* ½ mile west of Tent Rock Campsite on West Liebre Lookout Road, *G-7054.* Mono Co.: Sherwin Grade, Rock Creek, Route 395, *Ferris 12584.* Monterey Co.: Limekiln Creek west of Gonzales, *Hoover 9973;* creek below Metz, *Twisselmann 9190.* San Bernardino Co.: Grass Valley Lake, *Raven and Beeks 16770.* San Luis Obispo Co.: 3 miles north of Pozo, *Hoover 9906.* Santa Barbara Co.: Goleta salt marsh, *Pollard, Oct. 10, 1957;* San Miguel Island, *Greene, September 1886.* Tulare Co.: Redstone Park, *K. Brandegee, July 25, 1905;* Bakeoven Meadows, *J. T. Howell 26936.* Ventura Co.: Pt. Mugu, *J. T. Howell 3139;* Mill Canyon, Lockwood Valley, *Twisselmann 17544;* Santa Cruz Island, ¼ mile east of Main Ranch, *Wolf 4168.* OREGON. Harney Co.: Malheur Lake, Narrows, *Henderson 8604.* NEVADA. Esmeralda Co.: 1.5 miles west of Lida, *Alexander and Kellogg 2386.* IDAHO. Owyhee Co.: ½ mile north of Oreana, *Davis 2072.*

Subspecies *coronaria* occupies the most diverse series of habitats of any annual *Stephanomeria.* Striking morphological variation is found within populations in terms of ligule number, size, and color. The number of pappus bristles and the proportion of the bristle that is plumose are both higher in populations in the South Coast Ranges than in populations in the Sierra and eastward. Moderate reductions in fertility are found in experimental hybrids between populations representing these two groups. In the southern Sierra Nevada and mountains of southwestern Nevada, subspecies *coronaria* is found from 5000 to 9300 feet and subspecies *exigua* at lower elevations. Where the two subspecies meet, intergrading individuals are often found.

2. STEPHANOMERIA PANICULATA Nutt., Trans. Amer. Phil. Soc. 2: 7:428. 1841.

     Ptiloria paniculata Greene, Pittonia 2:132. 1890.

     Stephanomeria oregonensis Gandoger, Bull. Soc. Bot. Fr. 65:53. 1918. (Ochoco River, Oregon, *Cusick 2695*)

     Stephanomeria suksdorfii Gandoger, loc. cit. (Bingen, Washington, *Suksdorf 5867*)

Herbage glabrous or occasionally short pubescent on stems and involucres; heads solitary or clustered on short (5–7 mm) peduncles (fig. 2); heads averaging five florets; involucres subtended by appressed calyculate bracts; ligules various shades of pink or white; achenes averaging 3.8–4.2 mm in length, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 15–18 in number, completely plumose to the base, generally connate in groups of 2–4 at the thickened, heavily setulose bases, usually remaining adnate to the achene. **n = 8.**

Type. "On the Rocky Mountain Plains, towards the Colorado", 1834–35, *T. Nuttall.* (Holotype: GH!)

Distribution (fig. 1). Open sandy or volcanic soils around Mt. Shasta and occasionally south to Plumas County, California. More common in eastern Oregon, Washington, and Idaho, often growing as a weed along

roadsides, particularly in the Columbia River gorge. Flowers June to August.

Representative specimens. CALIFORNIA. Plumas Co.: between Taylorsville and Genesee, *J. T. Howell 28209.* Siskiyou Co.: Mt. Shasta, *Grant 5064;* on U.S. 97, ¾ mile south of turnoff to Highway A12, north of Weed, *G-6682.* OREGON. Jefferson Co.: 2½ miles west of Metolius on road to Round Butte, *G-6686.* Sherman Co.: 6 miles west of Arlington on 8ON, *G-6691.* Wasco Co.: 2 miles west of The Dalles on U.S. 30, *G-6687.* WASHINGTON. Douglas Co.: Rock Island, *Sandberg and Leiberg 2303.* Klickitat Co.: Columbia River, *Suksdorf 982.* Walla Walla Co.: Waitsburg, *Horner 28.* Yakima Co.: 5 miles south of Toppenish on U.S. 97, *G-704.* IDAHO. Canyon Co.: Falks Store, *MacBride 1687.* Elmore Co.: King Hill, *Nelson and Mac-Bride 1085.* Owyhee Co.: about 8 miles east of Silver City on road to Murphy, *G-719.*

Stephanomeria paniculata shows close phylogenetic affinities to *S. exigua* ssp. *coronaria.* It is self-compatible and is highly self-pollinating in the greenhouse. Correlated with its breeding system are short narrow ligules and reduced number of pollen grains.

3. **Stephanomeria diegensis** n. sp. Inter *S. exiguam* et *S. virgatam* quasi intermedia; ab *S. exigua* pappi setis non incrassatis, ab *S. virgata* acheniis sulcatis differt.

Heads solitary or clustered on short (3–4 mm) peduncles (fig. 2); heads averaging 11–13 florets; involucres subtended by reflexed calyculate bracts, glandular-puberulent; ligules various shades of pink or white on upper surface, generally purple-tinged on back; achenes averaging 1.9 to 2.3 mm long, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 19–21 in number; plumose on the upper 80–85% of their length, not thickened, distinct at the base, completely deciduous. **n = 8.**

Type. Near entrance to Torrey Pines State Park, San Diego County, California, August 15, 1966, *Gottlieb 66168.* (Holotype: UC)

Distribution (Gottlieb, 1971, fig. 3). Frequent in open, pioneer sites such as old clearings, the landward side of coastal sand dunes, chaparral openings, and sandy roadside embankments below 2000 feet from Santa Monica Mountains south to San Quintin, Baja California. Flowers August to November.

Representative specimens. CALIFORNIA. Los Angeles Co.: Santa Catalina Island, Descanso Canyon, *Millspaugh 4534;* canyon below Lemon Tank, San Clemente Island, *Raven 17978;* Mosquito Harbor, San Clemente Island, *Abrams and Wiggins 344;* Mandeville Canyon, Santa Monica Mountains, *Clokey and Templeton 4581;* U.S. 101, 0.2 miles east of Zuma Beach turnoff, Santa Monica Mountains, *Raven and Thompson 13721;* Inglewood, *Abrams 2979.* Orange Co.: Route 74 immediately west of Lower San Juan Campground, *G-6860.* San Diego Co.: La Jolla, *F. E. and E. S. Clements 269;* Del Mar, *Jepson 1607;* Coronado, *Spencer 1009;* Torrey Pines, *Raven and Wedberg 9474;* 4 miles north of Lakeside on Highway 67, *G-6637;* ¼ mile north of Rancho San Bernardo Road on U.S. 395, *G-66162;* 1½ miles west of Harbison Canyon Road on U.S. 8, *G-66164.* Ventura Co.: on Deer Creek Road, 2½

miles east of Route 1, *G-6945*. MEXICO. Baja California. 2 miles north of Rosario Beach, *Wiggins and Gillespie 3896;* San Quintin Bay, *Mason 2062a;* Middle Island, Coronado Islands, *Moran 6805;* South Cove, Todos Santos del Sur, *Philbrick and Benedict B68–421*.

The morphological characteristics of *Stephanomeria diegensis* are an amalgam of those of *S. exigua* and *S. virgata*. The evolutionary relationships of the species are fully described in Gottlieb, 1971.

4. STEPHANOMERIA ELATA Nutt., J. Acad. Nat. Sci. Phil, n.s., 1.173, 1847.

Herbage glabrous or short pubescent or glandular-pubescent on branchlets and involucres; heads solitary or clustered on short (3–7 mm) peduncles (fig. 2); heads averaging 9–15 florets; involucres subtended by strongly reflexed, slightly reflexed, or rarely appressed calyculate bracts; ligules various shades of pink or white on upper surface, purple-tinged on back; achenes averaging 2.8–4.5 mm in length, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 17–22 in number, generally completely plumose (pinnae may be sparse in proximal 10% of bristle), the bases various, either not thickened, not connate, and completely deciduous, or thickened, connate in groups of 2–4, and remaining on the achene. **n = 16.**

Type. Holotype: "Santa Barbara, Upper California", not located at Phil. Acad. Nat. Sci. or British Museum. Neotype: Devereux Dunes, University of California, Santa Barbara Campus, Goleta, California, October 11, 1971, *Gottlieb and Philbrick 7140,* deposited at UC.

Distribution (fig. 4). Populations with thickened and connate pappus bristles are found in chaparral openings, grassy meadows, and along roadsides from Monterey County to southwestern Oregon in the Coast Ranges and also on the western slopes of the Sierra Nevada from 500 to 4500 feet south to Fresno County. Populations with unthickened and distinct bristles are distributed near the coast from Marin to Santa Barbara counties. Flowers from July to October.

Representative specimens. OREGON. Douglas Co.: 5 miles north of Jackson County line on Highway 227, *G-697*. Lane Co.: Willamette River near Oakgrove, *Henderson 16508*. CALIFORNIA. Amador Co.: 1.5 miles west southwest of Rich Gulch, *Belshaw 2478*. Alameda Co.: Strawberry Canyon, Berkeley, *Tracy 1953*. Eldorado Co.: 1 mile south of Coloma, *J. T. Howell 5575*. Humboldt Co.: White Thorn Valley, *Tracy 5034*. Lake Co.: 4 miles from Middleton on Adams Springs Road, *J. T. Howell 5449*. Marin Co.: south end Bolinas Ridge, Mt. Tamalpais, *J. T. Howell 21552;* on bluffs above ocean east of lighthouse, Point Reyes, *G-6958*. Mariposa Co.: 7 miles southwest of Mariposa on Merced Road, *Stebbins 2652*. Monterey Co.: headwaters of Arroyo Seco, *Mason 5745;* Laureles Grade, *G-66123*. Napa Co.: Wooden Valley Grade, *Raven 3057*. Nevada Co.: west of Greenhorn Creek, *Raven 7979*. San Francisco Co.: Lake Merced, *J. T. Howell 716*. San Luis Obispo Co.: mouth of Hazard Canyon, Morro Bay, *Chambers 2474;* Baywood Park, Santa Isabel Avenue, *G-66132*. San Mateo Co.: Pt. San Pedro, *J. T. Howell 15369*. Santa Clara Co.: Mt. Hamilton, *J. T. Howell 11718;* Skyline Blvd., 4 miles south of junction with Page Mill Road, *G-66120*. Santa Cruz Co.: head of San Lorenzo River,

Fig. 4. Distribution of *Stephanomeria elata*.

Yates 4060. Sonoma Co.: Layton Mine, Austin Creek, *Hoffman 579*. Trinity Co.: Scott Mountain, 13.5 miles north of Carrville, *J. T. Howell 12831*. Yuba Co.: Camptonville, *J. T. Howell 28285*.

All the tetraploid populations of annual Stephanomerias are placed into *Stephanomeria elata*. These populations are self-compatible and are self-pollinating in the greenhouse. Substantial inter-population morphological variability is observed in the length, width, color, and number of florets and degree of reflexing of the calyculate bracts. In addition, two groups of populations can be distinguished on the basis of degree of thickening of the basal portion of the pappus bristles as described above. Populations with thickened bristles also have larger achenes, averaging 3.9–4.5 mm in length, whereas the achenes of populations without thickened bristles average 2.8–3.3 mm in length. Another difference is that 24–30% of the pollen grains of the former group of populations are tetracolpate. Where the two groups of populations overlap in Santa Cruz, Santa Clara, and Monterey counties, it is often difficult to assign individuals to one or the other. Because of their high degree of self-pollination, hybridization between the two groups has not yet been successful. Since the morphological differences are minor and intergrade individuals can be found, and since cytogenetic evidence (Gottlieb, 1969) suggests that the tetraploid populations are allotetraploid, by chromosomal doubling following interspecific hybridization between *S. exigua* and *S. virgata,* the tetraploid populations are placed in a single species.

Although I have been unable to locate the type specimen of *S. elata,* Nuttall's description is sufficiently clear in details of morphology that it is appropriate to apply this name to the tetraploid populations. No other name has ever been applied to tetraploid populations. Nuttall most likely described a small or depauperate specimen since he mentions that the specimen from which he drew his description had "a small terminal panicle". His statement that the flowers were "apparently blue" was probably based on the condition of the dried specimen; it is not unusual for ligules with strongly purple-tinged stripes on their lower surface to appear bluish when dry.

5a. STEPHANOMERIA VIRGATA Benth. ssp. VIRGATA, Bot. Sulph. 32. 1844.

        Stephanomeria tomentosa Greene, Bull. Calif. Acad. 2:152. 1886. (Holotype: collected by E. L. Greene, Santa Cruz Island, July and August 1886, ND 001751! ND 001753! ND 001754!)

        Ptiloria virgata Greene, Pittonia 2:130. 1890.

        Stephanomeria virgata var. *tomentosa* Munz, Aliso 4:100. 1958.

Herbage glabrous or tomentose on stems and involucres; heads solitary or clustered on short (3–7 mm) peduncles (fig. 2); heads averaging 8–9 florets; involucres subtended by strongly reflexed calyculate bracts; ligules various shades of pink or rarely white on upper surface, usually purple-tinged on back; achenes averaging 3.0–3.4 mm in length, five-sided with smooth or rugose but not grooved surfaces (fig. 3); pappus bristles averaging 23–28 in number, densely and completely plumose to the base, not thickened and distinct, completely deciduous. **n = 8.**

Type. San Pedro, Los Angeles County. (Holotype: Kew)

Distribution (Gottlieb, 1971, fig. 2). Chaparral openings and dry sandy hills in oak savanna from sea level to 6000 feet from southern San Luis Obispo to San Diego counties. Also abundant on roadsides and freeway embankments around Los Angeles. Flowers late July to October.

Representative specimens. CALIFORNIA. Los Angeles Co.: Mint Canyon Road 7 miles north of Solemint, *G-66155;* 1 mile south of Crystal Lake on Highway 39, *G-66157;* 4 miles south of Gorman on Gorman Post Road, *G-7055.* San Bernardino Co.: Cajon Pass, *Raven 16687;* Lytle Creek Road, ½ mile south of Applewhite junction, *G-66159.* San Luis Obispo Co.: between Suey Creek and Cuyama River, *Hoover 6480.* Santa Barbara Co.: ½ mile west of La Cumbre Lookout, *G-66148;* Point Sal Road, 1 mile west of Ranch, *G-6934.* Ventura Co.: 4 miles northeast of Devil's Heart Peak, *Simontacchi 137;* 2 miles south of Rose Valley Campground on Route 33, *G-66151.*

Historically, any annual *Stephanomeria* that had essentially fully plumose pappus was placed in this species. Now it is known that fully plumose pappus bristles are a feature of many of the taxa. *Stephanomeria tomentosa* refers to a tomentose form originally thought to be restricted to the California offshore islands; it has now been commonly found in many populations.

5b. **Stephanomeria virgata** ssp. **pleurocarpa** (Greene) n. comb.

> *Ptiloria pleurocarpa* Greene, Pittonia 2:131. 1890.
> *Ptiloria canescens* Greene, Pittonia 2:131. 1890. (Paratype: collected by E. L. Greene, Alameda, June, 1890. ND 001745!)
> *Stephanomeria virgata* var. *pleurocarpa* Hall, Univ. Calif., Publ. Bot. 3:258. 1907.

Herbage glabrous or tomentose on stems and involucres; heads solitary or clustered on short (3–7 mm) peduncles (fig. 2); heads averaging 5–6 florets; involucres subtended by appressed calyculate bracts; ligules various shades of pink or rarely white, occasionally purple-tinged on back; achenes averaging 2.2–3.6 mm in length, five-sided with smooth or rugose but not grooved surfaces (fig. 3); pappus bristles averaging 23–28 in number, densely and completely plumose to the base, not thickened and distinct, completely deciduous. **n = 8.**

Type. Redding, Shasta County, collected by E. L. Greene, 1889. (Holotype: ND 001621!)

Distribution (Gottlieb, 1971, fig. 2). Many soil types including shale, sandstone, serpentine, and volcanics. Widely distributed from southwestern Oregon in the Coast Ranges and Sierra Nevada (below 6000 feet) to northern Baja California. Also occasional populations in mountains of north central Nevada. Flowers July to November.

Representative specimens. OREGON. Curry Co.: mouth of Fall Creek on Illinois River, *Baker 4877.* Douglas Co.: 3 miles north of Drew on 227, *G-696.* Jackson Co.:

Elk Creek, Rogue River, *Henderson 13082.* NEVADA. Washoe Co.: Incline Road, Lake Tahoe, *Kennedy 1474.* CALIFORNIA. Alameda Co.: Redwood Ridge *Constance 421.* Amador Co.: 2 miles south southwest of Volcano, *Johannsen 21505.* Calaveras Co.: Big Trees, *Howden 12670.* Contra Costa Co.: Marsh Creek, *6* miles east of Clayton, *Rose 38308.* Fresno Co.: Hume Lake, *J. T. Howell 16150.* Humboldt Co.: Trinity River, near mouth of Willow Creek, *Tracy 5187.* Kern Co.: 7 miles west of Maricopa, *Twisselmann 1604.* Lake Co.: 1 mile below Hullville on Eel River, *Heller 6021;* southwest side of Snow Mountain, 5000 feet, *Stebbins 2066;* Bartlett Springs Road, north of Lucerns, *G-6699.* Mariposa Co.: Wawona, *J. T. Howell 583.* Mendocino Co.: Mendocino, *Brown 900.* Monterey Co.: along San Antonio River between Jolon and Santa Lucia Ranger Station, *Mason 5788;* 9 miles north of Parkfield on Road to 198, *G-7081.* Napa Co.: 1.3 miles east of Chiles Valley, *Raven 3950;* Mt. St. Helena, *Eastwood, 7956.* Plumas Co.: Sierraville, *Hanks 6566.* Riverside Co.: Chalk Hill, San Jacinto Mountains, *Hall 2631.* San Benito Co.: 4 miles north of The Pinnacles, *J. T. Howell 11538.* San Diego Co.: immediately south of boundary Cuyamaca State Park, Route 79, *G-6866.* San Luis Obispo Co.: between Rocky Butte and Pine Mountain, *Hoover 8399.* Shasta Co.: Burney Falls, *Rose 45222.* Sutter Co.: 4 miles south of Live Oak, *Heller 13834.* Tulare Co.: Paradise Creek, *Frost 7895.* Tuolumne Co.: Mather, *Mason 2176.*

Populations of this subspecies are occasionally sympatric with populations of *S. exigua* and subspecies *virgata.* Hybrid individuals have been found in all such contact zones. *Ptiloria canescens* refers to a pubescent form that is a genetic variant and one commonly found in many populations throughout the distribution.

Literature Cited

Ferris, R. S. 1960. Illustrated flora of the Pacific States. Vol. IV. Bignoniaceae to Compositae. Stanford: Stanford Univ. Press.

Gottlieb, L. D. 1969. The role of hybridization in the evolution of the annual species of *Stephanomeria* (Compositae). Ph.D. Thesis, Univ. of Mich.

————. 1971. Evolutionary relationships in the outcrossing diploid annual species of *Stephanomeria* (Compositae). Evol. 25:312–329.

Grant, V. 1953. The role of hybridization in the evolution of the leafy-stemmed Gilias. Evol. 7:51–64.

HERMAPHRODITIC FLOWERS IN CALIFORNIAN OAKS

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In late summer 1941, a shrub of *Quercus turbinella* Greene subsp. *californica* Tucker was noticed flowering out of season beside U.S. Highway 399 at the base of the north side of Pine Mountain, Ventura County. Here, at an elevation of 3900 feet, this small-leaved, sclerophyllous oak occurred in an open, xeric shrub association with *Ceanothus leucodermis* Greene and *Pinus monophylla* Torr. & Frem. Although this oak is common in the area, only the one shrub was observed to be flowering.

The inflorescences, arising from buds at the ends of the twigs or in the upper leaf axils, were much longer than normal—up to 5 cm in length (fig. 1,A). The stiff rachis commonly was more slender distally, and sometimes had a slightly zigzag course. In some spikes the several lower flowers were perfect and the rest staminate. In addition to these aberrant inflorescences, the shrub also bore many clusters of apparently normal staminate aments. In the aberrant inflorescences, the individual flowers were bracteate, up to 3.5 mm in length, and had the appearance of pistillate flowers (as, indeed, some of them were: fig. 1,C) with stamens added. The stamens were in an epigynous position (see fig. 1,B), centripetal to the very small perianth lobes.

All species of *Quercus* are normally monoecious. In *Q. turbinella* subsp. *californica,* the pistillate flowers occur one or two together, usually sessile in the axils of the upper leaves of the new shoots. The staminate flowers, which appear in much greater numbers, are in lax, elongated catkins borne on the lower portion of the newly elongating leafy shoot or emerging from buds clustered at the ends of the previous year's twigs.

In the present case, both the flowers and the time of flowering were unusual. My observations (and collection: *Tucker 373-A,* DAV) were made on August 9, 1941; however, in that general area, *Q. turbinella* subsp. *californica* normally flowers in April. Although no unusual environmental conditions were noted at the time, this unusual flowering must have been triggered by some sort of unusual conditions (and the *initiation* and early differentiation of these inflorescences and flowers must have occurred at least several weeks prior to that).

Again, in late summer 1947, the same type of peculiar flowering was noted on a shrub of *Q. durata* Jeps. in Marin County, beside the Fairfax-Alpine Dam road, opposite the south end of Carson Ridge (*Tucker 1588,* August 31, 1947. DAV). This oak, like *Q. turbinella,* is a drought-adapted, small-leaved, sclerophyllous shrub. The stiff, elongated, multi-flowered spikes bore mostly pistillate flowers, but a few of the flowers had small epigynous stamens, also. At this latitude, *Q. durata* normally flowers in May.

Fig. 1. Inflorescences and flowers of *Quercus turbinella* subsp. *californica*: A. Atypical inflorescences bearing mostly perfect flowers; B, An individual perfect flower; C, A pistillate flower (center) in an inflorescence composed largely of perfect flowers. (an: anther; st: style)

In the genus *Quercus,* instances of this sort may be quite rare, but probably not so rare as the paucity of published reports might indicate. Scaramuzzi (1958) reported similar atypical flowers in the Mediterranean oak, *Q. coccifera* L. She encountered this in mid-May rather than late summer, however, and noticed no disruptive agents in the external environment. In addition to hermaphroditic flowers, she also described two types of intersexual flowers in which either the stamens or the pistils were more strongly developed. I am aware of only one previously published account of unseasonal perfect flowers in the United States. Greene (1889–90) reported exactly this condition in *Q. agrifolia* Née and *Q. dumosa* Nutt., both from Santa Cruz Island, off the coast of southern California. Although he illustrated this condition of *Q. dumosa* (op. cit., Plate XXVIII), his figure is only a gross depiction of the inflorescences— the hermaphroditic nature of the flowers is not shown at all. It seems worthwhile, therefore, to put on record these instances I have observed and illustrations showing the actual flowers.

There is considerable evidence that the perfect flower represents the ancestral condition in the Fagaceae (Reece, 1938; Tucker, unpubl.), and that typical unisexual flowers represent a derived condition attained through evolutionary reduction—presumably by the accumulation of

gene mutations over a period of time—that ultimately suppressed initiation of the stamens in certain flowers (the pistillate flowers) and initiation of the gynoecium in others (the staminate flowers). But gene action is always expressed against a background of environmental conditions and, considering the readiness with which the "normal" sexual expression of certain flowers can be altered experimentally (e.g., *Cannabis*, Heslop-Harrison, 1959; *Cucurbita*, Nitsch et al., 1952), one can easily visualize similar effects being produced in nature by the infrequent occurrences of unusual environmental conditions. In other words, if an oak (which normally produces only unisexual flowers) were subjected to environmental conditions that differ markedly from the norm at the period of floral initiation and early development, this "latent" potential to produce hermaphroditic flowers might still be realized.

The external factors in the natural environment of foremost importance in floral initiation are usually temperature and light (Hillman, 1962). Any drastic deviation from the norm of mature floral organization (as in the present case) probably reflects some unusual condition in one or both of these factors during floral initiation and early development. However, the presence of normal staminate aments in the same flush of unseasonal growth—indeed, on the same branchlet—indicates that the unusual condition(s) must have affected only the pistillate spikes, producing three gross visible aberrations: (1) a much more elongated axis, (2) many more flowers than normal, and (3) the presence of stamens in some of them (i.e., altering them from pistillate to hermaphroditic).

In the oaks, flowers on the spring flush of growth are initiated the previous year. Thus, in *Q. alba*, Turkel et al. (1955) observed that both staminate and pistillate inflorescences are initiated during the year preceding anthesis, the staminate inflorescences being distinguishable as early as late June. Similarly, Conrad (1900) observed that in winter buds of *Q. velutina* the staminate flowers already had stamens well formed, and the carpels were evident in the pistillate flowers.

The aberrant inflorescences with which we are concerned, however, represent new flushes of growth in late summer, borne on the twigs formed that same spring. The conditions that induced the formation of these atypical inflorescences and flowers must have been operative only two or three months prior to these unseasonal August flowerings.

In my field notes for the *Q. durata* collection, this comment appears: "The unusual out-of-season aments may be correlated with the unseasonal rains of May and June of this year." A check of U.S. weather Bureau records (1941, 1947, 1964) indicates that there was, indeed, unusual precipitation in late spring and/or summer both in 1941 in Ventura County and in 1947 in Marin County. Ozena, in the upper Cuyama Valley in Ventura County—a weather station since 1906—is within a mile of the location of the *Q. turbinella* collection. Kentfield, in Marin County—a weather station since 1888, and the nearest one to the col-

lection site of *Q. durata*—is roughly seven miles (airline) east of the *Q. durata* locality.

Strangely enough, the seasonal precipitation records for these two years and localities were quite different. At the Ozena station, 1941 was an unusually wet year; at the Kentfield station, 1947 was comparatively a very dry year. A major point of similarity, however, may be noted. At Ozena, May was significantly wetter than normal in 1941. Similarly, at Kentfield, June was notably wetter than normal in 1947. These atypically late rains, *after the oaks put out their normal spring flush of growth,* may possibly have triggered this second flush of growth. On the other hand, the initiation and early development of these flowers most likely was the result of some other combination of factors (probably temperature and day length, and perhaps others). Temperature data for 1941 was not available for the Ozena station. Data for Kentfield for 1947, however, indicate temperatures slightly higher than normal during the several months preceding the aberrant flowering of *Q. durata* in August. The monthly mean temperatures for May, June, and July were respectively, 3.4, 3.1, and 1.7 °F above the long term mean monthly temperatures (based on a 51-year record).

Considering these aberrant inflorescences, once again, their most obviously deviant features are (1) their much greater length, and (2) more numerous flowers. Some insight as to the underlying causes may be gained from the study by Turkel et al. (1955), who noted that in the early development of the pistillate inflorescence in *Q. alba* a number of bractlets appear in rapid succession along the primordial inflorescence axis. A flower develops in the axil of each of the lower bractlets, and these flowers become the (one to several) functional pistillate flowers. In addition, however, rudimentary flowers in various stages of development occur at the apex of the axis. Macroscopically, this tip of the axis, with its bractlets and rudimentary flowers, appears merely as a slight continuation above the functional flowers. Also, in *Q. borealis* Michx. f. (*Q. rubra* L.), a member of the black oak subgenus, the primordial pistillate inflorescence contains a number of bracts arranged spirally on the axis, but floral apices form in the axils of only the two (or occasionally one) lowest bracts (Macdonald, 1971).

It seems likely that this early suppression of some of the pistillate flowers is a fairly general feature in *Quercus,* most species of which have short, few-flowered pistillate inflorescences at anthesis. This view gains credence, furthermore, when we consider the fact that a few Mexican and Central American species are *characterized* by elongated, multiflowered pistillate inflorescences (e.g., *Q. rugosa* Née among the white oaks, and *Q. urbanii* Trel. among the black oaks). In the related but generally more primitive genus *Lithocarpus,* elongated, many-flowered inflorescences are common (see Camus, 1948). These facts suggest that in species such as *Q. alba,* or *Q. borealis,* the production of only one or two mature pistillate flowers—when the *potential* for more development

is clearly present—may be the result of growth hormones that suppress this development. If, then, the "normal" auxin regime were upset on rare occasions by a marked change in environmental conditions, perhaps this potential would be realized and ancestral gene combinations still in the code, but long suppressed, would be re-activated to produce not only elongated, multi-flowered inflorescences but hermaphroditic flowers as well. Even so, it appears that it is only the rare individual that is capable of this kind of response, for this aberrant flowering has been observed only in single individuals—not throughout populations. However, fundamental answers to such questions of cause and effect must await further study, and as a subject for experimental morphogenesis this one would be interesting indeed.

LITERATURE CITED

CAMUS, A. 1948. Les chênes. Monographie du genre *Quercus*. Paris. 3 vols. text, 3 vols. atlas, publ. 1934–1954. (Vol. 3 of atlas, which includes plates of *Lithocarpus* spp., publ. 1948).

CONRAD, A. H. 1900. A contribution to the life history of *Quercus*. Bot. Gaz. 29:408–418.

GREENE, E. L. 1889–90. Illustrations of west American oaks. Bosqui Engraving and Printing Co., San Francisco.

HESLOP-HARRISON, J. 1959. Growth substances and flower morphogenesis. Jour. Linn. Soc. London (Botany) 56:269–281.

HILLMAN, W. S. 1962. The physiology of flowering. Holt, Rinehart, and Winston, New York.

MACDONALD, A. D. 1971. Floral development in the Amentiferae. Ph.D. Thesis, McGill University Library, Montreal, Canada.

NITSCH, J. P., E. B. KURTZ, JR., J. L. LIVERMAN, and F. W. WENT. 1952. The development of sex expression in cucurbit flowers. Amer. Jour. Bot. 39:32–43.

REECE, P. C. 1938. The morphology of the flowers and inflorescences of the Fagaceae. Ph.D. Thesis, Cornell University Library, Ithaca, New York.

SCARAMUZZI, F. 1958. Osservazioni su anomalie dei fiori in *Quercus coccifera* L. Nuovo Giorn. Bot. Ital. 45:380–388.

TURKEL, H. S., A. L. REBUCK, and A. R. GROVE, JR. 1955. Floral morphology of white oak. Bull. 593, Penn. State Univ., Agric. Expt. Station.

U.S. DEPT. OF COMMERCE, Weather Bureau: Climatological Data. 1941. Vol. 28:1, U.S. by sections: Alabama–Louisiana; 1947. Vol. 34:1, Ditto.

U.S. DEPT. OF COMMERCE, Weather Bureau. 1964. Climatic summary for the U.S. —Supplement for 1951 through 1960, Pt. 1–10.

NOTES AND NEWS

CYTISUS SCOPARIUS (L.) LINK IN NORTH CENTRAL IDAHO.—*Cytisus scoparius* (L.) Link is a very common adventive, that is well established and spreading rapidly in many places on the w. side of the Cascades, from Calif. to B.C. (Hitchcock, et al. 1961. Vascular Plants of the PNW.; Vol. 3). While the shrub is sometimes cultivated east of the Cascades, previous to this report, it was not known as an escape from there. Several large bushes of Scots broom were observed growing in the wild along the St. Joe River road near the Falls Ck. bridge, Shoshone Co., Idaho (*Layser and Phillips 1441*, WS).—EARLE F. LAYSER, Colville Natl. Forest, Colville, Washington 99114 and H. WAYNE PHILLIPS, Helena Natl. Forest, Helena, Montana 59601.

H. E. BROWN AND THE PLANTS OF THE "NORTH SIDE OF MOUNT SHASTA"

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A number of herbarium sheets in a dozen or more herbaria carry labels printed in blue ink with the legend that the specimens were collected by H. E. Brown on the "North Side of Mount Shasta, Siskiyou County, California". An effort has been made to determine the source of these specimens and the accuracy of the citation.

At first, I was interested in confirming the occurrence of a few more or less commonly cited or obvious records. The work was broadened to discover the extent to which such labeling occurred among the materials Brown collected. In Cooke (1941) I quoted from a letter received from A. A. Heller shortly before his death to the effect that Brown's collections in the area were lumped under Mount Shasta although quite a bit of the collecting was done on Mt. Eddy.

In the files of the library of the New York Botanical Garden is a "List of H. E. Brown's California Plants". Centered above the title on the first of four sheets is the legend "No. 1", possibly in H. E. Brown's handwriting. The list includes 530 species, although the highest number found on one of his labels is 917. According to Lanjouw and Stafleu (1954), Brown collected in "Pacific North America (Chiefly California)". They list eleven herbaria in which Brown collections may be found with the notation that 732 specimens are at NY and 807 are at US. Other herbaria listed include: B, BRSL, E, F, L, MANCH, MIN, MO, and P. A few records are reported to be in the Jepson Herbarium (Bacigalupi, letter), and the California Academy of Science (Howell, 1950). One specimen has been found in the Herbarium of the University of California, Berkeley. Cantelow and Cantelow (1957) gave a brief summary of Brown's activities based largely on my comments (Cooke, 1941).

The list mentioned above is without system, either taxonomic, geographic, or numeric. In a search for herbarium records of these plants, before the list became available, a few sheets were found in the New York Botanical Garden Herbarium. The results of this search were listed in 1941. When the Brown catalogue became available, certain obvious or familiar species were searched for at NY. It was soon apparent that before a useful search could be made the list should be rearranged following the system used in the herbarium in which the specimens were filed. An opportunity to search for additional records was found in December, 1969. At that time, 122 numbers of 118 species representing 73 genera of as many species of Mount Shasta plants were found. This represents records in 23 families, and 22 percent of the entire list. Of these records, 60 percent are from eight locations or dates on Mt. Shasta, 40

percent from several locations in four other California counties, and from several Oregon locations.

At the time of Brown's activities, the north side of the mountain was not as accessible as now. The railroad had not been completed, but the Military Pass road might have been available for foot or even wagon traffic. Assuming that Brown could have reached the base of the north side of the mountain at as low an elevation as 5,000 feet, he would have found a rather dry mountain. At present, if there is surface water from springs, the springs are on the steep walls of Whitney Creek and Bolam Creek canyons whose walls are formed largely of volcanic ash, outcroppings of lava flows, and lava dikes. There are no meadows in the sense of the heather meadows along Squaw Valley Creek and Panther Creek on the south side of the mountain. No wet-meadow type habitats have been observed on several trips to timberline in the Bolam area, on trips to the lava parks above Hotlum, or on trips into the Shasta red fir forest above Andesite.

Brown's Mt. Shasta records are found over at least eight labels. These may be divided into two major groups: "north side" and "south side". Each of the four "north side" labels carries the location: "California Plants Collected North Side Mt. Shasta, Siskiyou Co., by H. E. Brown." They vary as to altitude and date as follows: 1. "Altitude 5000–9000 feet. June 11–16, 1897;" 2. "Altitude 5000–10,000 feet. June 15–30, 1897;" 3. "Altitude 5000–9000 feet. July 1–15, 1897;" and 4. "Altitude 5000–10,000 feet. July 15–31, 1897."

The distribution of habitats in the region today strongly indicates that all species distributed with these labels were collected on the west side of the Sacramento Valley on the east slopes of Mt. Eddy and possibly adjacent mountains and ridges as far south as Castle Lake.

The remaining group of four labels is said to cover plants collected in the vicinity of Mount Shasta. These include: 1. "California Plants Collected near Mt. Shasta, Siskiyou Co. by H. E. Brown. Altitude 6000–7000 feet. June 1–15, 1897." 2. "California Plants Collected Near Sisson, Siskiyou Co. by H. E. Brown. Altitude 3555 feet. June 1-10, 1897." 3. "California Plants, Collected South Side of Mount Shasta, Siskiyou Co., by H. E. Brown. Altitude 5000–10,000 feet. July 1–15, 1897." 4. Same as (3) but dated: "July 15–31, 1897."

Probably it is no longer possible to determine the extent of Brown's travels in the Mt. Shasta area. It has been suggested that he worked in a store in Sisson (now the city of Mount Shasta). A few of the plants with these labels can be found today on the lower slopes of Mt. Shasta and in Strawberry Valley, the general area dominated by the community that used to be known as Sisson. However, most of the plants mounted over these labels occur in the lower valleys of the headwaters region of the Sacramento River and on the eastern slopes of the adjacent mountains of the Klamath Mountains such as Mt. Eddy and the ridges south to Castle Lake.

On the basis of lists obtained from specimens seen at NY, of the Heller letter cited above, and of my collecting trips on Mt. Shasta and observations in the Klamath Province, it is suggested that: 1. Brown never visited the "North Side of Mt. Shasta". The plants so labeled were probably collected in the Wagon Creek drainage of the east side of Mt. Eddy, directly across the valley and west of Mt. Shasta. 2. Some of the plants labeled as collected between 6000–7000 feet "near Mount Shasta" may have been collected on Mt. Shasta, but were probably collected on Mt. Eddy, especially if the altitude is cited correctly. 3. Of the plants collected "near Sisson", most were probably collected on the west side of the Upper Sacramento and Wagon Creek valleys. 4. Of the plants collected "south side of Mt. Shasta", some could have been collected between Sisson (now the city of Mount Shasta) and Wagon Camp, the location the Merriam Expedition chose as a base during the period from July 15 to Oct. 1 in the following year (1898). However, many of the species on Brown's list have not been seen in the area since Brown is supposed to have made his collections. Miss Wilkins and the botanical collectors of the Merriam Expedition made a very thorough survey of the species found in the area in which the expedition was based (Wagon Camp is at 5700 feet), that is, Wagon Camp and related areas.

On the basis of the information presented here, it is suggested than monographers be exceedingly careful about the citation of a plant collected by H. E. Brown "on Mount Shasta". It is entirely possible that the specimen was collected elsewhere. This could have been in the neighboring mountains, especially in the Wagon Creek drainage on Mount Eddy.

LITERATURE CITED

BROWN, H. E., undated. List of H. E. Brown's California plants. Privately printed, filed in the library of the New York Botanical Garden.

CANTELOW, E. D. and H. C. CANTELOW, 1957. Biographical notes on persons in whose honor Miss Eastwood named plants. Leafl. West. Bot. 8:83–101.

COOKE, W. B., 1941. First supplement to the flora of Mount Shasta. Amer. Midl. Nat. 26(1):74–84.

HOWELL, J. T., 1950. Plant types in the herbarium of the California Academy of Sciences. V. Wassmann Jour. of Biol. 8:251–254.

LANJOUW, J. and F. A. STAFLEU, 1954. Index herbariorum. Part II. Collectors. First installment A-D. Regnum Vegetabile 2:1–174.

MERRIAM, C. H., 1899. Results of a biological survey of Mount Shasta, California. North American Fauna 16:1–179.

NOTES AND NEWS

AVAILABILITY OF BAKER'S LIST OF SEED PLANTS.—Milo S. Baker's "A Partial List of Seed Plants of the North Coast Ranges of California" has been re-issued and is available by mail ($2.44 including tax and mailing charge) from either the Santa Rosa Junior College Bookstore, 1501 Mendocino Avenue, Santa Rosa, California 95401, or the Sonoma State College Bookstore, 1801 East Cotati Avenue, Rohnert Park, California 94928.

NOTES AND NEWS

T<small>RANSFER OF THE</small> N<small>ORTH</small> C<small>OAST</small> H<small>ERBARIUM</small>.—The collections of Milo S. Baker, numbering in excess of 15,000 unmounted specimens, have been donated to Sonoma State College by the Trustees of the Santa Rosa Community College. To date about 20% of the Baker collection, constituting the whole of the Compositae and a portion of the Gramineae, has been mounted with completion projected into early 1973. The name, North Coast Herbarium of California (NCC), as listed in *Index Herbariorum* will be maintained and henceforth will apply to the combined collections at Sonoma State College. Space for study is somewhat limited but definitely available and the welcome mat is out! Inquiry regarding loans should be addressed to Prof. Charles Quibell, Curator North Coast Herbarium, Department of Biology, Sonoma State College, Rohnert Park, California 94928.

A N<small>EW</small> C<small>OMBINATION AND A</small> N<small>EW</small> N<small>AME IN</small> H<small>ACKELIA</small> (B<small>ORAGINACEAE</small>).—My recently completed study of certain North American species of *Hackelia* necessitates some nomenclatural changes. It is unfortunate when a well established name, especially of a wide ranging species such as *Hackelia jessicae* (McGregor) Brand, has to be replaced by an earlier and unfamiliar one.

Hackelia micrantha (Eastwood) J. L. Gentry, comb. nov.
Lappula micrantha Eastwood, Bull. Torrey Bot. Club 30:497. 1903. *Hackelia eastwoodae* I. M. Johnston, Contr. Gray Herb. n.s. 68:47. 1923. nom. superfl.
Lappula macilenta Greene ex Baker, W. Amer. Pl. 1:18. 1902. nom. nud.
Lappula jessicae McGregor, Bull. Torrey Bot. Club 37:262. 1910. *Hackelia jessicae* Brand, Pflanzenr. IV. 252 (Heft 97):132. 1931. *Lappula floribunda* var. *jessicae* Jepson & Hoover in Jepson, Fl. Calif. 3:307. 1943.

Johnston in his publication on the restoration of the genus *Hackelia* (Contr. Gray Herb. n.s. 68: 43–48. 1923) proposed a new name, *H. eastwoodae* I. M. Johnst., because he thought that a homonym would be introduced if he transferred *Lappula micrantha* Eastw. to *Hackelia. Lappula micrantha* Eastw., not *H. micrantha* (Ledeb.) Opiz, is listed as the synonym of *H. eastwoodae* by him. However, the specific epithet in Ledebour's original description (Ledebour, C. F. 1829. Flora Altaica. 1:205. Berlin) and in the transfer by Opiz (Opiz, P. M. 1839. *In:* F. Berchtold, Oekonomisch-technische Flora Böhmens 2(2):146. Prague) is spelled m*a*crantha, not m*i*crantha as in the paper by Johnston. He apparently confused micrantha and macrantha. The name, *H. eastwoodae,* is illegitimate and must be rejected because it was nomenclaturally superfluous when published and it does not have priority over *H. jessicae.* Therefore the name, *H. micrantha* (Eastw.) J. L. Gentry, must be applied to the species previously known as *H. jessicae.*
    The Opiz combination, *H. macrantha* (Ledeb.) Opiz, does not appear in Index Kewensis. The basionym, *Echinosperum macranthum* Ledeb., is associated with a Central Asian species of *Lappula: L. macrantha* (Ledeb.) Gurke.
    My study has also confirmed the specific distinctiveness of the following species.

Hackelia cronquistii J. L. Gentry, nom. nov.
H. patens var. *semiglabra* Cronq. Leafl. W. Bot. 10: 39. 1963.

It is with much pleasure that this species is named for my mentor, Dr. Arthur Cronquist, who first pointed out the salient features of this species and who was the collector of the type specimen.
    These nomenclatural changes are published here to make them available for use in the forthcoming publication by C. L. Hitchcock and Arthur Cronquist, *Flora of the Pacific Northwest—An Illustrated Manual.*—J<small>OHNNIE</small> L. G<small>ENTRY</small>, J<small>R.</small>, Department of Botany, Field Museum of Natural History, Chicago, Illinois 60605.

New Distributional Records for Plants in the Pacific Northwest.—The extreme northeastern corner of Washington offers a great deal that is of interest to a botanist. In that area, the Rocky Mountain flora meets a notable southward extension of boreal elements, and imposed upon both of these is the interior wet belt with its coastal floristic components. The merging of these elements is reflected by a complex and diverse flora. Yet, with only a few exceptions and the author's investigations, this is a place that has been botanized but little. Plant collecting from this locality, in connection with an ongoing floristic study of Pend Oreille County, has continued to yield new distributional records and rare plants (Andrus, R. E. and E. F. Layser, *Sphagnum riparium* Ångstr. a new record for the western U.S. Bryologist 74: 211, 1971; Layser, E. F., A floristic study of Pend Oreille County, Washington. M.S. thesis, State Univ. New York College of Forestry, 1969; Layser, E. F., Notes on the flora of the Pacific Northwest, Madroño 21: 47–48, 1971). Summarized herewith are recent finds deserving mention:

Carex aenea Fern.   C. L. Hitchcock et al. (Vascular plants of the Pacific Northwest, Pt. 1, Univ. of Washington Press, 1969) state that this plant is "seldom collected in our range". Previously known from s. e. B. C., w. Mont. and Fremont Co., Idaho. It is new for Washington, *Layser 1247* (BH, WS), Sullivan Lk. (s. end), Pend Oreille Co.

C. buxbaumii Wahl. is reportedly a "widespread, but relatively uncommon and infrequently collected" species (Hitchcock et al. op. cit.). F. J. Hermann (Manual of the Carices of the Rocky Mountains and Colorado Basin, U.S.D.A. Handbook No. 374, 1970) considers the plant as "very local" in occurrence. *Layser 1828* (BH, WS, WTU), Lk. Thomas, Stevens Co.; *Layser 1840* (BH, WS), Diamond Lk., better Lk., Pend reille Co.

C. flava L. was reported from Mont., c. Idaho and s. B.C. in the Pacific Northwest (Hitchcock et al. op. cit.). It is here reported as new for the state of Washington. *Layser 1234* (BH, WS), Ledbetter Lk., Pend Oreille Co.

C. lasiocarpa Ehrh. var. *americana* Fern. was known from the Cascade Mts. in s. Wash., and from n. Idaho and w. Mont. (Hitchcock et al. op. cit.). This report constitutes the second station for the plant inWash. *Layser 1239* (BH, WS), Ledbetter Lk., Pend Oreille Co.

Delphinium glaucum Wats. is reported here as a disjunct occurrence of the species. Previously, the plant was known only from the Olympic and c. to s. Cascade Mts. (Hitchcock et al. op. cit., Pt. 2, 1964). *Layser 1814* (WS, WTU), Sherman Peak, Ferry Co.

Gaultheria hispidula (L.) Muhl. is known from "Labrador w. to B.C. s. into n. Idaho" (Hitchcock et al. op. cit., Pt. 4, 1959). It is reported here as an addition to Washington's flora. *Layser 1786* (BH, WS, WTU), Sema Meadows, Pend Oreille Co.

Hypericum majus (Gray) Britt. prior to this report was apparently represented from the Pacific Northwest by a single collection at Green Lake, near Seattle, that was made in 1891 (Hitchcock et al. op. cit., Pt. 3, 1961; C. V. Piper, Flora of the state of Washington, Contributions U.S. Natl. Herbarium Vol. XI, U.S. Govt. Print Office, 1906). *Layser 1797* (WS, WTU), Diamond Lk., Pend Oreille Co.

Muhlenbergia glomerata (Willd.) Trin.   Hitchcock et al. (op. cit. 1969) state, "the plant is rather rare; I have seen only one specimen from Wash. and none from Oregon, and it is not at all common in n. Idaho and W. Mont." *Layser 1784* (WS, WTU), Diamond Lk., Pend Oreille Co.

Nymphaea tetragona Georgi is noted by Hitchcock et al. (op. cit. 1964) to be "very rare in our area, where known from one station in Idaho and from . . . Whatcom Co., Wash." It is here recorded from Huff Lk., Pend Oreille Co. *Layser 1651* (WS).

Sagittaria subulata (L.) Buch. was previously known only from Thurston Co., Wash. in our area (Hitchcock et al. op. cit. 1964). This report constitutes a second station for the species in the Pacific Northwest. *Layser 1763* (WS, WTU), Lk. Thomas, Stevens Co.

Sanicula marilandica L.   Hitchcock et al. (op. cit. 1961) note the plant is known from "e. B.C., n. Idaho and probably extreme n.e. Wash." in our area. This confirms the species occurrence in Wash. *Layser 1667* (WS), NE¼ Sec. 3, T40N, R43E., Pend Oreille Co.—EARLE F. LAYSER, Colville, Natl. Forest, Colville, Wash. 99114.

REVIEWS

Wild Flowers of the United States. By H. W. RICKETT. Volume 5, The Northwestern States, 2 pts., 666 pp., illus. McGraw-Hill Book Co., New York. $57.50.

The most recent volume of this much-heralded series encompasses the Northwestern States, which are rather curiously interpreted to include not only western Washington and Oregon, but "California southward to the deserts". The present volume (in two parts) is the fifth in the series to be issued; only the Rocky Mountain region remains to be covered. The rather sumptuous production has had the generous financial backing of the National Committee for the Wild Flowers of the United States, headed by Mrs. David Rockefeller. The "wild flowers" of the title are all herbaceous; woody plants are omitted. Cacti are only sparingly treated, and "unattractive plants with small green flowers unlikely to attract the amateur" are also omitted. Even after this pruning, approximately 3,000 species are mentioned in the work.

The first pages of part one deal with such topics as the names of wild flowers; the morphology of flowers, fruits, and vegetative parts; and plant identification. There is a brief section aimed at discouraging amateurs from transplanting wildlings to their gardens. Next are a guide to the families represented in the book and an illustrated glossary. The main portion of the work is devoted to a family-by-family account of "northwestern" wild flowers, beginning with the Liliaceae. Each family is described very briefly, and there is a key-like guide to its genera. Following this is a generic account of the family, which is accompanied by color photographs illustrating various of the species that are discussed in the text. The species are very simply and briefly described and technical terminology is kept to a minimum.

Because I am a professional systematist, it is difficult to give a balanced appraisal of a work designed for the amateur. Not so many years ago, however, my only means of identifying wild flowers was by leafing through the few "popular" books available for western species and by linking drawings or photographs with the specimens in hand. Surely Rickett's series has provided a very elegant and—unfortunately—expensive means for interested amateurs to do the same thing almost anywhere in the United States. Any publication that enhances public interest in the native flora is to be applauded.

Nevertheless, the two parts covering most of the immediate Pacific Coast of the United States are not without deficiencies, botanical and otherwise. The composition and overall artistic quality of the photographs range from excellent to very poor, although in general the color rendition is good (a notable exception is the lurid photograph of *Centranthus ruber*). Examples of photographs of doubtful utility for the amateur are those of *Thalictrum occidentale, Romanzoffia suksdorfii,* and *Anthemis arvensis,* which illustrate little of assistance in naming these plants and are fulsome as well. A scale is unfortunately missing from all photographs, so that the flower of *Myosurus minimus* (which qualifies as one of those omittable "unattractive plants with small green flowers") is seemingly equal in size to that of *Nuphar polysepala.* I also question the desirability of illustrating several species of a genus when the distinguishing characters of the rather similar species are not evident from the photographs. For example, five yellow-flowered leafy-stemmed

oxalises are illustrated; I think it is virtually impossible to tell one from the other by the photographs. In this instance (to paraphrase a local politician), when you've seen one, you've seen 'em all. Also, I find it hard to believe that the photograph of *"Oxalis repens"* (listed as such, though the text states that "the correct name of this species is *O. corniculata*") is really that species; the size of the flowers relative to the leaves is excessive. I also doubt that the plethora of photographs of blue delphiniums will aid in their identification. Had photographs been used more economically, the price of the book accordingly could have been reduced. The book would be more easily used if a page reference to the textual discussion of each illustrated species were listed in the legend for each photograph, since in many instances the photographs and the description are separated by several pages. Another problem associated with the illustrations is the distribution of photographs of one genus into two or more plates where they are mixed with other genera; for example, *Campanula* appears in two plates, both of which also illustrate genera of other families. Likewise, the species of *Convolvulus* are relegated to two plates, which they occupy with other genera. Such an arrangement makes comparisons within a genus difficult. The concordance in detail between the text discussions and the illustrations generally is good. However, *Blennosperma nanum* is described as having yellow rays, which it typically does, but the single plant illustrated is the rather rare white-rayed form!

The photographs are mostly ones that have been taken in nature; however, the unesthetic courtyard of the Life Sciences Building on the Berkeley campus disfigures the background of at least one photograph (a potted *Limnanthes gracilis*) and one somehow suspects that the University of Washington greenhouse lurks behind the cloth backdrop to *Streptanthus glandulosus*. The fact that the locale for some of the photographs is not within the geographic area circumscribed by the book's title is indicated by an occasional unexpected fellow-traveller that appears in the photographs; for example, the eastern *Orontium aquaticum* ornaments the illustration of *Menyanthes trifoliata*.

The accuracy of identification seems to be quite good, though my colleagues have pointed out a few bloopers. California's pre-eminent weed specialist, T. C. Fuller, suggests that the illustration labeled *Centaurea jacea* is more likely that of *C. cyaneus;* that the illustration of *C. solstitialis* is really *C. melitensis* and vice versa; that the photograph labeled *Cirsium occidentale* is one of *C. pastoris;* and that the *Cirsium edule* is *C. nutans.* W. F. Hinton insists that *Eriogonum pyrolae-folium* is really *Calyptridium umbellatum.* R. C. Bacigalupi notes that the illustrations of *Lithophragma affine* and *L. parviflorum* are more correctly *L. hetero-phylla* and *L. tenella* respectively, and that *Saxifraga occidentalis* should be labeled *S. ferruginea.* His concern over the identification of *Downingia elegans* is understandable; it is *D. bacigalupii.*

I have also noted a few errors of fact. For example, *Bensonia* (= *Bensoniella*) *oregana* is said to grow "only in the mountains of southwestern Oregon". This mistake is understandable; although the genus has long been known from California, it was not included in Munz' 1959 *A California Flora* (although it did appear in the later Supplement). The occurrence of *Anemopsis californica* in southern Oregon is also overlooked. Another problem is the lack of an index at the end of part one, and in the index in part 2 there is no indication which part is referred to by the pagination.

Many of the drawbacks pointed out in the preceding discussion will not reduce the general utility of the work to the amateur audience for which it is intended. I question how widely such an expensive book will be used, although I understand that a series of smaller, less costly books will be abstracted from the present more comprehensive volume. All in all, this publication is an impressive work, a pleasure to the eye, and it should go a long way toward stimulating an interest in wild flowers on the part of the residents of the Far West who have yet fully to appreciate the riches of the natural world around them.—ROBERT ORNDUFF, Department of Botany, University of California, Berkeley 94720.

Annual Review of Ecology and Systematics. By RICHARD F. JOHNSTON, PETER W. FRANK, and CHARLES D. MICHENER, Eds. Vol. 1, 1970. ix + 406 pp. Annual Reviews Inc., Palo Alto. $10.

The Annual Reviews of Plant Physiology, Genetics, Entomology, and other fields of science are familiar to most of us. These apparently successful presentations are now to be joined by the Annual Review of Ecology and Systematics. The first volume of this new series was prepared under the editorial leadership of 5 animal ecologists, 2 plant ecologists, and 1 systematic entomologist. Therefore, the resulting poor emphasis on plant systematics should come as no surprise.

The first question to cross the mind of many readers of this volume will be: why? The diffuse and complicated field of ecology is immediately apparent to anyone who pages through the bulk of the journal, *Ecology.* The vast assemblage of subjects in this field does not present the cohesive units that characterize, for example, the major fields of plant physiology. Therefore, an annual review of ecology, by itself, would appear to be an almost unreachable objective. This judgment is borne out in the content of the first volume which includes 15 papers covering topics on philosophy, population genetics, anthropology, and endogenous rhythms as well as on plant ecology (4 papers), animal ecology (3 papers), plant systematics (3 papers), and animal systematics (1 paper).

Papers on plant systematics include: "Analysis of character variation in ecology and systematics", by Theodore J. Crovello; "Chemosystematics and ecology of lichen-forming fungi", by William Louis Culberson; and "The shapes and sizes of seeds", by J. L. Harper, P. H. Lovell, and K. G. Moore.

Crovello addresses his topic to those who wish to adapt ecological and systematic information to computer technology. It doubtless will be helpful to workers in that field. However, your reviewer is somewhat puzzled by a paper carrying this title but which fails to mention (among the 286 literature citations) such exemplary character variation studies as those of Woodson on *Asclepias,* or of Hall on *Juniperus.* It is amazing that a paper on this subject directs no comment to the various genetic systems, such as additive genes, epistatic genes, and complementary genes that regulate character expressions and variation. On the other hand, the author carefully emphasizes the obvious importance of punching the data cards by a compatible system for the rapid pooling and extraction of information.

The Culberson paper is only marginally systematic. In 16 pages it gives a good morphological, ecological, and chemosystematic treatise of lichens, one that would be most helpful in developing lecture material for a survey course on the non-vascular plants.

The paper by Harper, Lovell, and Moore is far more than an essay on the sizes and shapes of seeds. The topic is discussed in terms of seed production, genotypic control of seed size and shape, seed polymorphism, and ecological aspects of seed size and shape. In view of the highly significant but often neglected relationships that seeds have to evolution and systematics, this paper must be viewed as a useful contribution. It is supported by an impressive array of 117 literature citations.

It may well be that the most significant paper in this volume is "The units of selection" by R. C. Lewontin, who presents an erudite discussion of the selection of molecules, organelles, cells, gametes, individuals, and populations. One wonders why this paper could not have been included in the Annual Review of Genetics.

Hopefully, future volumes of this series will include such subjects as character displacement, protein electrophoresis, scanning electron microscopy, modern studies of pollen morphology, and other topics of pertinent systematic interest. However, the reviewer's unhappy conclusion is that the first volume will appeal primarily to ecological bibliophiles who think in terms of an unbroken set of the series rather than of selective, qualitative considerations. Good review papers involve much labor and time. It is to be hoped that the editors of this series will be able to accomplish the necessary planning and sufficiently advanced commitments to provide these vital requisites for a successful and meaningful series.—GEORGE W. GILLETT, Department of Biology, University of California, Riverside 92502.

World Vegetation Types. By S. R. EYRE, ed. 264 pp. Columbia University Press, New York. 1971. $12.50.

This is an anthology of papers, or rather of parts of papers and books by 21 recognized authorities in the field of vegetation. The editor points out in his forewcrd that his first aim has been to present a set of studies that are fairly representative of those main types of wild vegetation that, until recently, covered much of the land area of the earth; the second has been to include only that kind of work that takes cognisance of ecological status and vegetation development. These goals are not entirely reached as some of the papers contain nothing significant on ecology or community dynamics, and some major types of vegetation are ignored altogether, e.g. broad-leaved deciduous forests.

To prepare an anthology is a thankless job as readers are quick to miss their favorite works but this is inevitable, especially if the entire selection must be as limited as in this little volume. Nevertheless, the choice does not always appear to be the best. Thus the brief excerpt from Carl Sauer surely represents his less inspired writings when he concludes that grasslands "are an impoverished assemblage, not a fully developed organic household or community". If the editor meant to select writings which, in the main, attempt the functions of both description and interpretation, as he claims in the introduction, then the choice of Weaver and Albertson's "The Origin of the Mixed Prairie" is baffling as both authors have given such excellent descriptions of various prairie types.

However, the editor succeeded in presenting a variety of publications by some of the most illustrious authorities on vegetation, and some of the papers, as those by Richards, Beard, Keay, Jackson, Hastings and Turner, Keller, and Polunin permit a real insight into the nature of the formations they discuss. Other papers are often of the same quality although more limited in scope, e.g. those by Aubréville, Weaver and Clements, Cockayne, Cooper, Robbins, and others.

A comprehensive treatment of the vegetation of any area includes a discussion of structure, floristic composition, community dynamics, and ecological features. In this anthology, none of the authors treats the vegetation of their respective areas in such a comprehensive fashion. This may be due to their personal inclinations or to the fact that the presentations are, after all, only brief excerpts. The reader should therefore not expect a very systematic treatment of the various vegetation types. One the other hand, the combination of the papers by Richards, Beard and Aubréville on the rain forests of tropical lowlands does give him an excellent understanding of the nature and the complexities of this formation. The attempt to produce a similar effect by a combination of grassland papers is less successful.

The value of this anthology lies perhaps not so much in what it sets out to achive. It seems to lie rather in the fact that it illustrates a great variety of approaches to the study of vegetation. Thus, an author embarking on the investigation of a particular vegetation type may profit considerably from studying this anthology in order to assure a comprehensive and well organized presentation.

The book has a small set of illustrations, taken from the original works. Perhaps this is the natural and right thing to do. But it means that the illustrations for this anthology must be taken from printed versions, and this has distinct drawbacks, especially with regard to the technicalities of reproduction. Considering the superb photographs now available of so many vegetation types, one wonders whether it might not have been desirable to replace the old pictures with fresh and more effective ones. But this may not have been feasible.

The book closes with a selected bibliography of nine pages, concerning only the discussed vegetation types. It is a stimulating book and should be particularly useful as supplementary reading in university courses on vegetation.—A. W. KÜCHLER, Department of Geography, University of Kansas, Lawrence 66044.

The Biology of Parasitic Flowering Plants. By JOB KUIJT. 246 pp., 176 figs. and photographs. University of California Press, Berkeley. 1969. $15.00.

This masterly treatise brings together significant information on parasitic flowering plants from a vast and scattered literature—the first serious attempt to describe and compare the various modes of parasitism and plant structure in all eight unrelated groups of dicotyledons in which parasitism is found. Kuijt proposes that parasitism has arisen independently in each of these groups: (1) Santalales, (2) Scrophulariaceae (tribe Rhinantheae), (3) Rafflesiaceae and Hydnoraceae, (4) Balanophoraceae, (5) *Cuscuta,* (6) *Cassytha,* (7) Lennoaceae, (8) *Krameria.* Each group is treated in monographic fashion with a scholarly discussion of such pertinent aspects as general habit and nature of the plants, flowers, pollination, embryoylogy, fruits and seeds, dispersal methods, and mode of parasitism, all of which are illustrated with an abundance of excellent drawings by the author and photographs. In addition, there is a valuable discussion of the phylogenetic relationships of each group often supplemented by original comments and observations. The introductory chapter traces the historical development of man's awareness of parasitism and presents a fascinating account of the role of parasitic plants in medicine, magic, folklore, and commerce. It is interesting to read of the historical appreciation of sandalwood (*Santalum* spp.) and to learn how its sale led to the rise of the Hawaiian monarchy of King Kamehameha and to the virtual destruction of the magnificent Hawaiian groves of *S. freycinetianum.* An entire chapter is devoted to a description of the various haustorial connections and the intricacies of their development. This chapter is superbly illustrated, showing the artist Kuijt at his best. Another chapter on the physiological aspects of parasitism is probably more abbreviated (15 pages) than those who are ecologically or physiologically oriented would prefer, but such aspects as germination, nutrition and water economy, effects on host, and host specificity are thoroughly summarized. Kuijt criticizes the use of the terms "facultative" and "obligate" (in referring to green parasites of the family Scrophulariaceae) as having little meaning since plants that are facultative under the ideal conditions of cultivation are always obligate parasites in nature. This is doubtless true but his further argument that *Cuscuta* can also complete its life cycle when supplied a nutrient medium hardly seems pertinent. Kuijt, in rejecting these terms and the concepts they represent, fails to consider the usefulness of the terminology for indicating an evolutionary degree of parasitism in the Rhinanthoid Scrophulariaceae. Certainly, green parasites that are (facultatively) able to complete their life cycle without a host even under greenhouse conditions are less advanced down the road toward parasitism than the plants that (obligately) must have a host (or its equivalent nutritional medium) present. The last chapter on evolutionary aspects speculates on the origin and evolution of the haustorial connection and considers the evolutionary modifications, often highly reduced and not infrequently quite bizarre, that the parasites have undergone.

In spite of the huge amount of material that has been summarized for this treatise, one is impressed by some of the large gaps in our knowledge of parasitic plants, especially in such groups as Rafflesiaceae, Hydnoraceae, and Balanophoraceae, and Kuijt is careful to point out those areas where even basic information is lacking. It would be well for those botanists who have these plants accessible to note those cases where they could supply original and useful observations.

This book, of quarto size with double column format, is a particularly handsome one and the author and the University of California Press are to be congratulated on their achievement.—LAWRENCE R. HECKARD, Jepson Herbarium, University of California, Berkeley 94720.

Flora of the Australian Capital Territory. By NANCY T. BURBIDGE and MAX GRAY.
447 pp. Australian National University Press, Canberra. 1970. $12 (Australian)
[Available in US from International Scholarly Book Services, Box 4347, Portland,
Oregon 97208. $14.30]

The Australian Capital Territory, an area of some 940 square miles which in-
cludes the capital city of Canberra, forms part of the eastern Australian tablelands
and is an enclave in southeastern New South Wales. Its latitude is closely com-
parable with that of the highest peaks of the Sierra Nevada but Australia's moun-
tains scarcely attain half the altitude of the Californian summits. It therefore may
come as a surprise to find well-developed alpine herbfields on several mountain areas
in Australia, in particular above a tree-line at c. 1850m at Mt. Kosciusko. The
highest ranges in the Capital Territory (to 1920m) are only some 50 miles north
of the Kosciusko plateau and just reach tree-line conditions. The predominant vege-
tation is *Eucalyptus* forest and woodland, with subalpine heaths and bogs included
at the upper altitudes, and with grasslands in the lower and drier parts.

The location, altitude, and prevailing soils exclude many of the vegetation types
which most commonly come to mind as distinctively Australian. The semi-desert
shrub-lands of the arid interior, the species-rich heaths which characterize sands of
the southwest and the east coast of the continent, and the rainforests of the north-
east must all be sought elsewhere.

Among the 1324 species included in this Flora (of which 289 are naturalized)
grasses form the largest component with 67 genera. Excellent line drawings by
Dr. Burbidge illustrate about one third of the species and represent most genera.
The keys appear very satisfactory and the descriptions are quite detailed. The
authors have investigated many critical groups rather than merely presenting a
compilation of existing information. Of particular value are the brief ecological
characterizations of each species, the comments on unresolved taxonomic problems,
and the inclusion in the keys of species as yet unnamed. A valuable bibliography
gives reference to relevant modern works; a glossary, vegetation map and brief
notes on the region are also included.

This excellent and attractively presented Flora will be useful throughout the
southeastern Australian tableland areas. I recommend it highly for any library
which aims at including major works on the Australian flora.—BARBARA G. BRIGGS,
National Herbarium of New South Wales, Royal Botanic Gardens, Sydney,
Australia.

Cacti of the Southwest --Texas, New Mexico, Oklahoma, Arkansas, and Louisiana.
By DEL WENIGER. xvi + 249 pp., 64 color plates. University of Texas Press,
Austin. n. d. (9 July 1970). $25.00.

One cannot help but be impressed with Mr. Weniger's detailed accounts of his
collections and observations of cacti presented in this book. He manifests a keen
understanding of the combinations of characteristics that separate natural groups,
and his descriptions and comments on these taxonomic factors along with discus-
sion of ecological parameters comprise what could have been a real contribution to
the study of cacti. It is therefore almost tragic that such a potentially great book
instead should be an enigma. Beginning with the title and continuing throughout
the book there occur many peculiarities and questions. Why call a book *Cacti of
the Southwest* when it deals with the South Central States? Why is there no date
on the title page? Why are there proposed 2 new specific epithets, 15 recombina-
tions at the species level and 21 recombinations at the variety level only to have
them become invalid, *nomina nuda* because of the lack of proper Latin descriptions
and references to basionyms? Why are there no literature citations? Why are there
no scientific data or references presented to support statements such as "results of
our own chromatographic studies seem important here" in aligning genera? For
whom is this book intended? One supposes that it would be particularly appealing

to the amateur cactophile and to the lay public in general, mainly because of the 185 beautiful color photographs, one for every taxon described. Yet the text becomes too involved with descriptions and relatively sophisticated academic questions relating to interpretations of the International Code of Botanical Nomenclature for the average reader. It is certainly not acceptable as a scientific publication for obvious reasons. Mr. Weniger states that the material presented in his book "is much simplified and rendered as nontechnical as possible". This should not excuse him from following certain prescribed and generally accepted rules and terms in presenting biological information. For example roses of the West Indies did not change "in order to adapt to more arid conditions"; pereskias are not primitive but rather have retained primitive characteristics; Engelmann is not abbreviated Eng. but instead Engelm.; generic names are not capitalized when used in a generalized sense, e.g., opuntias; and cacti are spiny not thorny.

The field of cactology is in dire need of thorough and detailed systematic studies of the family. Mr. Weniger has demonstrated real ability in his exceptionally clear and interesting writing style, his expert photography and his insight in the biology of cacti. We look forward to contributions he may make in the scientific literature.— DAVID L. WALKINGTON, Department of Biology, California State University, Fullerton 92634.

MADROÑO

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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

A FLORISTIC STUDY OF POINT ARENA,
MENDOCINO COUNTY, CALIFORNIA

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In 1967 the Pacific Gas and Electric Company (PG&E) decided that a botanical survey should be made of the site of their proposed generating plant on Point Arena, Mendocino Co., California. The primary purpose of the study was to determine whether any rare species were present. In 1967 three collecting trips were made to Point Arena and in 1968 five more trips. Most of our work was concentrated on PG&E's property, but a quick survey of the entire point demonstrated that PG&E property contained a nearly complete flora of the whole point except for the species of the brush-covered north-facing slopes on the north side of the peninsula. In addition a few common natives were found on the ungrazed lands near the lighthouse.

The PG&E property on Point Arena contains approximately 1000 acres. It is bounded on two sides by ocean bluffs and on the landward sides is surrounded by adjacent areas of the point where the terrain and flora are continuations of the terrain and flora of the study site. Aside from the spectacular rock formations of the ocean bluffs this is not, at first glance, a biologically prepossessing area. The main topographic features are two marine terraces, one with an altitude of 40–80 feet above sea level and the other with an altitude of 200 feet. These terraces are separated by a short steep slope with a few small outcroppings of siliceous shale of the Miocene Monterey Formation. On the lower terrace there are several vernal pools at the base of the steep slope, while the northeast end of the terrace has a large swampy area with a grove of dwarfed *Pinus muricata*. The upper terrace contains a large swampy vernal pool as well as several small swampy areas near the top of the slope separating the two marine terraces. Two small streams arise in the swamps of the upper terrace and flow towards the north while a third small stream rises in the swampy areas of the lower terrace and flows west into the ocean.

The presence in this small area with its relatively uniform topography of many microhabitats produced by streams, swamps, and vernal pools, as well as ocean bluffs, siliceous shale outcrops, and variations in the thickness of the soil on the marine terraces, results in the presence of an unexpectedly large number of taxa: 205 species and subspecies (or varieties) distributed in 145 genera and 63 families were collected on this site. Since there has been overgrazing by sheep as well as intermittent grazing by

horses and dairy cows, many of the species are uncommon and some were undoubtedly missed. It is anticipated that with removal of the sheep in 1970 these infrequent species will become more common. In addition the composition of the weedy element can be expected to change radically while the native species that occur in the ungrazed areas nearby can be expected gradually to invade the study area. The removal of the sheep will also result in the recovery of the severely pruned North Coastal Scrub Community whose remains are common on the upper marine terrace.

The abandoned farmyard, surrounded by windbreaks of *Cupressus macrocarpa*, naturalized cultigens, and barnyard weeds was not included in this study.

Eight plant communities are recognized on this site:

1. Coastal bluff. This floral element has been severely damaged by sheep and most of the individuals are restricted to inaccessible places. A few of the species were not collectible and could not be identified and hence do not appear on the plant list. Most of the bluff species are members of the widespread ocean bluff flora of northern California: *Erigeron glauca, Dudleya farinosa, Eriophyllum staechadifolium, Allium dichlamydeum,* and *Lupinus variicolor.*

2. The overgrazed grassland just back of the coastal bluffs was rich in depauperate individuals of species that are not, even under ideal circumstances, very tall: *Microseris bigelovii, Cicendia quadrangularis, Sagina occidentalis,* and *Eryngium armatum.*

3. The vernal pools and swampy areas of the lower marine terrace, except for the swamps of the pygmy forest, tend to be poor in species: *Ranunculus flammula* var. *ovalis, Chrysanthemum leucanthemum,* and *Eleocharis acicularis.*

4. The pygmy pine forest is rich in shrubby species and perennial herbs: *Ledum glandulosum* var. *columbianum, Vaccinium ovatum, Gaultheria shallon, Erigeron supplex, Aster chilensis, A. subspicatus, Iris douglasiana, Camassia quamash, Lilium maritimum, Gentiana sceptrum, Castilleja latifolia,* and many others.

5. The siliceous shale outcrops of the slope are distinguished by the presence of species not found elsewhere: *Clarkia* sp., *Brodiaea coronaria* var. *macropoda, B. laxa, B. peduncularis, Corethrogyne californica* var. *obovata,* and *Lupinus bicolor* ssp. *umbellatus. Clarkia* was never found while in bloom and the *Corethrogyne* was extremely prostrate, except for its erect peduncles.

6. The vernal pools on the upper terrace near Highway 1 were rich in typical vernal pool species: *Isoetes howellii,* which was rare, *Lythrum hyssopifolia, Eryngium armatum, Oenanthe sarmentosa, Allocarya bracteata, A. reticulata* var. *rossianorum, Galium trifidum* ssp. *subbiflorum, Centunculus minimus, Veronica scutellata,* and *V. americana.*

7. The swamps bordering the two north-flowing streams, especially the one originating in the vernal pools of the upper terrace, also possess

many species. The latter has a dense shrub and low tree growth as well as many ferns and herbaceous perennials. Many of the species are represented by only a few individuals: *Lysichiton americanum, Habenaria dilatata, Botrychium multifidum* ssp. *silaifolium, Blechnum spicant, Athyrium felix-femina* vars., *Sidalcea calycosa, Myrica californica, Ledum glandulosum,* and *Marah oreganus,* while *Lilium maritimum, Camassia quamash, Gentiana sceptrum, Spiranthes romanzoffiana,* and *Iris douglasiana* are common in the grassland on the margins of the swamps.

8. Coastal scrub. *Gaultheria shallon, Vaccinium ovatum, Ceanothus griseus, Rosa gymnocarpa, R. nutkana, Rubus vitifolius,* and *Iris douglasiana.* Except for the *Iris* these species have been severely damaged by the sheep and this community is not, at present, a prominent feature of the study area.

Although no narrow endemics were found on Point Arena, either because there never have been any or because the sheep have eliminated them, the swamp communities to which many of the species belong do not appear to be common on the North Coastal Plain. According to Hans Leschke at least one of the swamp species, *Carex phyllomanica,* is rare in California. It is useful, therefore, to have a record of the species that occur here, at the end of a long period of land abuse from overgrazing, in an area from which nearly all the original tree and shrub communities had been removed, though vestiges still exist elsewhere on Point Arena to indicate what the original state probably was.

The authors wish to thank John Tomas Howell and Hans Leschke for their assistance in identifying difficult taxa. Vouchers for all the taxa have been deposited in the herbarium of the California Academy of Sciences. Excerpts from this botanical study constitute one of the appendices to the environmental statement on Point Arena being prepared by PG&E.

ISOETACEAE. *Isoetes howellii* Engelm.

EQUISETACEAE. *Equisetum telmateia* Ehrh.

OPHIOGLOSSACEAE. *Botrychium multifidum* (Gmel.) Rupr. ssp *silaifolium* (Presl.) Clausen.

ASPIDIACEAE. *Athyrium filix-femina* (L.) Roth. var. *sitchense* Rupr., and f. *strictum* (Gilbert) Butters, *Polypodium scouleri* H. & S., *Polystichum munitum* (Kaulf.) Presl.

BLECHNACEAE. *Blechnum spicant* (L.) Smith.

PINACEAE. *Pinus muricata* D. Don.

LILAEACEAE. *Lilaea scilloides* (Poir.) Haum.

POACEAE. Festuceae. *Briza minor* L., *Bromus marginatus* Nees, *B. mollis* L., *B. sterilis* L., *Cynosurus echinatus* L., *Dactylis glomerata* L., *Festuca dertonensis.* (All.) A. & G., *Glyceria pauciflora* Presl, *Poa annua* L., *P. compressa* L., *P. pratensis* L., *P. unilateralis* Scribn.

Hordeae. *Hordeum brachyantherum* Nevski, *H. hystrix* Roth, *H. leporinum* Link, *Lolium perenne* L.

Aveneae. *Aira caryophyllea* L., *A. praecox* L., *Avena sativa* L., *Danthonia californica* Bol., *Deschampsia caespitosa* (L.) Beauv. ssp. *holciformis* (Presl) Lawr., *Holcus lanatus* L., *Tristetum cernuum* Trin. var. *canescens* (Buckl.) Beal.

Agrostideae. *Agrostis alba* L., *A. pallens* Trin., *A. palustris* Huds., *Alopecurus geniculatus* L., *Calamagrostis nutkaensis* (Presl) Steud., *Polypogon monspeliensis* (L.) Desf., *Stipa pulchra* Hitchc.

Phalarideae. *Anthoxanthum odoratum* L.

Paniceae. *Panicum pacificum* Hitchc. & Chase.

CYPERACEAE. *Carex gynodynama* Olney, *C. obnupta* Bailey, *C. phyllomanica* Boott, *C. salinaeformis* Mkze., *C. subbracteata* Mkze., *Eleocharis acicularis* (L.) R. & S., *Scirpus cernuus* Vahl var. *californicus* (Torr.) Beetle, *S. koilolepis* (Steud.) Gleason, *S. microcarpus* Presl, *S. setaceus* L.

ARACEAE. *Lysichiton americanum* Hult. & St. John.

LEMNACEAE. *Lemna minor* L.

JUNCACEAE. *Juncus bolanderi* Engelm., *J. bufonius* L., *J. effusus* L., *J. lesuerii* Bol., *J. patens* Mey., *J. phaeocephalus* Engelm., *J. tenuis* Willd. var. *congestus* Engelm., *Luzula subsessilis* (Wats.) Buch.

LILIACEAE. *Camassia quamash* (Pursh) Greene, *Lilium maritimum* Kell., *Maianthemum dilatatum* (Wood) N. & M., *Zigadenus fremontii* Torr.

AMARYLLIDACEAE. *Allium dichlamydeum* Greene, *Brodiaea coronaria* (Salisb.) Engl. var. *macropoda* (Torr.) Hoover, *B. laxa* (Benth.) Wats., *B. peduncularis* (Lindl.) Wats.

IRIDACEAE. *Iris douglasiana* Herb., *Sisyrinchium bellum* Wats., *S. californicum* (Ker.) Dryand.

ORCHIDACEAE. *Habenaria dilatata* (Pursh) Hook., *Spiranthes romanzoffiana* C. & S.

SALICACEAE. *Salix lasiolepis* Benth., *S. sitchensis* Sanson.

MYRICACEAE. *Myrica california* C. & S.

BETULACEAE. *Alnus oregona* Nutt.

URTICACEAE. *Urtica urens* L.

POLYGONACEAE. *Eriogonum latifolium* Sm., *Polygonum aviculare* L., *Rumex acetosella* L., *R. conglomeratus* Murr.

AIZOACEAE. *Mesembryanthemum chilense* Mol.

PORTULACACEAE. *Montia perfoliata* (Donn) Howell, *M. sibirica* (L.) Howell.

CARYOPHYLLACEAE. *Cerastium viscosum* L., *Sagina crassicaulis* Wats., *S. occidentalis* Wats., *Silene gallica* L., *Spergula arvensis* L., *Spergularia rubra* (L.) J. & C. Presl, *Stellaria media* (L.) Cyrill., *S. sitchana* Steud. var. *bongardiana* (Fern.) Hult.

RANUNCULACECE. *Ranunculus californicus* Benth. var. *cuneatus* Greene, *R. flammula* L. var. *ovalis* (Bigel.) Benson, *R. uncinatus* D. Don.

PAPAVERACEAE. *Eschscholzia californica* Cham.

BRASSICACEAE. *Brassica campestris* L., *Cardamine oligosperma* Nutt., *Dentaria californica* Nutt., *Nasturtium officinale* R. Br.

CRASSULACEAE. *Dudleya farinosa* (Lindl.) Britt. & Rose, *Tillaea aquatica* L.

SAXIFRAGACEAE. *Ribes sanguineum* Pursh var. *glutinosum* (Benth.) Loud.

ROSACEAE. *Alchemilla occidentalis* Nutt., *Fragaria chiloensis* (L.) Duchn., *Potentilla egedii* Wormsk. var. *grandis* (Rydb.) Howell, *Rosa gymnocarpa* Nutt., *R. nutkana* Presl, *Rubus parviflorus* Nutt., *R. vitifolius* C. & S.

FABACEAE. *Lathyrus vestitus* Nutt., *Lotus aboriginum* Jeps., *L. corniculatus* L., *L. formosissimus* Greene, *L. micranthus* Benth., *L. purshianus* (Benth.) Clem. & Clem., *L. subpinnatus* Lag., *Lupinus bicolor* Lindl. ssp. *umbellatus* (Greene) Dunn, *L. nanus* Dougl., *L. variicolor* Steud., *Medicago hispida* L., *M. lupulina* L., *Trifolium appendiculatum* Loja, *T. barbigerum* Torr., *T. macraei* H. & A., *T. wormskioldii* Lehm., *Vicia americana* Muhl. ssp. *oregana* (Nutt.) Abrams, *V. angustifolia* Reichard.

GERANIACEAE. *Erodium cicutarium* (L.) L'Her., *Geranium dissectum* L., *G. molle* L.

OXALIDACEAE. *Oxalis pilosa* Nutt.

LINACEAE. *Linum angustifolium* Huds.

POLYGALACEAE. *Polygala californica* Nutt.

CALLITRICHACEAE. *Callitriche verna* L.

LIMNANTHACEAE. *Limnanthes douglasii* R. Br.

RHAMNACEAE. *Ceanothus griseus* (Trel.) McMinn, *Rhamnus californica* Esch.

MALVACEAE. *Malva parviflora* L., *Sidalcea calycosa* Jones.

HYPERICACEAE. *Hypericum anagalloides* C. & S.

VIOLACEAE. *Viola adunca* Sm.

LYTHRACEAE. *Lythrum hyssopifolia* L.

ONAGRACEAE. *Camissonia ovata* (Nutt.) Raven, *Epilobium watsonii* Barb. var. *franciscanum* (Barb.) Jeps.

APIACEAE. *Eryngium armatum* (Wats.) Coult. & Rose, *Heracleum lanatum* Michx., *Oenanthe sarmentosa* Presl, *Perideridia gairdneri* (H. & A.) Math.

ERICACEAE. *Gaultheria shallon* Pursh, *Ledum glandulosum* Nutt. var. *columbianum* (Piper) Hitchc., *Vaccinium ovatum* Pursh.

PRIMULACEAE. *Anagallis arvensis* L., *Centunculus minimus* L.

PLUMBAGINACEAE. *Armeria maritima* (Mill.) Willd. var. *californica* (Boiss.) Lawr.

GENTIANACEAE. *Cicendia quadrangularis* (Lam.) Griseb., *Gentiana sceptrum* Griseb.

POLEMONIACEAE. *Navarretia mellita* Greene.

HYDROPHYLLACEAE. *Nemophila menziesii* H. & A.

BORAGINACEAE. *Allocarya bracteata* (Howell) Jtn., *A. reticulata* (Piper) Jtn. var. *rossianorum* Jtn., *Myosotis versicolor* (Pers.) Sm.

LAMIACEAE. *Pogogyne serpylloides* (Torr.) Gray ssp. *intermedia* Howell, *P. zizyphoroides* Benth., *Prunella vulgaris* L., *Satureja douglasii* (Benth.) Briq., *Stachys chamissonis* Benth., *S. emersonii* Piper, *S. rigida* Nutt. ssp. *quercetorum* (Heller) Epl.

SOLANACEAE. *Solanum nodiflorum* Jacq.

SCROPHULARIACEAE. *Castilleja latifolia* H. & A. ssp. *mendocinensis* Eastw., *Gratiola ebracteata* Benth., *Mimulus guttatus* Fisch., *Orthocarpus castillejoides* Benth., *O. erianthus* Benth., *O. pusillus* Benth., *Veronica americana* (Raf.) Schw., *V. scutellata* L.

PLANTAGINACEAE. *Plantago bigelovii* Gray, *P. hookeriana* F. & M. var. *californica* (Greene) Poe, *P. lanceolata* L., *P. major* L., *P. juncoides* Lamk. var. *californica* Fern.

RUBIACEAE. *Galium trifidum* L. var. *subbiflorum* Weig., *Sherardia arvensis* L.

CAPRIFOLIACEAE. *Lonicera involucrata* (Richards.) Banks.

CUCURBITACEAE. *Marah oreganus* (T. & G.) Howell.

CAMPANULACEAE. *Campanula californica* (Kell.) Heller.

ASTERACEAE. Heliantheae. *Wyethia angustifolia* (DC.) Nutt.

Madiinae. *Madia anomala* Greene.

Helenieae. *Eriophyllum staechadifolium* Lag., *Helenium bolanderi* Gray, *Lasthenia macrantha* (Gray) Greene var. *pauciaristata* Gray.

Astereae. *Aster chilensis* Nees, *A. subspicatus* Nees, *Baccharis pilularis* DC. ssp. *consanguineus* (DC.) Wolfe, *Bellis perennis* L., *Corethrogyne californica* DC. var. *obovata* (Benth.) Kuntze, *Erigeron glaucus* Ker-Gawl, *E. supplex* Gray, *Solidago spathulata* DC.

Anthemideae. *Achillea borealis* Bong., *Chrysanthemum leucanthemum* L., *Cotula coronopifolia* L., *Soliva sessilis* R. & P.

Senecioneae. *Erechtites prenanthoides* (Rich.) DC., *Petasites palmatus* (Ait.) Gray.

Inuleae. *Anaphalis margaritacea* (L.) B. & H., *Evax sparsiflora* (Gray) Jeps., *Gnaphalium luteo-album* L., *G. purpureum* L.

Cynareae. *Cirsium breweri* (Gray) Jeps., *C. quercetorum* (Gray) Jeps., *C. vulgare* (Savi) Ten.

Cichorieae. *Hypochoeris radicata* L., *Leontodon leysseri* (Wallr.) Beck, *Microseris bigelovii* (Gray) Sch.-Bip., *M. paludosa* (Greene) Howell, *Sonchus asper* L., *S. oleraceus* L.

INFORMATION ON CHEMISTRY AND POLLINATION BIOLOGY RELEVANT TO THE SYSTEMATICS OF NEMOPHILA MENZIESII (HYDROPHYLLACEAE)

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In 1941, Constance described a paradoxical situation in *Nemophila menziesii* H. & A. s.l. The apparent contradiction involves inter-taxon sterility (Chittenden and Turrill, 1926; Rick, 1946; and Cruden, 1967) and "morphologically intermediate" flower types that suggest introgression. I present data from two divergent sources, flavonoid chemistry and pollination biology, to explore two questions: 1) whether the taxa usually included in *N. menziesii* s.l. are specifically distinct and 2) the nature and origin of variation encountered in the North Coast Ranges. First I review the distribution and floral morphology of *N. menziesii* s.l. and present data that suggest there are species-specific flavonoid profiles and that *Nemophila menziesii* s.l. is a species aggregate of three closely related species. Data obtained from a study of bees that are obligate collectors of *Nemophila* pollen corroborate the chemical data. Finally I present a model to reconcile the morphological variation, inter-taxon sterility, and specificity of *Nemophila* pollinators.

Three taxa that are closely related to *N. menziesii* s.l. and are sometimes included within it are *N. atomaria* Fisch. & Mey., *N. liniflora* Fisch. & Mey., and *N. integrifolia* (Parish) Abrams. For the purposes of this paper I refer material from San Bernardino Co. to *N. integrifolia*. Although *N. rotata* Eastw. from Point Loma, San Diego Co., and *N. integrifolia* are usually considered as synonymous (Constance, 1941; Munz, 1959), I hesitate to make the taxonomic decision to use *N. rotata,* as I have not examined the Point Loma specimens.

Nemophila menziesii s.str. (*N. insignis* Dougl. ex Benth.) is the well known baby blue-eyes. The corollas are blue with a clear white center. In the Sierra Nevada, southern California, and the South Coast Ranges the blue area reflects UV light. In the North Coast Ranges the blue area absorbs UV light. In *N. atomaria* the corolla is typically white with rows of blue-black dots radiating from its center. This species is found from Santa Clara and Santa Cruz counties, California, north to Washington Co., Oregon. The corolla absorbs UV light. The corollas of *N. liniflora* are whitish with blue to purple veins and absorb UV light. This species is found from Santa Clara Co. north to Mendocino Co., California. *Nemophila integrifolia* is a poorly understood taxon from southern California. The corollas are variable in size, range in color from deep blue to whitish, and absorb UV light.

I emphasize UV reflectivity because of its role in attracting pollinators. Bees see UV as a distinct color and the combination of UV and

blue produces in the bee's eye "bee violet" (Daumer, 1958). Thus a bee can discriminate between a blue flower that reflects UV and one that absorbs UV.

Throughout most of their distributional ranges the four taxa of *Nemophila* are relatively distinct and easily differentiated. However, in the North Coast Ranges one finds, even in the same population, apparent recombination types among *menziesii, atomaria,* and *liniflora.* It is because of these "obvious" intermediates that the various taxa have been maintained as subspecies rather than species (Constance, 1941; Munz, 1959).

Floral variation is also encountered in the South Coast Ranges. Whereas typical *N. menziesii* has a clear, white center, many individuals in the South Coast Ranges have dots and dashes radiating from the center of the corolla similar to those in *N. atomaria.* Further, some populations in San Benito and Monterey counties are variable with respect to UV-reflectivity.

Chromatographic Studies

Thirty to forty corollas from each population were covered with acidified ethanol, whose volume was later reduced under vacuum. The condensed extract was spotted on 24 x 18 inch sheets of 3 MM Whatman chromatography papers. The sheets were run descending. The solvent used for the long dimension consisted of ethyl acetate; tertiary butyl alcohol; glacial acetic acid; and water (5:4:1:3 v:v). The short dimension was run in 15% acetic acid. The dried sheets were examined under UV light and UV light plus ammonia fumes. All the spots appear purple in UV light with the execption of number one (see Fig. 1), which fluoresced yellow in UV light and UV light plus ammonia fumes. In UV light plus ammonia fumes some spots remained dark (shaded spots in Fig. 1) and the other fluoresced a yellowish-green (clear spots in Fig. 1). No attempt was made to identify the various chemical compounds. The populations studied and the spots present are listed in Table 1. Three populations of *N. maculata* were studied and are included for comparison.

The populations studied fall into three distinct groups with respect to the flavonoid profiles from corolla tissue. Indeed the differences between the taxa in *N. menziesii* s.l. are as great as the differences between them and *N. maculata.* Although the number of populations sampled is small they represent a broad segment of the distributional range and morphological variation within each taxon.

Although there is intra-taxon variation with respect to most compounds, the presence or absence of particular compounds does serve to differentiate the various taxa. Without exception, *N. atomaria* lacks spots 2, 3, 15, and 16, which are usually present in *N. menziesii* and *N. integrifolia,* and with one exception its has spots 9 and 10, which are usually absent in *N. menziesii.* Likewise, *N. menziesii* lacks spots 4 and 14, which are usually present in *N. atomaria* and *N. integrifolia.* The chemical spe-

cificity is maintained even in mixed populations, e.g., at the Chiles-Pope Valley Road and Arnold Drive localities where *N. menziesii* s.str. and *N. liniflora* occurred in mixed populations.

If introgression were occurring one might anticipate its discovery in such mixed populations. Yet the chemical profiles from the Chiles-Pope Valley populations are representative of their respective taxa, and the profiles from Arnold Drive exhibit variation normally encountered in the two species. Careful comparison with other populations of the taxon in question shows that similar variation exists in populations that are geographically disjunct from the other species. For example, populations of *N. menziesii* s.str. from the Sierra Nevada lack spots 3 and 7. Likewise, the Berry Summit (Humboldt Co.) population of *N. atomaria* lacks spot 4. The lack of spot 14 in the Arnold Drive *N. atomaria (liniflora)* population is suggestive of introgression, but spot 14 is also absent from the Trinity Road (Sonoma Co.) population, which morphologically is typical *atomaria* with no evidence of introgression.

As a consequence of my work on the pollinators of *N. menziesii* s.l. (Cruden, 1972) I assumed *N. liniflora* to be a segregate of *N. atomaria*. This assumption is confirmed by the chromatographic results. The populations listed under *N. atomaria* in Table 1 represent both *N. atomaria*
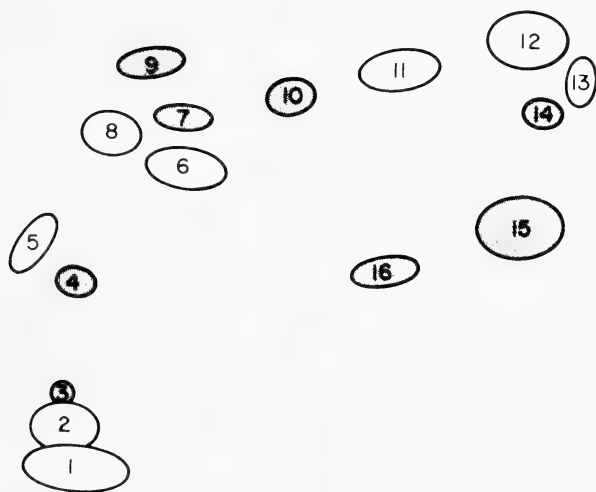
FIG. 1. Composite profile of flavonoid compounds present in corollas of *Nemophila menziesii* s.l. and *N. maculata*. Shaded spots remain dark in UV and ammonia fumes. Light spots appear yellowish-green in UV and ammonia fumes.

TABLE 1. PRESENCE OF COMPOUNDS IN POPULATIONS OF NEMOPHILA MENZIESII AGGREGATE

Locality	Spot Number															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
N. atomaria																
Humboldt Co. Berry Summit Rt. 229	+				+	+		+					+	+		
Marin Co. McClure's Beach	+			+	+	+		+					+	+		
Sonoma Co. Triniti Rd.	+			+	+	+		+					+			
Arnold Drive (_N. liniflora_)							+									
Napa Co. Chiles-Pope Valley Rd. 3.2 mi.S. Pope Valley (_N. liniflora_)	+			+		+			+					+		
N. menziesii																
Lake Co. Sawmill Flat	+	+			+	+		+		+	+	+	+		+	
Rt. 175 2 mi. S. Rt. 29	+	+	+		+	+		+		+	+	+	+		+	+
Napa Co. Chiles-Pope Valley Road 3.2 mi. S. Pope Valley	+	+	+		+	+	+	+			+	+	+		+	+
Sonoma Co. Sonoma Mt. Rd.	+	+	+		+	+	+	+			+	+	+		+	+
Arnold Drive	+	+	+		+	+	+	+			+	+	+		+	+
Contra Costa Co. Camino Diablo and Vasquez Road	+	+	+		+	+	+	+	+			+	+		+	+
San Benito Co. Lonoak Rd. 10 mi. E. Rt. 101	+	+	+		+	+	+	+			+	+	+		+	+
Monterey Co. Jolon-Bradley Rd.	+	+	+		+	+	+	+	+		+	+	+		+	+
Jolon-King City Rd.	+	+	+		+	+	+	+			+	+	+		+	+
Nevada Co. Rt. 49 1.8 mi. N. county line	+	+	+		+	+	+	+			+	+	+		+	+
Amador Co. ca. 1 mi. S. Jackson City	+	+	+		+	+		+		+	+	+	+		+	+
Tuolumne Co. Rt. 49 and Mokelumne River	+	+	+		+	+	+	+		+	+	+	+		+	+
Madera Co. Crystal Springs	+	+	+		+	+	+	+		+	+	+	+		+	+
Bass Lake	+	+	+		+	+		+		+	+	+	+		+	+
Fresno Co. 4 mi. S. Alder Springs	+	+	+		+	+		+			+	+	+		+	
Riverside Co. 3.4 mi. S. Idyllwild	+	+	+		+			+			+	+	+		+	+

TABLE 1. (Continued)

Locality	Spot Number															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
N. integrifolia																
San Bernardino Co. 3.8 mi. E.																
Arrowhead Ranger Station	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+
0.1 mi. E. Arrowhead Ranger Station	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+
Rt. 38 and Skinner Cr.	+	+	+	+	+	+	+	+	+		+	+	+	+	+	
N. maculata																
Madera Co. Bass Lake	+	+			+	+	+	+		+	+	+	+	+		
Crystal Springs	+	+			+	+		+			+	+	+	+		
Fresno Co. 4 mi. S. Alder Springs	+				+	+		+			+	+	+			

and *N. liniflora*. On morphological grounds the Arnold Drive and Chiles-Pope Valley Road populations are referable to *N. liniflora,* the others are typical *N. atomaria*. As there are no discernible differences in the profiles of the two taxa, I suggest the proper alignment of *N. liniflora* is with *N. atomaria,* not *N. menziesii*. This is contrary to the suggestions of previous workers (Constance, 1941; Munz, 1959).

Although the number of populations studied in the North Coast Ranges is small, the results substantiate the major taxonomic decisions of earlier workers that two taxa are sympatric in the region. Those plants that appear to be introgressants can usually be assigned to one taxon or the other. For example, plants with *menziesii*-like flowers, i.e., bluish with a white center and colored veins are referable to *N. menziesii,* and, likewise, plants having essentially *atomaria* flowers with blue-edged corolla lobes are referable to *N. atomaria*.

HYBRIDIZATION STUDIES

A second line of evidence suggests that introgression may occur, albeit rarely, between *N. atomaria* and *N. menziesii* s.str. Chittenden & Turrill (1926) and Rick (1946) both reported that crosses between plants referable to *N. atomaria* and *N. menziesii* were unsuccessful. Both Chittenden & Turrill (1926) and Rick (1946; pers. commun.) performed many crosses. In no instance were inter-taxon crosses successful. I have performed a small number of crosses between *N. menziesii* s.str. from Sawmill Flat (Lake Co.) and *N. atomaria* from Warm Springs Road (Sonoma Co.). Reciprocal crosses were made. Thirteen crosses using *N. menziesii* as the pollen parent were unsuccessful, but one of seven crosses using *N. atomaria* as the pollen parent was successful, producing a capsule with mature seed. Three selfings of *N. atomaria* were successful indicating that the pollination technique was satisfactory. The few seeds realized from the one successful cross were not germinated. The results suggest that hybridization in natural populations must be a rare event.

OLIGOLECTIC BEES ON NEMOPHILA

The systematic implications of the following discussion depend on an appreciation of the relationship between an oligolectic bee and its pollen source. An oligolectic species as presently understood is one ". . . in which the individual members of the population, throughout its range and in the presence of other pollen sources, consistently and regularly collect pollen from a single plant species or a group of related plant species, turning to other sources, if at all, only in the face of a local pollen shortage" (Linsley and MacSwain, 1957). The flight period, distribution range, and indeed the whole economy of the bee is tied to that of its host (pollen) plant. The emphasis on pollen source derives from the important role pollen plays in the life of the bee. In solitary bees, including oligolectic bees, pollen is the primary food source of the larvae, the adults utilizing nectar and sometimes pollen as nutrients (Linsley, 1958). Thus

the oligolectic bee is tied to its pollen source in the same way a host spe-
cific parasite is tied to its host. Because of the specificity of the oligolec-
tic relationships it should be possible to gain new insights with respect
to the host plant by studying the bee. Indeed, the presence of an un-
known *Cucurbita* in Ecuador was predicted on the basis of the occur-
rence there of a bee known to be oligolectic on *Cucurbita* (Hurd, pers.
commun.).

Four bees are known to be oligolectic on *N. menziesii* s.l. (Cruden,
1972). *Andrena nemophilae* Ribble has been collected on *N. menziesii*
s.l. throughout California. This bee is a broadly adapted oligolege in
that it collects pollen from all the taxa included in *N. menziesii* s.l. The
three remaining species are narrowly adapted oligoleges, i.e., are co-
adapted to a single pollen source (Cruden, 1972).

Andrena macrocephala Ckll. is widely distributed in southern Califor-
nia, in the Coast Ranges north to Napa and Yolo counties, and in the
Sierra Nevada north to Madera Co. Throughout its distributional range
Andrena macrocephala has been collected primarily on *Nemophila men-
ziesii* (Cruden, 1972). In the North Coast Ranges this bee has been col-
lected on *N. atomaria* (including *N. liniflora*), but where *N. menziesii*
and *N. atomaria* occur in mixed populations the bee exhibits a strong
preference for *N. menziesii*. For example, at the Chiles-Pope Valley
Road population seven of eight females were captured on flowers of *N.
menziesii*. A subspecies of *A. macrocephala*, *A. m. tetleyi* Linsley, was
collected on *N. integrifolia* at Tetley Park, San Bernardino County
(Linsley, 1938). I collected bees from five populations of *N. integrifolia*
and failed to see, let alone collect, this bee. Thus the available data sug-
gest that *A. macrocephala* visits *N. menziesii* in preference to both *N.
atomaria* and *N. integrifolia* (see also Table 2).

Andrena torulosa LaBerge is found in the Coast Ranges from Santa
Clara Co., California, north to Washington Co., Oregon. The distribution
of *A. torulosa* mirrors that of its host plant, *N. atomaria* (including *N.

TABLE 2. FLOWER RECORDS OF BEES OLIGOLECTIC ON
NEMOPHILA MENZIESII AGGREGATE

Bee	N. menziesii		N. atomaria		N. integrifolia	
	Local.	Individ.	Local.	Individ.	Local.	Individ.
Andrena macrocephala	20	216	4	9	2	9
Andrena torulosa	6	32	8	109		
Andrena crudeni	18	93				
Andrena nemophilae	10	76	4	10	1	12

liniflora). Only in the southern North Coast Ranges does *A. torulosa* regularly visit flowers other than those of *N. atomaria*. There it is an important pollinator of non-reflective *N. menziesii* although the bee populations were small when associated with *N. menziesii*. In mixed populations of *N. atomaria* and *N. menziesii* this bee shows a strong preference for *N. atomaria*. At the Chiles-Pope Valley Road population 26 of 27 individuals captured were taken on flowers of *N. atomaria*.

Andrena crudeni LaBerge is an oligolege of *N. menziesii* s.str. and to date is known primarily from reflective populations in the South Coast Ranges from San Luis Obispo Co. north to Santa Clara Co., in the Sierra Nevada from Kern Co. north to Nevada Co., and two locations in southern California. Of the 20 populations I studied this bee was associated with its host plant 18 times. On two occasions, *A. crudeni* was found on flowers of *N. maculata*.

Andrena torulosa and *A. crudeni* are closely related species in subgenus *Nemandrena* whose members all are apparently oligolectic on *Nemophila menziesii* s.l. (LaBerge, 1971; Cruden, 1972). A third species, *A. subnigripes* Viereck, is known only from *N. menziesii* s.str. in Fresno and Tulare counties, California. At the end of the flowering season, when *Nemophila* pollen is scarce, both *A. torulosa* and *A. crudeni* may collect pollen from *Limnanthes* (Limnanthaceae) and *Platystemon* (Papaveraceae). Such late season foraging activity is characteristic of other oligolectic bees (Thorp, 1969).

The floral specificity of *Andrena macrocephala, A. torulosa* and *A. crudeni* corroborate the suggestion from the chemical data that *N. atomaria* (including *N. liniflora*) and *N. menziesii* s.str. are specifically distinct. The failure of Chittenden and Turrill (1926) and Rick (1946) to demonstrate inter-taxon fertility is further evidence for the specific relationship of the two taxa. How then may one explain the obvious evidence of gene exchange between the two taxa?

Variation in Nemophila: An Explanation

The variation observed in present *Nemophila menziesii* and *N. atomaria* may be explained in either of two ways; i.e., introgression subsequent to speciation or gene exchange prior to speciation. Two lines of evidence support introgression as a reasonable explanation. First there is the morphological variation described above which suggests past gene exchange. Second there is evidence from hand pollinations that limited hybridization is possible. Although hybridization is a requisite for introgression, it dos not necessarily result in introgression.

The case of introgression between two subspecies of the house mouse, *Mus m. musculus* and *M. m. domesticus,* in Denmark (Selander, 1970) is particularly relevant. The two subspecies hybridize freely in a narrow band across Jutland producing fertile hybrids but limited gene exchange. The degree of introgression varies from allele to allele and the frequencies of introgressant alleles are usually low. Selander (1970) and

others suggest 1) that genomes are co-adapted and 2) that the genetic as well as the external environment is important to co-adapted genes. Thus an allele with a high fitness value in its normal genetic environment is likely to have a low fitness value in a foreign genetic environment.

In comparison with *M. m. musculus* and *M. m. domesticus, N. menziesii* and *N. atomaria* are also genetically and ecologically distinct, indeed more so than in *Mus*. In contrast, hybridization is apparently an uncommon event. If introgression is proportional to hybridization, is it reasonable to attribute to introgression the loss of reflectivity in *N. menziesii* in the North Coast Ranges and the presence of "atomaria" spots in *N. menziesii* in the South Coast Ranges? In contrast to *Mus* an "introgressed" character has replaced a "co-adapted" character in both regions.

An alternative explanation of the observed variation is gene exchange prior to speciation. I suggest that the events that resulted in the geographical isolation of the ancestral *N. menziesii* s.l. population also re-resulted in the isolation of the ancestral *Andrena crudeni-torulosa* population. Given today's 1:1 relationship between the bees and plants it seems probable that the ancestral *N. menziesii* s.l. population and *Andrena crudeni-torulosa* population also enjoyed an oligolectic relationship. Geographical isolation also resulted in ecological divergence. Today *N. menziesii* is a member of communities dominated by plants derived from the Madro-Tertiary geoflora whereas *N. atomaria* is a member of communities dominated primarily by species derived from the Arcto-Tertiary geoflora.

What event might explain the geographical separation and subsequent genetic and ecological differentiation of a once continuous population into two discrete entities? I suggest that the incursion of seas over what is now the South Coast Ranges during the Miocene was the event which resulted in geographical isolation of the ancestral plant and bee populations.

During the late Miocene–early Pliocene times the South Coast Ranges composed an archipelago of greater or lesser extent (Axelrod, 1956; Oakeshott, 1971). During these periods the Madro-Tertiary geoflora expanded tremendously. Evidence from Miocene and Pliocene floras (Axelrod, 1956) suggests that the regions probably inhabited by *N. menziesii* s.str. during this period, i.e., the southern Sierra Nevada and the archipelago, were dominated by Madro-Tertiary communities whereas the northern element *(N. atomaria)* lived in regions dominated by Arcto-Tertiary communities.

Given the model of a once continuous population that was geographically separated by a long incursion of seas over the South Coast Ranges, we must hypothesize a population whose floral characters varied clinally over the region of submergence. As evolution proceeded in the resultant populations blue and UV reflectivity were selectively advantageous in the Sierra Nevada populations, whereas white, spotted, non reflective flowers were selected in the North Coast Ranges. The blue-edged corollas in the

North Coast Ranges are thus attributable to "relict", genes in the "ato-maria" gene pool. Likewise the "atomaria" spots in the "menziesii" gene pool may be considered relictual. It is perhaps fortuitous that the present day occurrence of variation in UV reflectivity in San Benito and Mon-terey counties corresponds quite nicely with the Miocene-Pliocene archi-pelago. It is also in the South Coast Ranges that "atomaria" spots are most prevalent. It seems possible that the Miocene archipelago served as a refugium for intermediate type plants.

The final observation requiring an explanation is the dramatic break between UV reflective and non-reflective populations south and north of the Sacramento River respectively. Obviously, in *Nemophila men-ziesii* s.l. it is selectively advantageous to be non-reflective north of the Sacramento River. I suggest that in the southern North Coast Ranges *Andrena torulosa* played a role by preferentially visiting non-reflective and low-reflective variants in the *N. menziesii* population as the latter migrated into the North Coast Ranges as today *A. torulosa* is an impor-tant pollinator of *N. menziesii* s.str. in the North Coast Ranges.

SUMMARY

Nemophila menziesii s.l. is a species aggregate including *N. menziesii, N. atomaria* and *N. integrifolia*. The three species are morphologically and chemically distinct and *N. menziesii* and *N. atomaria* are reproduc-tively isolated. The specific nature of the three taxa is reflected in the specificity and flower preferences of three bees oligolectic on *N. atomaria* and *N. menziesii*. The close relationship of the three species is suggested by the broadly adapted oligolectic bee *Andrena nemophilae*. I suggest that the incursion of Miocene seas over what is now the South Coast Ranges resulted in the geographical isolation of a once continuous popu-lation into two segments, now recognized as *N. atomaria* and *N. men-ziesii*. As so little is known of *N. integrifolia* I have not included it in my discussion other than to indicate the specific nature of the flavonoid pro-file from corolla tissue.

LITERATURE CITED

AXELROD, D. I. 1956. Mio-pliocene floras from west-central Nevada. Univ. Calif. Publ. Geol. Sci. 33:1–322.
CHITTENDEN, R. J., and W. B. TURRILL. 1926. Taxonomic and genetic notes on some species of *Nemophila*. Kew Bull. Misc. Inform., No. 1.

Constance, L. 1941. The genus *Nemophila* Nutt. Univ. Calif. Publ. Bot. 19:341–398.
Cruden, R. W. 1967. Genecological studies in *Nemophila menziesii* H. and A. (Hydrophyllaceae). Doctoral Thesis [Botany] University of California, Berkeley.
————. 1972. Pollination biology of *Nemophila menziesii* with comments on the evolution of oligolectic bees. Evolution (in press).
Daumer, K. 1958. Blumenfarben, wie sie die Bienen sehen. Z. Vergleich. Physiol. 41:49–110.
LaBerge, W. E. 1971. A new subgenus of *Andrena* found in California and Oregon (Hymenoptera:Andrenidae). Pan-Pac. Entomol. 47:47–57.
Linsley, E. F. 1938. Studies in the Andrenidae of North America I. Calif. Acad. Sci. Proc. Ser. 4. 23:263–282.
————. 1958. The ecology of solitary bees. Hilgardia 27:543–599.
———— and J. W. MacSwain. 1957. The nesting habits, flower relationships, and parasites of some North American species of *Diadasia* (Hymenoptera: Anthophoridae). Wasman J. Biol. 15:199–235.
Munz, P. A. 1959. A California flora. Univ. Calif. Press, Berkeley.
Oakeshott, G. B. 1971. California's changing landscapes. McGraw Hill Book Company, New York, 388 pp.
Rick, C. 1946. Studies of natural populations in the *Nemophila menziesii-atomaria* complex. Amer. J. Bot. 33:825 (Suppl. 9a).
Selander, R. K. 1970. Biochemical polymorphism in populations of the house mouse and old-field mouse. Symp. Zool. Soc. Lond. 26:73–91.
Thorp, R. W. 1969. Systematics and ecology of bees of the subgenus *Diandrena* (Hymenoptera:Andrenidae). Univ. Calif. Publ. Entomol. 52:1–146.

NOTES AND NEWS

L. H. Shinners' Collection of Anthophilous Hymenoptera Deposited in Dallas Museum of Natural History.—Dr. Lloyd H. Shinners, the late Director of the Herbarium, Southern Methodist University, Dallas, Texas, had a special interest in pollinating insects. Details of his life have been described by D. S. Correll (Brittonia 23:101–104. 1971) and W. F. Mahler (Sida 4(3):228–231. 1971). During the period 1948–1960, he collected over 8,500 insects, mainly bees and wasps. Virtually all the insects were taken on identified flowering hosts and each insect was assigned a numbered label. As identified insects were returned from taxonomic specialists, he developed a file of insect-flower associations. Three-quarters of the collection is from Texas and provides a rich record of phenological, geographical, and host relationships in an area little studied from the viewpoint of floral biology. Thirteen other states are represented, especially Missouri (11% of specimens). Although the collection was damaged by pests, much unstudied material and the file have been deposited in the Dallas Museum of Natural History. Inquiries for the loan of material should be directed to Mr. Hal P. Kirby, Director, P.O. Box 26193, Dallas Museum of Natural History, Dallas, Texas 75226.—Howell V. Daly, Division of Entomology, University of California, Berkeley 94720.

TAXONOMY OF AMAURIA (COMPOSITAE-PERITYLINAE)

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The genus *Amauria*, with its three known species, is endemic to the Baja California peninsula and a few associated islands. Bentham (1844) proposed the genus to accommodate a single species, *A. rotundifolia*, which was collected during the voyage of H.M.S. Sulphur. The other two species recognized here are *A. brandegeana* (Rose) Rydb. and the recently discovered *A. carterae* (Powell, 1972a).

Amauria has not always been regarded as a distinct genus. In fact, Rose (1890) described *A. brandegeana* as a member of *Perityle* Benth., and Brandegee (1893), although apparently unaware of Rose's species, hastened to submerge *A. rotundifolia* with *Perityle* while stating that "the longdoubtful [sic] genus *Amauria* disappears at last from our flora". Rydberg (1914) revived *Amauria* and placed it with three other small genera, *Eutetras, Oxypappus,* and *Microspermum,* in the subtribe Amaurinae as part of his Helenieae in the *North American Flora.* Subsequent workers have not openly challenged *Amauria* as a generic entity, including Everly (1947) who last monographed *Perityle.* Actually, Everly did not mention *Amauria,* but she evidently agreed with Rydberg's treatment since *A. brandegeana* and *A. rotundifolia* were not included in her concept of *Perityle.* Furthermore, I have seen numerous sheets of the latter two species that were annotated as Amaurias by Everly in 1947.

The present study of *Amauria* was undertaken as part of my recent systematic investigations of *Perityle* and related genera (Powell and Tsang, 1966; Powell, 1968a; 1968b; 1969; 1972b). These investigations have shown that *Amauria* is closely related to *Perityle* and also *Eutetras.* Turner (1966a; 1966b) has suggested that *Eutetras* and the Amaurinae (Rydberg, 1914), excepting *Microspermum,* should be merged with the Peritylinae (Rydberg, 1914), and I agree. Thus, as presently reconstituted, the subtribe Peritylinae includes *Perityle, Pericome, Amauria,* and *Eutetras* as closely allied members, and *Oxypappus* of more distant and questionable relationship.

Generic Relationships and Characteristics

The close relationship of *Amauria, Perityle,* and *Eutetras* was indicated above. More specifically, *Amauria* is morphologically close to the Baja Californian endemic *Perityle crassifolia* and the weedy *P. emoryi* of sect. *Perityle* (Powell, unpublished). The taxa are similar in vegetative and floral characteristics (white rays, yellow discs), except that the Amaurias have distinctive 4-angled achenes that are epappose, and the Perityles are characterized by 2(–3)-angled achenes with a pappus of bristles and/or squamellae. The achenes of *Eutetras* (south-central Mexi-

co) are also 4-angled, a factor that doubtless inspired Rydberg's (1914) classification, but the pappus of bristles and scales readily distinguish the genus (Turner, 1966a). I believe that *Eutetras, Amauria,* and *Perityle crassifolia* (and the Peritylinae) had common ancestry emanating from the Sierra Madre Occidental of Mexico (Powell, in press). Other information regarding the proposed generic affinities is discussed below.

In addition to the distinctive, epappose achenes of *Amauria,* certain ontogenetic features of the capitula help to distinguish the genus. As heads mature, the involucral bracts reflex to a position nearly parallel with the peduncle and the achenes are spread like a 3-dimensional Japanese fan. Disc corollas remain more or less aggregated in a single clump and separate in early unison from maturing achenes. The achenes of *Amauria* are shed as soon as the heads are mature. In *Perityle,* generally speaking, involucral bracts merely spread or become moderately reflexed as heads mature, and disc corollas are not so readily or simultaneously separated from achenes. The achenes of *Perityle* are more persistent at maturity. In certain species of *Perityle,* however, including those presumably related to *Amauria,* the bracts of mature heads may eventually reflex to the peduncle, but the florets are somewhat persistent. The bracts of *Eutetras* are merely spreading at maturity (and later reflexing), while those of *Pericome,* unlike the other genera, are coalescent or only partially separated even in older heads.

CHROMOSOME NUMBERS

The chromosome number of both *Amauria rotundifolia* and *A. brandegeana* is $n = 18$, as determined from five collections of each species (Powell, 1968b; 1972c). An individual plant from one collection of *A. rotundifolia* was reported as $n = ca\ 17$, but two other plants of the same collection were clearly $n = 18$ (Powell, 1968b). *Amauria carterae* is reported here as $n = 20$ or $n = 18$ plus 4 univalents or fragments. The uncertain counts were obtained from seed progeny of the holotype *(Carter 5439).* Through observation of late diakinesis, metaphase I, and anaphase I stages, I was not able to determine whether four small chromosomes were achiasmatic and early separating homologues, nonhomologous univalents, or centric fragments. Presumably achiasmatic and precociously dividing bivalents and fragments are frequently observed aspects of meiotic behavior in species of *Perityle* (Powell, 1968b).

A base number of $x = 18$ is suggested for *Amauria.* Although confirmation of the base number must await further chromosomal study of *A. carterae,* $x = 18$ is supported by the counts for *A. rotundifolia* and *A. brandegeana* and by the numbers of *Eutetras* $(x = 18)$ and *Pericome* $(x = 18)$. The base number of *Perityle* is not established; sect. *Perityle,* to which *Amauria* is allied through *P. crassifolia* $(n = 19, 18)$ and *P. emoryi* $(n = 50–58)$ is $x = 17, 18,$ or 19 (Powell, 1968b, where *P. incompta* = *P. crassifolia;* 1972c).

Experimental Hybridizations

The three species of *Amauria* have been utilized in artificial green-house crosses. The techniques employed in the production and analysis of hybrids were essentially the same as those reported elsewhere (Powell, 1970). The parental stocks were grown from seeds, flowered in about 60 days, and were self-incompatible. Seed-set occurred rarely in uncovered heads of *A. brandegeana,* but probably as a result of insect cross-pollination.

The following interspecific crosses were attempted: *A. brandegeana* × *A. rotundifolia; A. carterae* × *A. rotundifolia; A. brandegeana* is a short-lived annual and was not available at the time *A. carterae* was brought into flower. Reciprocal crossability was high in both of the above combinations as judged by near 100% recovery of filled achenes. Results: 1.) *A. brandegeana* × *A. rotundifolia*—seed germination was poor, and only two F_1's were grown to maturity. The hybrids readily flowered, and pollen stainability averaged 34%. Meiosis was regular. An attempt to obtain F_2 hybrids was unsuccessful. Crossability of the F_1's was low, and the small number of achenes with F_2 embryos did not germinate. 2.) *A. carterae* × *A. rotundifolia*—nearly all the achenes have germinated, but most of the delicate seedlings have died without passing the cotyledon stage. Four F_1 hybrids have been obtained and these are vigorous. Data from flowering stages are not yet available.

I have not observed any evidence of natural hybridization in *Amauria,* although the limited interfertility data and distribution of the taxa suggest such a possibility. The species are geographically sympatric (fig. 1) but I have not seen any ecologically sympatric populations in the field, nor have I seen any mixed collections among the specimens that were borrowed for examination. Morphological study of *A. brandegeana* and *A. rotundifolia,* and their hybrids, has shown that it would be difficult to detect hybridization by vegetative features alone, but that achene pubescence might be a reliable indicator. The achenes of artificial F_1 hybrids were pubescent on the faces and angles with the type of hairs that usually characterize *A. rotundifolia* (see Taxonomy).

A few intergeneric hybrids with *Amauria* have been synthesized. Results of these crosses are to be presented elsewhere (Powell 1972b), but the hybrid combinations and a summary of results are indicated below: *Eutetras palmeri* × *A. brandegeana; E. palmeri* × *A. rotundifolia; Pericome caudata* × *A. rotundifolia.* All of the crosses were successful, with about 20–50% seed set, and F_1 hybrids were obtained. The F_1's were floriferous, pollen stainability ranged from 2% for *P. caudata* × *A. rotundifolia* to 87% for *P. crassifolia* × *A. rotundifolia,* and meiosis in all cases was very irregular. In spite of the intergeneric crossibility and moderate interfertility, the genera seem to be genetically isolated since only a few backcrosses were obtained (they were sterile), and no F_2's could be synthesized.
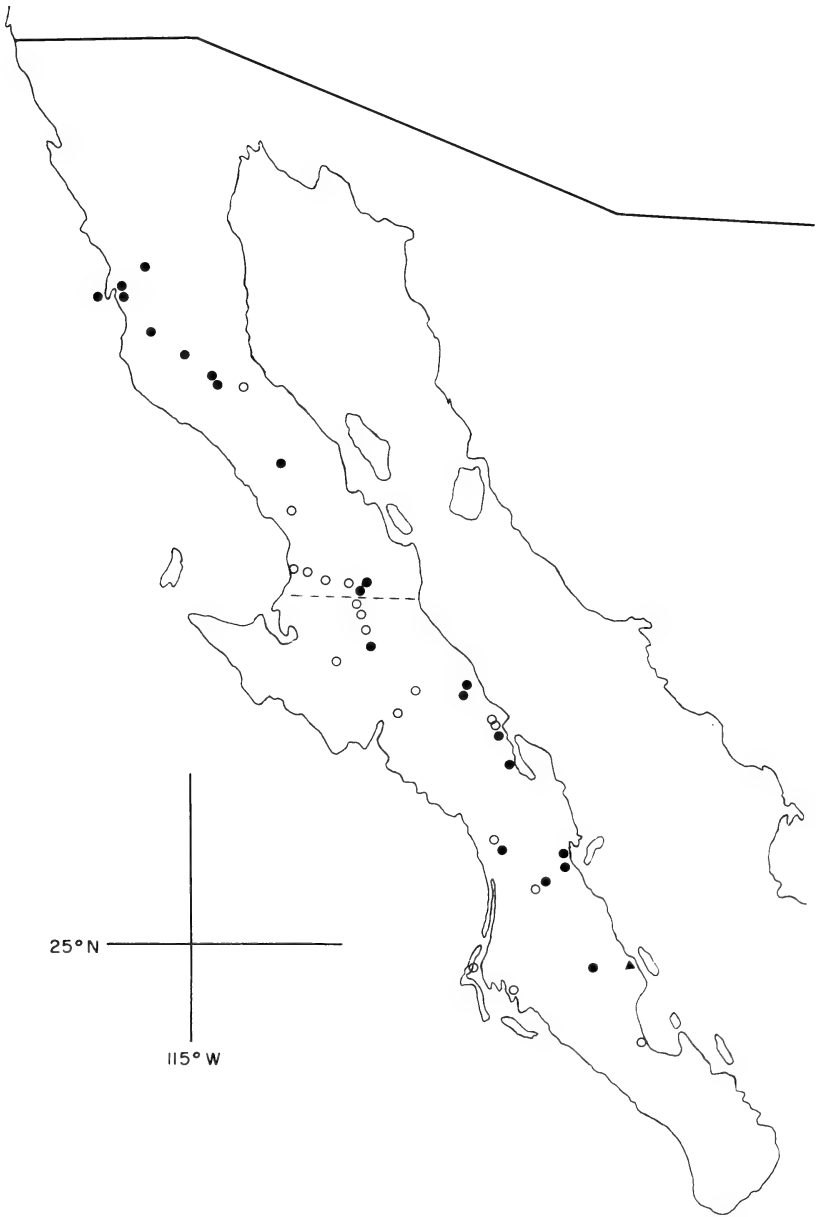
FIG. 1. Distribution of *Amauria* species: *A. carterae* (triangle); *A. rotundifolia* (closed circles); *A. brandegeana* (open circles).

Taxonomy

Amauria Benth., Bot. Voy. Sulph. 31. 1844.

Plants suffrutescent or suffruticose perennials 10–45 cm high, or deli-
cate to robust annuals 10–80 cm high, branching from the base and
distally, minutely and densely glandular-puberulent to glandular-pubes-
cent, especially above; leaves opposite and alternate, rather succulent
and thick or thin, sparsely or densely glandular, 1–7(–9) cm long, 0.5–
4.5(–6.0) cm wide, cordate, cordate-reniform, ovate, or ovate-deltoid in
outline, pedately cleft or divided into 3–5 segments or shallow to deeply
lobed, the margins and segments serrate-dentate to doubly so; petioles
of lower leaves 0.5–4.0(–5.0) cm long, upper leaves shorter-petioled, or
sessile; capitulescence of one to several heads borne on peduncles 1–4
cm long; heads radiate, 5–9 mm high, 5–12 mm wide; receptacles usu-
ally flattened, rarely short-conical; involucres campanulate to hemispher-
ical; bracts numerous, in two equal series, 4–6 mm long, 1.0–2.5 mm
wide, oblanceolate to narrowly obovate, keeled or flattened, glandular-
pubescent to essentially glabrous, reflexing to peduncle at maturity; ray
flowers 10–20, ligules white, oblong to broadly so or subspathulate, 5.5–
10.0 mm long, 1.8–5.0 mm wide, usually 3-toothed at apex; disc flowers
numerous, corollas yellow, 4-lobed, readily dehiscent at maturity, 2.0–3.5
mm long, throats tubular-funnelform to narrowly campanulate, 1–2 mm
long, lobes acute, 0.4–0.6 mm long; styles 1.0–1.6 mm long, slender and
tapering to a point, or subspathulate and obtuse; achenes black, linear,
somewhat flattened but with 4 angles, the angles 2 and 2 closer together,
faces glabrous or pubescent with curled hairs, the angles ciliate with an-
trorsely curled hairs, short antrorsely-appressed hairs, or longer twisting
or curled hairs; pappus absent or a callous crown present; anthers 1.0–
1.5 mm long; base chromosome number, $x = 18$.

Type species, *A. rotundifolia* Benth.

KEY TO SPECIES

Leaves pedately cleft or divided into 3–5 major segments; achenes ca
        1.5 mm long . . . . 1. *A. carterae*
Leaves shallowly to deeply lobed; achenes 2.0–3.5 mm long.
        Achene faces glabrous, angles with straight or slightly curved
          and appressed hairs . . . 2. *A. rotundifolia*
        Achene faces and angles pubescent with peculiar incurled hairs
                  3. *A. brandegeana*

1. **Amauria carterae** Powell, Madroño 21:456–458. 1972. fig. 2.

    TYPE: Mexico: Baja California Sur. Sierra de la Giganta, Cerro
    Mechudo, 600 m, ca Lat 25°55′N, Long. 110°45′ W, 21 Feb
    1970, *A. Carter 5439* (Holotype, UC!).

Plants low perennials, forming clumps 10 cm high and 20 cm broad,
upper stems densely and minutely glandular-puberulent; leaves succu-
lent, minutely glandular-puberulent; 1–2 cm long, 0.5–1.0 cm wide, pe-
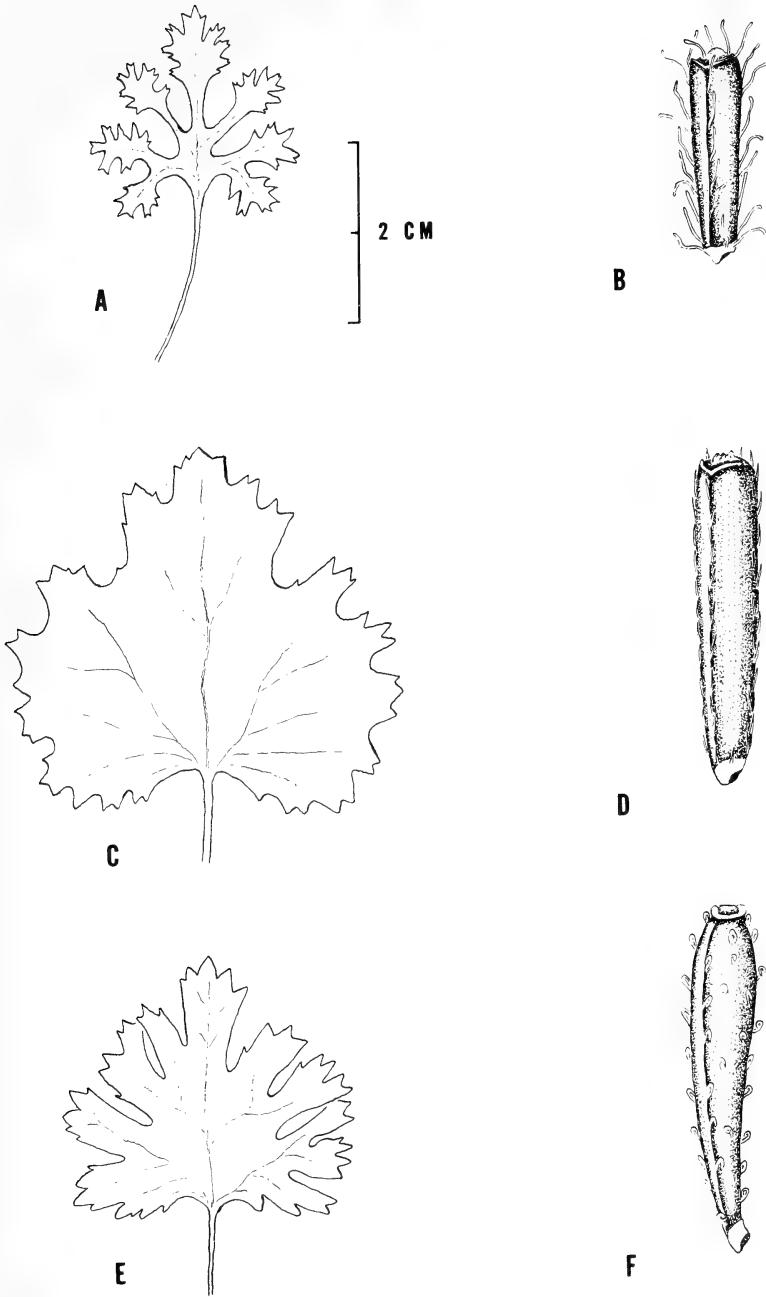
FIG. 2. Representative leaf shape ($\times$ 1) and achene morphology ($\times$ 15) of *Amauria* species: A and B, *A. carterae;* C and D, *A. rotundifolia;* E and F, *A. brandegeana.*

dately cleft, or divided with 3 (–5) major segments, the segment margins shallow-lobed or indented and crisped; petioles 0.7–1.1 cm long; capitulescence essentially of solitary heads borne on peduncles 1–2 cm long; heads 5–6 mm high, ca 5 mm wide; involucres campanulate; bracts 5–6 mm long, 1.0–1.3 mm wide, oblanceolate, not keeled, essentially glabrous or minutely puberulent; ray flowers ca 18, ligules oblong to subspathulate, 5.5–7.5 mm long, 2.0–2.5 mm wide; disc corollas 3.0–3.5 mm long, throats tubular-funnelform, ca 1.5 mm long; styles slender, ca 1.6 mm long, tapering to a fine point; achenes ca 1.5 mm long, linear, faces glabrous, the angles sparsely ciliate with rather long hairs, the white hairs usually twisting or curling or somewhat antrorsely appressed; pappus absent; anthers ca 1.5 mm long; chromosome number, **n = 20** or **n = 18** plus 4 univalents or fragments.

Known only from the type collection (fig. 1).

This species was described from a single specimen, the holotype, after observing that its distinctive morphology was maintained in seed progeny. As compared to the other Amaurias, *A. carterae* appears closest to *A. rotundifolia* from which it is easily delimited by the following characters: Low, clumped habit; minute glandular-puberulence; pedately cleft or divided leaves; smaller heads; rather thin, essentially glabrous bracts; slender styles tapering to a fine point; and achene features.

2. AMAURIA ROTUNDIFOLIA Benth., Bot. Voy. Sulph. 31. 1844. fig. 2.

    TYPE: MEXICO: Baja California (?): San Quintin. (Holotype, K).

        Perityle fitchii Torr., Pacif. R.R. Rep. 4:100. 1857. TYPE: "California" (probably Lower California), *Rev. A. Fitch, s.n.* (Holotype, NY!)

        Laphamia peninsularis Greene, Bull. Calif. Acad. 1:8. 1884. TYPE: MEXICO: Baja California, Scammon's Lagoon, collector unknown. (Fragment of type, US! Isotype, GH!).

        Perityle rotundifolia (Benth.) T. S. Brandeg., Zoe 4:210. 1893.

Plants suffruticose, spreading perennials, 20–45 cm high, or bushy annuals to 80 cm high, upper stems branching, densely glandular-pubescent; leaves glandular-pubescent, 2–1(–9) cm long, 1.0–4.5(–6.0) cm wide, usually cordate to cordate-reniform, or ovate to ovate-deltoid, shallowly lobed, rarely deeply so, and serrate-dentate to doubly so; petioles of lower leaves 1.0–3.5(–5.0) cm long, upper leaves shorter-petioled; capitulescence of several heads borne on rather stout peduncles 1–4 cm long; heads 6–9 mm high, 7–12 mm wide; involucres hemispherical; bracts 4.5–6.0 mm long, 1.8–2.5 mm wide, broadly oblanceolate to narrowly obovate, keeled, glandular-pubescent; ray flowers 12–20, ligules oblong, 7–10 mm long, 1.8–2.0 mm wide; disc corollas 3.0–3.5 mm long, throats tubular-funnelform, 1.8–2.0 mm long; styles linear 1.0–1.5 mm long, tapering to a point; achenes 2.0–2.5(–3.5) mm long, linear, faces glabrous, angles ciliate with short antrorsely appressed hairs, the whitish

hairs pointed and straight to slightly curved; pappus absent; anthers ca 1.5 mm long; chromosome number, $n = 18(17)$.

Found throughout the middle two-thirds of the Baja California peninsula and San Martin Island especially in rocky or bluff habitats but also in sandy soil. Apparently flowering the year around, but less often during the hot summer months. (fig. 1).

Representative specimens: Mexico: Baja California. San Martin Island, *Anthony 218* (CAS, GH, POM, UC, US); San Martin Island, *T. Brandegee s.n.* (GH, UC, US); 4.5 km N of Catavina, *Carter, Alexander, and Kellogg 1882* (GH, US); 8.8 km N of Catavina, *Carter and Kellogg 3004* (GH, SD, US); San Quintin, *Epling s.n.* (NY); Rancho San Luis, *Harbison s.n.* (SD); 4 mi S of Barril, *Harbison 41620* (SD); grade between Barril and Calmalli, *Harbison 41858* (RSA, SD, UC); 35 mi N of Punta Prieta, *Harbison and Stover s.n.* (SD); Hassler Cove, San Martin Island, *Moran 10510* (SD, UC, US); ca 5 mi SW of El Potrero, *Nelson and Goldman 7256* (US); San Quintin Bay, *E. Palmer 706* (ARIZ, CAS, GH, NY, US); 56 mi N of Arroyo de Catavina, *Porter 167* (CAS, GH); Calmalli, *Purpus 176* (US); 5–10 mi N of Catavina, *Wiggins 4391* (US); ca 5 mi W of Los Emes, southern Sierra San Pedro Martir, *Wiggins 9921* (US); sand dunes W of San Quintin Bay, *Wiggins 11895* (DS, SD, TEX, UC, US). Baja California Sur. Purisima, *Brandegee s.n.* (UC, US); Arroyo Hondo, N side of Cerro de la Giganta, *Carter, Alexander, and Kellogg 2021* (US); W peak of Pilon de las Parras, W of Loreto, *Carter and Sharsmith 4235* (NY, US); Mulege, *Johnson 3676* (CAS, GH, NY, UC, US); Cayuca Ranch, Loreto, *Jones 27736* (POM, UC); Volcan las Tres Virgenes, *Moran 11694* (SD, UC); N of Cerro San Luis, *Moran and Hendrickson s.n.* (SD); ca 44 mi S of El Arco, *Powell and Sikes 1652* (SRSC); ca 20 mi W of Santa Rosalia, *Powell and Sikes 1654* (SRSC); bluff road around Bahia de la Concepcion, *Powell and Sikes 1660* (SRSC).

Amauria rotundifolia always can be distinguished from *A. brandegeana* by achene pubescence, as indicated in the key to species. Additionally, this taxon usually is readily identified by its leaves, which are cordate or cordate-reniform and not deeply lobed. For some specimens, however, the leaves are rather deeply and somewhat irregularly lobed, and thus resemble *A. brandegeana* in this character. When compared to *A. brandegeana* other useful diagnostic features of *A. roundifolia* include: Lignescent basal stems and perennial habit; thicker leaves that are less densely glandular-puberulent; larger heads; wider bracts; more numerous ligules; longer disc corollas; styles tapering to a point; and achenes with no callous crown. According to the label-data of other collectors and my own limited field observations, *A. rotundifolia* occurs most typically as a perennial in the crevices of rocky bluffs. The taxon also exists as a soil-dwelling annual, according to label data, and I have seen one annual population in the field *(Powell and Sikes 1652)*. Seemingly it is the soil-dwelling forms that most resemble *A. brandegeana* in habit characteristics.

The holotype of *A. rotundifolia* has not been examined, but Bentham's description (particularly achene morphology) leaves little doubt about its validity. Rose (1890) has formulated useful explanations with regard to the synonymy.

3. AMAURIA BRANDEGEANA (Rose) Rydb., N. Amer. Fl. 34:30. 1914.
   fig. 2.
   Perityle brandegeana Rose, Bot. Gaz. 15:114. 1890. TYPE:
   MEXICO: Baja Calif., Lagoon Head, 6–15 Mar 1889, *E. Palmer
   800* (Holotype, US! Isotypes, ARIZ! CAS! GH! NY! US!).

Plants delicate or robust annuals, 10–45 cm high, upper stems glandu-
lar-pubescent and short-hirsute; leaves short-hirsute and glandular-
pubescent to sparsely so, 2–7 cm long, 1.5–4.0 cm wide, cordate, ovate,
or ovate-deltoid, shallowly to deeply 3–5 lobed with the segments irregu-
larly serrate or dentate, usually doubly so; petioles of lower leaves 0.5–
4.0 cm long, upper leaves sessile or shorter-petioled; capitulescence of
several heads borne on peduncles 1–4 cm long; heads 6–8 mm high, 6–9
mm wide; involucres campanulate to hemispherical; bracts 4–5 mm long,
1.0–1.5 mm wide, oblanceolate to broadly so, keeled, glandular-puberu-
lent; ray flowers 10–18, ligules broadly oblong or subovate, 5–9 mm
long, 2–5 mm wide; disc corollas 2.0–2.5 mm long, throats tubular-
funnelform to narrowly campanulate, ca 1.0 mm long; styles flattened,
slender, ca 1.0 mm long, slightly spatulate and obtuse; achenes 2.0–2.5
mm long, linear, angles and faces pubescent with brownish peculiarly in-
curled hairs the entire achene length; pappus absent, but with a callous
crown; anthers ca 1.0 mm long; chromosome number, **n = 18.**

A winter annual of southern Baja California (State) and most of Baja
California Sur including Magdalena Island. Flowering Oct.-Apr. (fig. 1).

Representative specimens: MEXICO: Baja California. ca 15 mi N of El Arco,
Powell and Sikes 1649 (SRSC); 17 mi S of Rancho Rosarito, *Powell and Turner
1809* (SRSC); Miller's Landing, *Wiggins 7755* (TEX, US); 10 mi S of San Augus-
tine, *Wiggins 7589* (TEX); 35 mi S of Punta Prieta, *Wiggins 11303* (GH, UC, US);
Rancho Mesquital, *Wiggins 11334* (GH, UC, US). Baja California Sur. 56 km S of
El Arco, *Carter, Alexander, and Kellogg 1941* (GH, US); eastern bajada of Sierra
Calvario, Sierra Viscaino, *Gentry 7384* (ARIZ, UC); Magdalena Island, *Orcutt 53*
(CAS, GH, NY, US); Estero Salinas, *Porter 463* (CAS); 30 mi S of Santa Rosalia,
Powell and Sikes 1658 (SRSC); 25 mi S of El Arco, *Powell and Turner 1819*
(SRSC); ca 11 mi N of Mulege, *Powell and Turner 1834* (SRSC); 26 mi W of
San Javier, *Powell and Turner 1846* (SRSC); 27 mi N of San Ignacio, *Sikes and
Babcock 293* (SRSC); 4 mi SE of El Arco, *Thomas 8313* (DS); 22 mi S of Pozo
Aleman, *Wiggins 7850* (TEX, US); 12 mi N of La Purisima, *Wiggins 11469* (CAS,
GH, UC, US); Estero Salinas, *Wiggins 11476* (CAS, GH, UC, US); 3.5 mi N of
Aripes, W end of Bahia de la Paz, *Wiggins 14667* (CAS, TEX, UC); 9.5 mi S of
El Solito, Viscaino Desert, *Wiggins 15130* (CAS); 34 mi SW of San Ignacio, *Wig-
gins 15195* (CAS, GH).

The superficial appearances of *A. brandegeana* and *Perityle emoryi*
are strikingly similar. In fact, herbarium specimens of the two taxa have
been misidentified by numerous workers, and occasionally they were
erroneously annotated by Everly, who was familiar with both species. I
have found that herbarium specimens of *A. brandegeana* can best be
identified macroscopically by the presence of rather long ligules (5–9
mm), but this character is variable, and usually it is necessary to resort
to microscopic examination of the achenes. The achenes of *A. brandege-*

ana are epappose, 4-angled, and have unique, in-curled hairs on the faces and angles, while the achenes of *P. emoryi* are typically 2-angled, pubescent only on the margins, and have a pappus of a bristle and/or squamellae. However, in many populations of *P. emoryi,* especially on Magdalena Island (Powell, unpublished), the outer achenes are 3-angled, epappose, and pubescent on the surfaces as well as the margins. In such cases, particularly in inferior specimens, species identification is difficult. I have considered the possibility that the two taxa might occasionally hybridize, but there is as yet no evidence for the idea. The species are geographically sympatric in Baja California, although apparently not populationally mixed, and both are known to occur on Magdalena Island. Distributional considerations suggest that the endemic *A. brandegeana* and the widespread, weedy *P. emoryi* do have ecological differences. Chromosomal data offer little support for the possibility of hybridization since numerous counts for *P. emoryi* (Powell, 1968b) indicate that it is always hexaploid. There have been no counts of *P. emoryi* from Magdalena Island.

In addition to the characters already mentioned, *A. brandegeana* is distinguished from *A. rotundifolia* by: Annual habit; thinner leaves which are densely glandular-pubescent; smaller heads; narrower bracts; fewer ligules; shorter disc corollas; obtuse styles; achenes with a callous crown.

LITERATURE CITED

BENTHAM, G. 1844. Botany of the Voyage of H.M.S. Sulphur. 31–32.

BRANDEGEE, T. S. 1893. Southern extension of California flora. Zoe 4:210.

EVERLY, M. L. 1947. A taxonomic study of the genus *Perityle* and allied genera. Contrib. Dudley Herb. 3:375–396.

POWELL, A. M. 1968a. Additional discussions pertaining to the congeneric status of *Perityle* and *Laphamia* (Compositae). Sida 3:270–278.

————. 1968b. Chromosome numbers in *Perityle* and related genera (Peritylanae-Compositae). Amer. J. Bot. 55:820–828.

————. 1969. Taxonomy of *Perityle* section *Pappothrix* (Compositae-Peritylanae). Rhodora 71:58–93.

————. 1970. Natural intersectional hybridization in *Perityle* (Compositae). Brittonia 22:3–10.

————. 1972a. New species of *Perityle* and *Amauria* (Compositae). Madroño 21:456–458.

————. 1972b. Artificial hybridizations in the subtribe Peritylanae (Compositae-Helenieae). Amer. J. Bot. 57:760–768.

————. 1972c. *In* IOPB chromosome number reports. Taxon 21:344.

————. In press. Taxonomy of *Perityle* section *Laphamia* (Compositae-Peritylanae). Sida.

————, and H. S. Tsang. 1966. Preliminary chromatographic studies of *Laphamia* and related genera of Compositae. Southw. Nat. 11:190–195.

ROSE, J. N. 1890. Preliminary notes on *Perityle*. Bot. Gaz. 15:113–119.

RYDBERG, P. A. 1914. Carduaceae-Helenieae-Peritylanae. N. Amer. Fl. 34:11–27.

TURNER, B. L. 1966a. Taxonomy of *Eutetras* (Compositae-Helenieae). Southw. Nat. 11:118–122.

————. 1966b. Taxonomy of *Oxypappus* (Compositae). Sida 2:431–433.

HIGH POLYPLOIDY AND THE ORIGIN OF
BALSAMORHIZA MACROPHYLLA (COMPOSITAE)

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Balsamorhiza comprises about 12 species of perennial sunflowers native to the western and northwestern United States and adjacent parts of Canada. Strong morphological and ecological evidence suggests that when ecological barriers are broken between most species of *Balsamorhiza*, natural hybridization occurs (Maguire, 1942; Ownbey and Weber, 1943). *Balsamorhiza macrophylla* Nutt. is therefore unusual in being one of the few entities in the genus in which natural hybridization is unknown. Although the species is relatively uniform, it is intermediate in a number of characteristics between certain species pairs with which it is sympatric or nearly so.

Cytological examination has indicated that *B. macrophylla* is a high polyploid, with $n = 100 \pm 2$ (Table 1). Since related species all have $n = 19$ (Weber, 1946; and Table 1), *B. macrophylla* is so far known only as an approximate decaploid, with no intermediate ploidy levels recorded.

In this report the putative origin of *Balsamorhiza macrophylla* is discussed, as a basis for further investigations, in terms of the available karyological data and some morphological comparisons. These comparisons have been extended to the genus *Wyethia*, which is so closely related to *Balsamorhiza* that the distinction of the two genera has been questioned (Weber, 1946).

Materials and Methods

Qualitative morphological comparisons were made from living material of *B. macrophylla* Nutt., *B. sagittata* (Pursh) Nutt., *B. hookeri* Nutt. vars. *hispidula* (Sharp) Cronq. and *idahoensis* (Sharp) Cronq. and *Wyethia amplexicaulis* Nutt. (Table 2). Field data include notes on occurrence in relation to plant association, soil type, elevation, and water regime, and were collected for all the above-mentioned taxa and for some putative hybrid populations. Limited breeding experiments have also been undertaken.

Cytological observations were made from squash preparations of meiotic pollen mother cells. Buds were fixed in ethanol:acetic acid (3:1), stored in 75% ethanol under refrigeration, squashed in 1% aceto carmine, and examined with phase contrast. Voucher specimens have been deposited in the Garrett Herbarium, University of Utah (UT).

TABLE 1. NEW CHROMOSOME NUMBERS IN BALSAMORHIZA

Species	Gametic number	Locality
B. hookeri var. hispidula	19,20 (fig. 1,2)	Mouth of Big Cottonwood Canyon, Salt Lake Co., Utah, N. Helton 5.
B. hookeri var. idahoensis	19	3 mi. n. of Sweet, Gem Co., Idaho, N. Helton 27.
B. macrophylla	100±2 (fig. 3)	Parleys Canyon at cutoff to East Canyon, Salt Lake Co., Utah, N. Helton 52.

OBSERVATIONS AND DISCUSSION

Chromosome numbers and meiotic behavior. Chromosome numbers of **n** = **19** have been reported for *B. sagittata, B. deltoidea, B. careyana, B. rosea, B. serrata* and *Wyethia amplexicaulis* by Weber (1946). In the present study chromosome numbers of **n** = **19** have been confirmed for *B. sagittata* and *W. amplexicaulis,* and for putative hybrids between *B. sagittata* and the two varieties of *B. hookeri.* New species records have been made for the two varieties of *B. hookeri* and for *B. macrophylla* (Table 1). The only exceptions to the number **n** = **19** were in one population of *B. hookeri* var. *hispidula* from which **n** = **20** was also recorded (figs. 1, 2), and in *B. macrophylla* from which the recorded number was **n** = **100** ± **2** (fig. 3).

Balsamorhiza macrophylla is therefore approximately 10-ploid in relation to its congeners, and may be separated by a sharp karyological discontinuity. In the Compositae the only species known with chromosome numbers equalling or possibly exceeding that of *B. macrophylla* are three species of *Werneria* of the Peruvian highlands, with numbers of **2n** = ca **206** and **2n** = ca **213** (Diers, 1961).

Chromosome pairing behavior in the diploid taxa appeared to be normal, except for a low frequency of cells in populations of *B. hookeri* var. *hispidula,* in which anaphase bridges and lagging chromosomes were observed and also for some irregularity in some hybrid plants. Pairing behavior in *B. macrophylla* was highly regular (fig. 3), as most chromosomes were associated in normal bivalents, and maximum association observed was four quadrivalents. Diploidization is thus essentially complete in the materials examined.

Morphological comparisons. Balsamorhiza contains two sections, *Artorhiza* and *Balsamorhiza,* that are closely related but show some clear morphological differences. The two sections are also generally distinct ecologically (see below). Section *Artorhiza* is characterized by large, deep-seated caudices surmounted by multiple crowns, and the leaves generally have entire margins. Section *Balsamorhiza,* however, has much smaller caudices and often produces short, thick rhizomes that eventually produce separate rosettes, and mature plants have a simple crown bearing a single rosette of variously pinnatifid leaves.

Table 2.   Morphological Characteristics in Balsamorhiza and Wyethia

	B. sagittata	B. hookeri var. hispidula	B. macrophylla	W. amplexicaulis
Stem:				
length	2 to 6.5 dm	0.6 to 3 dm	3 to 10 dm	3 to 8 dm
vestiture	tomentose	pilose-hirsute, eglandular	pilose-glandular to glabrate	glabrate
Basal leaf:				
shape	deltoid	oblong-lanceolate	oblong-lanceolate	oblong-lanceolate
margin	entire	pinnately divided	pinnate or pinnately cleft	entire to denate
length	30 cm	10 to 40 cm	30 to 60 cm	20 to 40 cm
width	5 to 15 cm	c.5 to 15 cm	6 to 15 cm	5 to 15 cm
vestiture:				
abaxial	silvery tomentose to velutinous	sparsely hispid, hispid-pilose to hispidulose on margins	crisp hirsute to glabrous, hirsute-ciliate on margins	glabrous
adaxial	cinereous-strigulose	globular-resinous hispid, hispid-pilose to hispidulose on veins	glandular, crisp hirsute on veins, glabrous	glabrous
Phyllary:				
shape	ovate-lanceolate to lanceolate	linear to linear-lanceolate	lanceolate, oblong-lanceolate	ovate-lanceolate
apex	acuminate or attenuate	acute to acuminate	acute to acuminate	acute to acuminate
Ray:				
shape	oblong-lanceolate	not available	broadly oblong-elliptical	ovate-lanceolate
no. per head	mostly 13 to 21 (8 to 25)	10 to 16	8 to 16	6 to 16
length	2 to 4 cm	2.5 to 3 cm	3.5 to 5.5 cm	2.5 to 5 cm
Head:				
no. per peduncle	solitary or 2 or 3	solitary	solitary	several, occasionally solitary
diameter	6 to 8 cm	4.5 to 6 cm	8 to 12 cm	4 to 10 cm
Achene:				
length	7 to 8 mm	6 to 7 mm	8 to 10 mm	8 to 10 mm
pappus	absent	absent	absent	present
Root:				
habit	deep tap-root	carrot-like tap-root	deep tap-root	deep tap-root
surface	rough	smooth	smooth	smooth
Caudex habit	multiple crown of erect branches	simple crown	multiple crown of erect branches	multiple-crown of erect branches
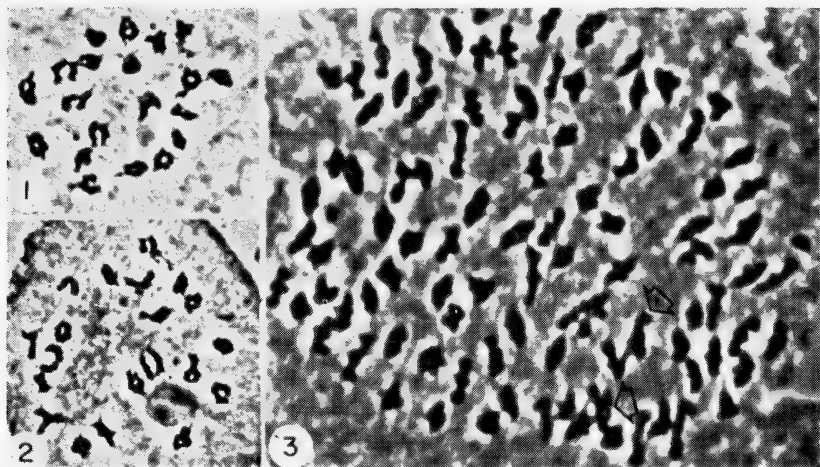
FIGS. 1–3. Meiotic chromosomes (diakinesis) in *Balsamorhiza*. 1 and 2, *B. hookeri* var. *hispidula*, **n = 20** (× ca 800); 3, *B. macrophylla*, **n = ca 100** (× ca 1080), multivalents indicated by arrows.

Morphological comparisons are provided in Table 2 for *B. sagittata* (sect. *Artorhiza*), *B. hookeri* var. *hispidula* (sect. *Balsamorhiza*), *B. macrophylla* and *W. amplexicaulis. Balsamorhiza macrophylla* is usually placed in section *Balsamorhiza* because of its pinnately dissected leaves. However, the root-caudex of *B. macrophylla* has characteristics intermediate between the two sections, viz., a large taproot with multiple crowns that produce rhizomes in immature plants.

Analysis of the morphological characters expressed in *B. sagittata, B. hookeri* var. *hispidula* and *B. macrophylla* indicates that the latter has features that are intermediate between the other two taxa. *Balsamorhiza macrophylla* is similar to *B. hookeri* var. *hispidula* in root habit, basal leaf shape, basal leaf margin, distribution of trichomes on the basal leaf surfaces, and trichome characteristics of the phyllaries (Table 2). The characters common to *B. macrophylla* and *B. sagittata* are the multiple-crowned caudex, shoot habit, length of root and shape of phyllary. However, *B. macrophylla* has some characters that are unknown in these or any other species of the genus, viz., glabrous stems and basal leaves (including the petiole base) and the large size of the stems, leaves, heads, phyllaries, and achenes. These characteristics do occur in *Wyethia. Balsamorhiza macrophylla* thus appears to combine characters of the two sections of the genus, and perhaps also of the genus *Wyethia*.

Geographic distribution and ecological requirements. There are some differences in the broad habitat requirements of the two sections of *Balsamorhiza* and only rarely do species of the two sections occur in close proximity. Species of section *Artorhiza* seem to prefer deep, well-drained,

often rocky but fairly fertile soils. In contrast, members of section *Balsamorhiza* mostly occupy shallow, sterile, rocky soil, primarily in xeric habitats. *Balsamorhiza macrophylla* and another meadow species, *B. incana,* are notable exceptions.

Balsamorhiza macrophylla is not widespread; it occurs in large populations in the lower and middle montane areas of northern Utah, southwestern Idaho, western Wyoming, and southwestern Montana. The ranges of *Balsamorhiza hookeri* and *B. sagittata* either widely overlap or interdigitate with that of *B. macrophylla* (fig. 4). *Balsamorhiza hookeri* var. *hispidula* is found in small populations throughout the Great Basin at relatively low elevations along the foothills of various mountain ranges. Populations of this species sometimes occur in close proximity to those of *B. macrophylla* along the western slopes of the Wasatch Mountains in north central Utah. *Balsamorhiza sagittata* is the most widely distributed species in the genus; its range overlaps the ranges of both the above-mentioned species and extends as far north as southern British Columbia, south to California, east to the Black Hills of South Dakota, and into western Colorado. In northern Utah, *B. sagittata* occurs primarily in lower montane regions where it is often close to populations of both *B. macrophylla* and *B. hookeri* var. *hispidula.*

Wyethia is confined to the western United States. Two species occur within the area of *B. macrophylla* (Weber, 1946), and one of these, *W. amplexicaulis,* is distributed in close proximity to the three species of *Balsamorhiza* mentioned above.

Ecological studies of foothill grasslands on the Wasatch Mountains present good evidence that *B. sagittata* and *B. macrophylla* belong to separate and distinct plant associations (Kleiner and Harper, 1966). *Balsamorhiza sagittata* is found primarily in a stable community containing equal percentages of annuals and perennials. By contrast, *B. macrophylla* favors a more disturbed habitat characterized by a higher percentage of annuals. Further investigation by Ludwig (1969) produced statistical evidence that *B. sagittata* and *B. macrophylla* also have different soil preferences. While *B. sagittata* occupies soils of high rock content, low percent clay, and comparatively low moisture content, *B. macrophylla* is found in soils of significantly lower rock content, high percent clay, and higher moisture content. Ludwig's analysis did not include *B. hookeri* var. *hispidula,* but observations made during the present study indicate that this species prefers sterile, rocky soils of low water content.

Balsamorhiza macrophylla also appears to have a level of frost tolerance higher than other species of the genus. During breeding experiments it was observed that both enclosed and exposed heads of *B. sagittata* plants were killed by late frost, while heads of adjacent plants of *B. macrophylla* were unaffected. Other parts of the plants of both species showed no apparent damage. It may be noted that *W. amplexicaulis* also has high frost tolerance (Weber, 1952). While *W. amplexicaulis* occurs
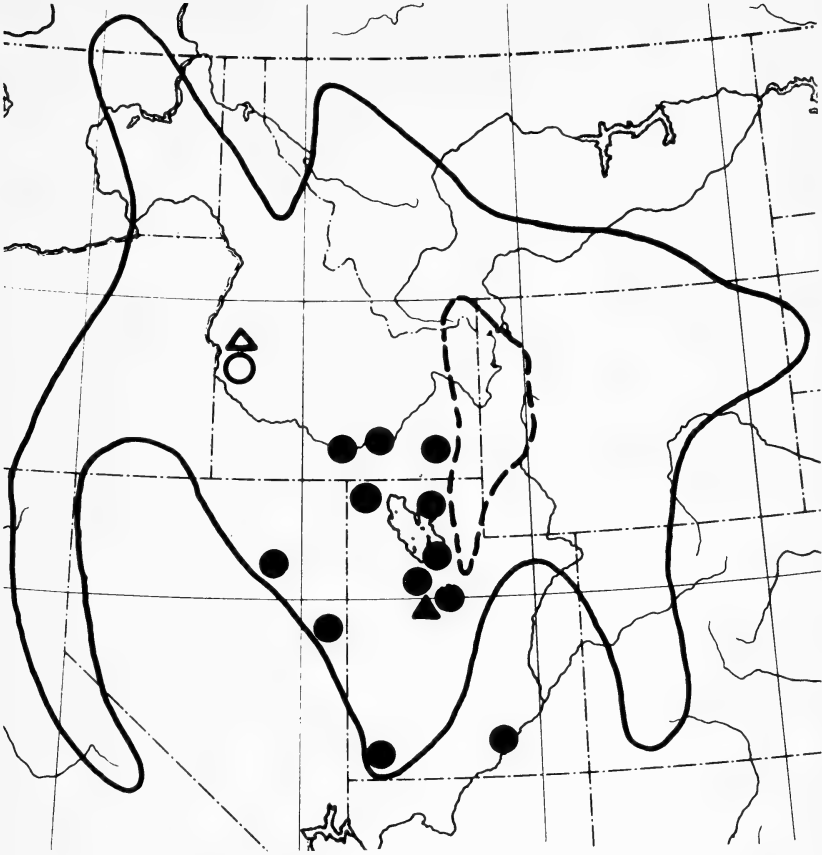
Fig. 4. Western United States, showing approximate distribution of four *Balsa-morhiza* entities and putative hybrids. *B. sagittata,* solid line; *B. macrophylla,* dash line; *B. hookeri* var. *hispidula,* solid disk; *B. hookeri* var. *idahoensis,* open disk; *B. sagittata* × *hookeri* var. *hispidula,* solid triangle; *B. sagittata* × *hookeri* var. *idahoensis,* open triangle.

in a different plant association than either *B. sagittata* or *B. macro-phylla,* its soil preferences with regard to percent of rock, clay, and water are almost identical to the soil preferences of *B. macrophylla* (Kleiner and Harper, 1966; Ludwig, 1969).

Hybridization in Balsamorhiza. Floral initiation in *Balsamorhiza* occurs at least four years after seedling establishment. Extended breeding tests have not been made, and observations on breeding have been made entirely in the field.

Several cases of natural hybridization in *Balsamorhiza* have been reported. Intersectional hybridization has been described by Maguire (1942), Ownbey and Weber (1943) and Stutz (in Drobnick and Plummer, 1966). Ownbey and Weber (1943) have drawn attention to the

curious situation that infrasectional isolation seems to be stronger than intersectional isolation, and discussed the phenomenon in relation to introgression and the origin of new taxa.

An analysis has been made of the recombination of some characters in a putative hybrid population between *B. sagittata* and *B. hookeri* var. *hispidula* found in Provo Canyon, Utah Co., Utah. The relationship between leaf base characters (sagittate in *B. sagittata* and acute in *B. hookeri* var. *hispidula*) and leaf margin characters (entire in *B. sagittata* and pinnately divided in *B. hookeri* var. *hispidula*) is approximately linear (fig. 5). The distribution is widely scattered on either side of the regression line, however, indicating a considerable amount of recombination. Field observations confirmed that putative hybrids more nearly resembling one parent generally occurred in close proximity to populations of that parental species. The approximately linear relationship between leaf base and leaf margin recorded in the above analysis, and the high frequency of individuals morphologically close to parental types suggest that backcrossing and introgression may be taking place.

Reciprocal crosses were attempted in the field, involving *B. sagittata, B. hookeri* var. *hispidula* and *B. macrophylla*. Inflorescence buds of these three species were also kept enclosed in cheesecloth covers for the duration of the flowering period. The only seeds obtained were from the crosses *B. sagittata* × *B. hookeri* var. *hispidula* (33 seeds) and *B. macrophylla* × *B. hookeri* var. *hispidula* (7 seeds). The seeds were planted in flats in the following fall. A low percentage of seeds of *B. sagittata* × *B. hookeri* var. *hispidula* germinated early in the next spring, but no seeds of the *B. macrophylla* × *B. hookeri* var. *hispidula* cross germinated. The seedlings were accidentally killed later in the season.

The results of the crossing program, being very limited, must be interpreted with caution. It may be suggested (1) that the species tested will cross in some combinations, and at least in one case produce viable seed, and (2) that the species are not self-pollinated (at least without the aid of a pollen vector). Apomixis is not likely to be involved.

There are no published accounts of natural hybridization involving *B. macrophylla,* nor of hybridization between *Balsamorhiza* and *Wyethia*.

General Discussion

Balsamorhiza macrophylla appears to have an anomalous position with regard to the current taxonomy of the genus. It is intermediate between the two sections of the genus in its combination of morphological characters and in some aspects of its habitat requirements. The species also has some morphological and physiological characters that are unusual in *Balsamorhiza* but are present in the closely related genus *Wyethia*. The geographic distribution of the species is consistent with a putative hybrid origin from parental stocks in the two sections of *Balsamorhiza* and perhaps also in *Wyethia*.
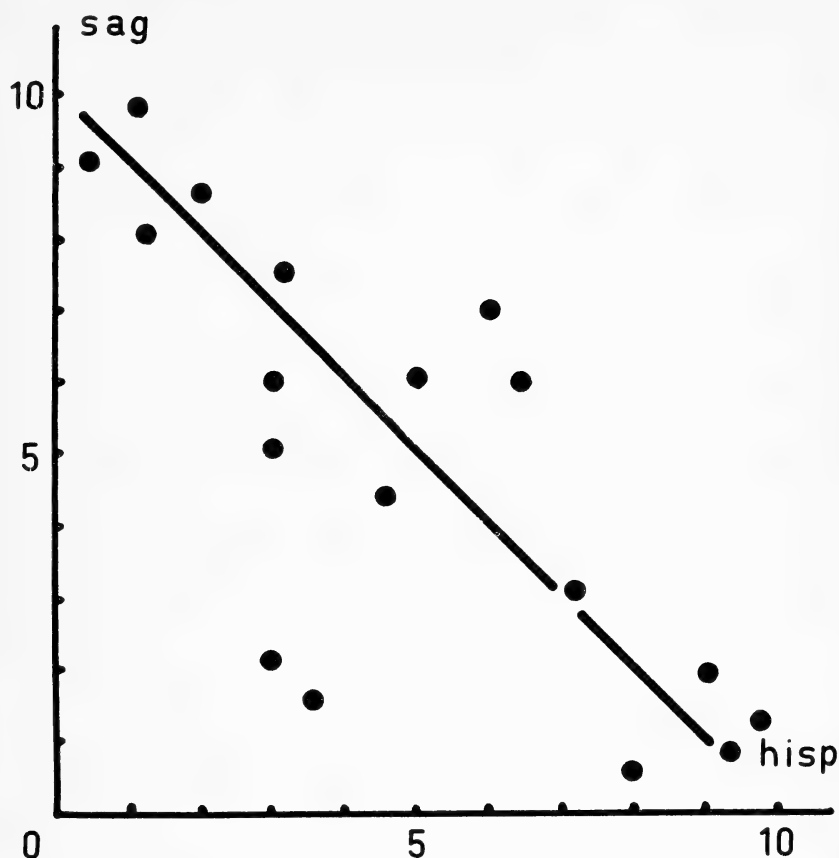
Fig. 5. Relationship between leaf base and leaf margin characters in a putative hybrid population between *B. sagittata* (sag) and *B. hookeri* var. *hispidula* (hisp). Character expression has been estimated on 10-point scales.

Intersectional hybridization in *Balsamorhiza* is well documented. It is clear from studies of segregation in putative hybrids between *B. sagittata* and *B. hookeri* var. *hispidula* that many characters of *B. macrophylla* may be derived from this parental combination, and they may reasonably be regarded as putative parents of the latter species. It is also possible, of course, that selection and adaptation in a hybrid population derived from these parents may also result in the establishment of characters that occur in neither parent. Thus, while some characters of *B. macrophylla*, such as glabrous stems and frost tolerance, may be taken subjectively to indicate involvement of *Wyethia* in the origin of *B. macrophylla*, there is no other evidence for this proposition, and these characters may also have been established following segregation and selection

in infrageneric hybrids. It is further possible that characters such as frost tolerance may be a consequence of polyploidy *per se* (Löve and Löve, 1957). Conversely *B. macrophylla* has no characters in common with *B. sagittata* that are not also expressed in *Wyethia amplexicaulis,* and an origin for *B. macrophylla* from a simple intergeneric cross could also be proposed. A more intensive morphological analysis is obviously required to clarify the relationships of the species.

Balsamorhiza macrophylla nevertheless appears to be a hybrid entity that has been fixed by polyploidy. The very high ploidy level involved, and the relatively high fertility of the diploid hybrids examined, indicate that the establishment of polyploidy has not been primarily in response to selection against partial sterility. The high ploidy level recorded must have been established in response to very strong selection for conservation of an adaptive genotype. This is borne out by the apparent uniformity of the entity.

An important requirement for further study is a detailed analysis of variation in *B. macrophylla* throughout its range, coupled with an intensive cytogeographic survey. It is important to determine the extent of the ca 10-ploid state, and whether any other ploidy levels exist in the species. It may be noted that the present chromosome count is from near the southern extremity of the distribution of the species. A search for other ploidy levels and an analysis of variation in this taxon will have an important bearing on our understanding of its age, origin, and taxonomic status.

Conclusions

Morphological, ecological, and cytological considerations suggest that *B. macrophylla* has had its origin through hybridization. The origin of the species may have been through a wide cross involving members of the two sections of *Balsamorhiza* and/or *Wyethia,* bringing together the vigorous, somewhat weedy nature of some taxa, the soil requirements of others, and such characters as frost tolerance. It is suggested that the new form was successful in disturbed habitats with deep soils at mid elevations in the Wasatch and similar mountain ranges. This adaptive biotype has been conserved by establishment of a high polyploid race. Further understanding of the origin of *B. macrophylla* requires an intensive morphological and cytogeographic analysis.

Acknowledgments

LITERATURE CITED

DIERS, L. 1961. Der Anteil an Polyploiden in den Vegetationsgürteln der Westkordillere Perus. Z. Bot. 49:437–488.

DROBNICK, F. and A. P. PLUMMER. 1966. Progress in browse hybridization in Utah. Western Assoc. State Fish Game Comm. Proc. pp. 203–211.

KLEINER, E. F. and K. T. HARPER. 1966. An investigation of association patterns of prevalent species in Red Butte Canyon, Salt Lake County, Utah. Proc. Utah Acad. Sci. 43:29–36.

LÖVE, A. and D. LÖVE. 1957. Arctic polyploidy. Proc. Genet. Soc. Can. 2:23–27.

LUDWIG, J. 1969. Environmental interpretation of foothill grassland communities of northern Utah. Ph.D. Thesis, Department of Biology, University of Utah, Salt Lake City.

MAGUIRE, B. 1942. Three natural hybrids of the Compositae in *Wyethia* and *Balsamorhiza*. Amer. J. Bot. 19:695. (Abstract).

OWNBEY, M. and W. A. WEBER. 1943. Natural hybridization in the genus *Balsamorhiza*. Amer. J. Bot. 19:695. (Abstract).

WEBER, W. A. 1946. A taxonomic and cytological study of the genus *Wyethia,* family Compositae, with notes on the related genus *Balsamorhiza*. Amer. Midl. Naturalist. 35:400–452.

————. 1952. The glabrate form of *Wyethia arizonica.* Leafl. W. Bot. 5:223–225.

NOTES AND NEWS

HAPLOPAPPUS LYALLII GRAY (COMPOSITAE), A NEW RECORD FROM CALIFORNIA—*Haplopappus lyallii* Gray is a cespitose perennial found in alpine habitats between elevations of 5,500 and 11,000 feet in the northwestern U.S. and British Columbia. On August 11, 1970, I collected this species in northern Trinity Co., Calif. (T36N, R11W, Sec. 12; *Ferlatte & Howard 1308*: HSC, UC), approximately 230 miles from its nearest known localities in the Blue Mts. of Baker Co., Oregon, and the mountains of northeast Nevada (Hitchcock, C. L., et al. 1955. Vascular Plants of the Pacific Northwest. Part 5: Compositae, by Arthur Cronquist, Univ. of Wash. Press, Seattle, p. 220.). There are approximately two dozen plants growing in dry, decomposed granite at an elevation of 8,800 feet on the west ridge of Thompson Pk. *Haplopappus lyallii* has also been collected about one mile to the south on the crest between Canyon Cr. and the Rattlesnake Cr. drainage (T36N, R11W, Sec. 13; *J. O. Sawyer 2337*: HSC, July 22, 1970). Associated species include the following: *Hieracium gracile* Hook., *Draba howellii* Wats., *Lupinus lobbii* Gray ex Greene, and *Pinus albicaulis* Englem.—WILLIAM J. FERLATTE, California Department of Agriculture, Sacramento 95823.

MALACOTHRIX TORREYI (COMPOSITAE) IN CALIFORNIA.—Apparently *Malacothrix torreyi* Gray has been collected in California on only one or two occasions. One collection was made by Annie M. Alexander and Louise Kellogg on June 4, 1946, "seven miles east of Eagleville, Modoc Co., elevation 5150 feet" (UC). However, the state line is exactly six miles east of Eagleville, though undoubtedly unmarked or poorly marked in this area, and it is likely that this collection is actually from Nevada. A second and slightly less equivocal record of this species in California was made on July 2, 1967, on disturbed gravelly soils derived from basaltic rock at about 8500 feet just north of Masonic Peak in Mono Co. (*Hardham 15084*, CAS). The two dominant species at this site, *Pinus monophylla* and *Artemisia tridentata,* were of scattered occurrence and associated species were infrequent. The *Malacothrix* occurred on the upper margins of the pinyon community and was not observed at lower elevations.—CLARE B. HARDHAM, Creston Star Route, Paso Robles, California 93446, and GORDON H. TRUE, JR., 142 Margarita Drive, San Rafael, California 94901.

THE SOUTHERN EXTENSIONS OF TSUGA MERTENSIANA (MOUNTAIN HEMLOCK) IN THE SIERRA NEVADA

David J. Parsons

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The distribution and habitat preference of the most southerly extensions of *Tsuga mertensiana* (Bong.) Carr, commonly known as mountain hemlock, have never been fully documented. A dominant element of the subalpine forest to the north, the mountain hemlock in the southern Sierra Nevada of California is confined to scattered stands at elevations above 9,000 feet. At this end of its range the tree shows a strong preference for cooler, north-facing, granitic slopes, being commonly found in small compact stands at the heads of north or east-facing canyons or in sheltered ravines where snow lingers well into summer (Storer and Usinger, 1963).

Available literature, herbarium records, and communication with persons familiar with the high country of California indicated that the most southerly extension of *T. mertensiana* would be found in the southern part of Kings Canyon National Park. An intensive field search in this and adjacent areas of the High Sierra produced knowledge of a total of five distinct stands, three in Fresno County and two in Tulare County, which almost surely represent the most southerly outposts of this subalpine species. A reference by Sudworth (1908) to mountain hemlock in the San Jacinto mountains remains unverified and doubtful; this very possibly represents a *Pinus flexilis* location.

The five sites can be localized as follows (see fig. 1):

I. Silliman Creek (36°38′N; 9,650–9,800 ft. elevation). A small stand (50–70 individuals) of trees is located on the south side of Silliman Creek, about ½ mile below Silliman Lake on the northern border of Sequoia National Park (Triple Divide Pk. quad). Noted by Pusateri and Marshall in 1943 (personal communication) the Silliman Creek stand appears to be the southernmost confirmed stand of *T. mertensiana*. It is the only stand to be found within Sequoia National Park and one of two within Tulare County.

II. Vidette Meadows (36°45′N; 9,200–9,800 ft. elevation). A stand of mountain hemlock exists on north to northeast facing slopes on the south side of Bubbs Creek in lower Vidette Meadows, Kings Canyon National Park (Mt. Pinchot quad). The stand extends down Bubbs Creek towards Junction Meadow for nearly a mile.

III. Sphinx Creek (36°45′N; 9,600–9,900 ft. elevation). This small stand occupies a north slope along one of the upper forks of Sphinx Creek (Triple Divide Pk. quad) in Kings Canyon National Park and just over the Fresno County line in Tulare County. Approximately eleven miles to the northeast of the Silliman Creek site, this stand is the second most southerly location.

IV. Avalanche Creek (36°45′30″N; 9,050–10,000 ft. elevation). The largest stand (several hundred individuals) of *T. mertensiana* encountered in the present study
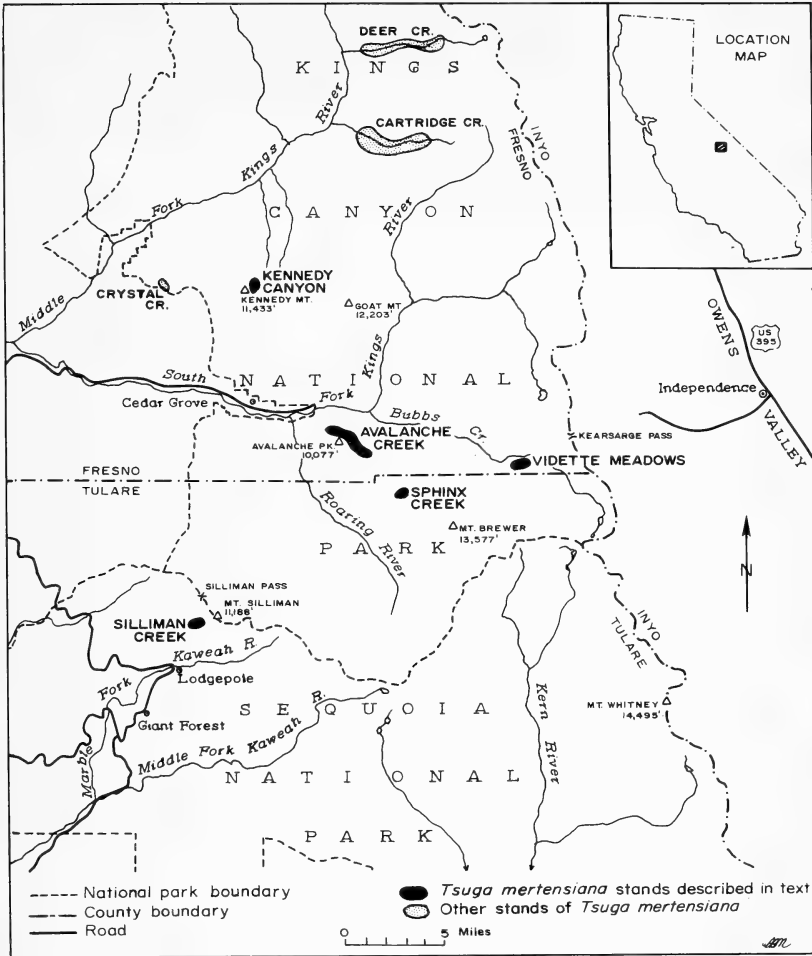
FIG. 1. Southern extensions of *Tsuga mertensiana* in the Sierra Nevada.

was found in the Avalanche Creek basin of Kings Canyon National Park (Marion Pk. quad), several miles to the west of Sphinx Creek site. This stand is located chiefly on north- to northeast-facing slopes.

V. Kennedy Canyon (36°53′N; 9,550–9,750 ft. elevation). Nine miles northwest of the Avalanche Creek site a stand of over 100 trees was located at the head of Kennedy Canyon (Marion Pk. quad). Equidistant between the Middle and South Forks of the Kings River, the Kennedy Canyon site is about seven miles north of Cedar Grove. Situated chiefly on northeast slopes, this stand includes the largest individuals encountered in the study (Table 1).

The Silliman Creek stand lies within the Kaweah River drainage while those at Vidette Meadows, Sphinx Creek, and Avalanche Creek are in

the drainage of the South Fork of the Kings River. Northward, through the drainage of the Middle Fork of the Kings (e.g., Kennedy Canyon, Crystal Creek, Cartridge Creek and Deer Creek—see fig. 1), stands of mountain hemlock become more extensive and more numerous.

The above-mentioned southern outposts of mountain hemlock are all on the western slopes of the Sierra. Only as far south as the latitude of Bishop does the species cross to the east side of the Sierra crest. There is a stand of a few mature trees and several smaller ones some two miles south of Lake Sabrina (Mt. Goddard quad), Inyo County, in a fault fracture in the granite between Emerald Lakes and Topsy Turvy Lake (37°10′30″N). This is apparently the highest occurrence of the species anywhere; the trees grow close to the 10,800-foot contour. A second stand (40 to 60 trees) lies a few miles to the north, immediately southeast of Horton Lake (Mt. Tom quad) at a latitude of 37°19′30″N and at an altitude of 10,000 feet.

Among the topographic variables that appear especially to influence the southernmost distribution of mountain hemlock are elevation and aspect. The altitudinal range of the species in the areas concerned is remarkably narrow. It varies from 9,050 to 10,000 feet on the western side of the Sierra and 10,000 to 10,800 feet on the eastern side. Northwards the tree is found at gradually lower elevations and in greater abundance. The north-facing aspect of the slopes on which all stands were encountered protects the trees from the hot, drying effects of the mid-day summer sun. Such sites are also likely to hold a snow cover late into summer.

In all cases the trees were found growing on parent material of granitic origin. They were found only where substantial amounts of mineral soil were available, and seemed to prefer loose, coarse-textured soils that maintained moderate but not excessive amounts of moisture throughout the summer. The lush undergrowth of moss and wildflowers so characteristic of these southern stands of *Tsuga* are further evidence of the moisture conditions and high humus content of the soils that are associated with the species in these areas. Talus slopes found above each of the five localities appear to be important in optimizing habitat conditions for the species due to the resultant moistening of the soil by seep water that drains from the rocky surface above.

The mountain hemlock is able to achieve upright posture and large dimensions even at the southern extremes of its distribution (Table 1). Sequoia and Kings Canyon National Park files contain a photograph of a mountain hemlock "with an estimated diameter of 72 inches and a height of 150 feet" found at the head of Crystal Creek (fig. 1). It has been suggested that "the tree might be larger than the S.A.F. champion for the species" (personal communication; John McLaughlin, Park Superintendent). Farther north, where it occurs as a dominant tree, the mountain hemlock is seldom known to achieve heights as great as 150 feet or diameters over 65 inches. Further evidence of the apparent present ecological suitability of these southernmost sites for mountain hem-

lock is seen in the large number of healthy juvenile trees in each of the areas studied. Reproduction is clearly vigorous, even in the southernmost Silliman Creek location. However, the hemlock here is never in the pure stands so typical of more northern locations but instead is interspersed with such other subalpine conifers as *Pinus contorta, P. monticola, P. balfouriana,* or *Abies magnifica.*

TABLE 1. SELECTED GROWTH FORM MEASUREMENTS OF
TSUGA MERTENSIANA FROM ITS SOUTHERNMOST EXTENSIONS

Location	Needle length (inches)	Cone length (inches)	Maximum diameter (inches)	Maximum height (feet)
Silliman Creek	.60–.75	1.8–2.0	35.0	80
Vidette Meadows	.25–.70	1.0–2.5	43.0	99
Sphinx Creek	.75–.80	1.8–2.2	28.4	80
Avalanche Creek	.30–.60	1.8–2.8	30.2	85
Kennedy Canyon	.30–.60	2.0–2.5	39.5	100
Horton Lake	.50–.70	2.4–3.2	28.5	62

ACKNOWLEDGMENTS

LITERATURE CITED

STORER, T. I., AND R. L. USINGER. 1963. Sierra Nevada natural history. Univ. of California Press, Berkeley, Calif.
SUDWORTH, G. B. 1908. Forest trees of the Pacific slope. Washington, D.C.

NOTES AND NEWS

HELEN M. GILKEY, 1886–1972.—Dr. Helen M. Gilkey, for many years a Professor and Curator of the Herbarium in the Department of Botany at Oregon State University, died recently at the age of 86. Dr. Gilkey moved to Corvallis in 1903, where she attended the university (then Oregon Agricultural College) and received her master's degree in 1911. In 1912, she entered the University of California, Berkeley, where she served as an illustrator for the departments of Botany and Physiology while working for her doctorate. She received the Ph.D. in 1915, submitting as her thesis a revision of the Tuberales of California, a work that was later published. Dr. Gilkey remained at Berkeley until 1918, when she moved back to Corvallis as an Assistant Professor and as Curator of the Herbarium. During her time at Corvallis, Dr. Gilkey continued as a world authority on the Tuberales and also authored or co-authored a number of books and articles on the flora of the Pacific Northwest, the most widely known being a Handbook of Northwest Flowering Plants, which went through several editions. She retired in 1951 and received the Distinguished Service Award of Oregon State University in 1969.

A PRELIMINARY REPORT OF THE MYXOMYCETES
FROM THE STATE OF IDAHO

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Four Myxomycetes previously have been reported from Idaho. *Prototrichia flagellifera* (Berk. and Br.) Rost. recorded by Macbride (1899) is synonymous with *Prototrichia metallica* (Berk.) Massee reported by Martin (1949), who also indicated *Arcyria versicolor* Phill. from this State. *Diderma lyallii* (Massee) Macbr. and *Physarum albescens* Macbr. were recorded by Hagelstein (1944) as was the latter species by Macbride and Martin (1934). The 36 species listed in this paper bring the total number of Myxomycetes found in Idaho to 40.

Most specimens were collected on decaying organic matter, usually wood, during the summer months of 1969 at elevations from 5,200 to 5,800 feet. The collections were obtained primarily from three different areas located near the mountainous central portion of the state: in the vicinity of the YMCA Camp Ponderosa north of McCall in Valley County; Camp Ee-Da-How north of Idaho City; and an area 12 miles northeast of Lowman. The latter two areas are both in Boise County. At least one collection of each species has been deposited in the University of California Herbarium at Berkeley and other available specimens given to the University of Idaho. The species names are those accepted by Martin and Alexopoulos (1969).

CERATIOMYXACEAE

Ceratiomyxa fruticulosa (Müll.) Macbr. Twelve miles northeast of Lowman.

LICEACEAE

Licea minima Fries. Near Camp Ee-Da-How, Idaho City.

L. variabilis Schrad. Twelve miles northeast of Lowman.

Tubifera ferruginosa (Batsch) J. F. Gmel. Near Camp Ee-Da-How, Idaho City.

RETICULARIACEAE

Lycogala epidendrum (L.) Fries. Near Camp Ee-Da-How, Idaho City.

Reticularia lycoperdon Bull. Near Camp Ee-Da-How, Idaho City.

R. splendens Morgan. Near Camp Ee-Da-How, Idaho City.

CRIBRARIACEAE

Cribraria argillacea (Pers.) Pers. Near Camp Ee-Da-How, Idaho City.

C. aurantiaca Schrad. Twelve miles northeast of Lowman.

C. microcarpa (Schrad.) Pers. Near Camp Ee-Da-How, Idaho City.

C. minutissima Schw. Twelve miles northeast of Lowman.

C. piriformis Schrad. Near Camp Ee-Da-How, Idaho City.

C. rufa (Roth) Rost. Near Camp Ee-Da-How, Idaho City.

Lindbladia tubulina Fries. Near Camp Ee-Da-How, Idaho City.

<center>Trichiaceae</center>

Arcyodes incarnata (Alb. and Schw.) O. F. Cook. Twelve miles north-east of Lowman. Although this species has been reported from Oregon, Massachusetts, Iowa, and Nevada, it is not commonly found and is considered rare.

Arcyria incarnata (Pers.) Pers. Near Camp Ee-Da-How, Idaho City.

Trichia botrytis (J. F. Gmel.) Pers. Near Camp Ponderosa, McCall.

T. decipiens (Pers.) Macbr. Near Camp Ee-Da-How, Idaho City.

T. varia (Pers.) Pers. Near Camp Ee-Da-How, Idaho City.

<center>Stemonitaceae</center>

Comatricha nigra (Pers.) Schroet. Twelve miles northeast of Lowman.

C. suksdorfi Ellis and Ev. Near Camp Ee-Da-How, Idaho City.

Enerthenema melanospermum Macbr. and Mart. Twelve miles north-east of Lowman.

E. papillatum (Pers.) Rost. Twelve miles northeast of Lowman.

Stemonitis axifera (Bull.) Macbr. Near Camp Ee-Da-How, Idaho City.

S. flavogenita Jahn. Near Camp Ee-Da-How, Idaho City.

S. fusca Roth. Near Camp Ponderosa, McCall.

S. hyperopta Meylan. Near Camp Ee-Da-How, Idaho City.

<center>Physaraceae</center>

Fuligo septica (L.) Wiggers. Near Camp Ee-Da-How, Idaho City.

Leocarpus fragilis (Dicks.) Rost. Near Camp Ponderosa, McCall.

Physarum decipiens Curt. Near Camp Ee-Da-How, Idaho City.

P. leucophaeum Fries. Near Camp Ee-Da-How, Idaho City. This species is not commonly found and has only been reported from California in the Western United States.

P. notabile Macbr. Near Camp Ponderosa, McCall, and Camp Ee-Da-How, Idaho City.

P. viride (Bull.) Pers. Twelve miles northeast of Lowman.

<center>Didymiaceae</center>

Diderma alpinum Meylan. Near Camp Ee-Da-How, Idaho City.

Didymium minus (Lister) Morgan. Near Camp Ee-Da-How, Idaho City.

D. squamulosum (Alb. and Schw.) Fries. Twenty-seven miles north-east of Boise toward Idaho City, Boise County.

<center>Literature Cited</center>

Hagelstein, R. 1944. Mycetozoa of North America, Mineola, 306p.

Macbride, T. H. 1899. North American Slime-Moulds, London, 231p.

————., and G. W. Martin. 1934. The Myxomycetes. The Macmillan Company, New York, 339p.

Martin, G. W. 1949. North American Flora 1:1–190.

————., and C. J. Alexopoulos. 1969. The Myxomycetes. University of Iowa Press, Iowa City, 560p.

NOTES AND NEWS

New Distributional Records for Washington Plants.—While working on my master's thesis at Mount Rainier National Park in 1969 and 1970 I noted four species that have not been recorded from the area previously. Two of these, *Ivesia tweedyi* Rydb. and *Astragalus alpinus* L., have never been recorded from west of the summit of the Cascade Mountains. These species were found growing together in only one location in the northeast corner of the park. They were dominant in a small lithosolic community, firmly stabilizing the soil on a ridgetop that runs north and south. *Ivesia tweedyi* has been found previously in only Chelan, Kittitas, northern Yakima, and Stevens counties, Washington, and in Shoshone and Idaho counties, Idaho. *Astragalus alpinus* is a circumpolar species previously known in Washington only from Okanogan and Pend Oreille counties. Another species, *Trollius laxus* Salisb., was first found several years ago in an isolated valley in the park by Arthur E. Haines, a former park naturalist; he did not notice it to be widespread at that time. I have found it to occur throughout the northeast section of the park in moist and wet subalpine areas. Often it is found with the almost equally widespread *Ranunculus alismaefolius* Geyer, the last of the four species.

The park has been thoroughly studied by numerous taxonomists and plant collectors. It is possible that *Ivesia tweedyi* and *Astragalus alpinus* could have been overlooked because they occur in only one small, isolated locality. On the other hand, with their widespread distributions, it seems unlikely that *Trollius laxus* and *Ranunculus alismaefolius* would have been missed unless their introduction to the park had been within the last 25–50 years or their distribution has increased considerably during that time.

The present distributions of *Trollius laxus* and *Ranunculus alismaefolius* coincide closely with the increased distribution of elk *(Cervus canadensis)* in the moist subalpine meadows in the northeast part of the park. Elk are rapidly increasing and have been spreading in the park, particularly recently. Years ago an introduction of elk from Kittitas County was made near Enumclaw and elk have spread into the park from Yakima County for at least forty years. Both plant species also occur in these counties. *Ivesia tweedyi* is known from these same counties too, but is a viscid plant and undoubtedly is not a palatable species. On the other hand, *Trollius laxus* and *Ranunculus alismaefolius* grow lushly in moist areas and *R. alismaefolius* is often grazed. Seeds may also be transported on elk hooves. It will be interesting to note if the distributions of *Trollius laxus* and *Ranunculus alismaefolius* follow the present spread of elk into moist subalpine meadows of the park where neither has been known previously.—Marcia J. Hamann, Department of Botany, Washington State University, Pullman 99163.

REVIEW

A Flora of Tropical Florida. By Robert W. Long and Olga Lakela. xvii + 962 pp., 125 line figures, 1 map and 1 plate of 5 portraits. University of Miami Press, Miami. 1971. $29.50.

Tropical Florida as defined in this Flora is restricted to the three most southern counties of the peninsula: Collier, Dade, and Monroe. The area covered is 5082 square miles or approximately 9% of Florida. If comparisons are helpful, the area covered is a little more than ⅕ as large as Connecticut and Rhode Island, almost 10 times as large as Marin County, California, somewhat more than 3.5 times as large as the area covered by California's Santa Cruz Mountains, or about 1.5 times as

large as San Luis Obispo County, California. The last three examples are included since each has had published relatively recently an outstanding local flora.

Professor Joseph Ewan contributed a brief but interesting account of the botanical exploration of tropical Florida. The introduction also includes a sketch of the geological history of southern peninsular Florida, an account of the origin and composition of the flora followed by a 3-page outline of the plant communities represented. The vast majority of this bulky volume (3⅝ pounds and about 3 inches thick) is occupied by brief descriptions and the various keys leading to the identification of the 179 families, 762 genera, "approximately 1650 species", and 190 subspecies or varieties of vascular plants. The uniformity of the printed text is broken by 125 full-page illustrations of representative species of the majority of the families. On the whole these seem to be more successful in the floral details than the habit sketches; seemingly much was lost in reproduction.

Clearly the book is not meant as a field guide; its bulk alone would preclude that admirable justification of a local flora. The typography, although easy to read, is needlessly wasteful of space and not especially pleasing to the eye due at least in part to its uniformity. The use of more varied typography would have both saved space and made for a more attractive page.

The authors established their neutrality in the persistent controversy over subspecies vs. variety by accepting the monographers "own use of the categories". This is slightly preferable to accepting only subspecies under the mistaken impression that the International Code of Botanical Nomenclature requires the use of the category "subspecies" if only one rank is recognized. Personally I believe readers would have been far better informed if the authors of the present flora had briefly stated their understanding of these categories and indicated how, in their opinion, the infraspecific variants encountered in tropical Florida fitted into their conceptual framework. As it is the reader may be perplexed by the recognition of numerous infraspecific variants that apparently for the most part are not ecologically isolated in so small an area.

One does not obtain a clear picture from this flora as to the frequency of the taxa within tropical Florida; in fact one is sometimes uncertain as to a taxon's actual occurrence in the stated area in spite of its inclusion in the book. This feeling of uncertainty is heightened by the admission that "some species are included in this flora based on the prediction that they eventually will be found". Biogeography is poorly served by such a policy. Extraterritorial ranges given for the taxa often ignore data presented in the recent literature (*e.g.* apparently neither *Vaccinium myrsinites* Lam. nor *Eriocaulon ravenelii* Chapm. is known from North Carolina as stated).

More attention to the literature would have prevented the acceptance of such obviously erroneous binomials as *Ilex caroliniana* (Walt.) Trel. (a later homonym of a binomial by Philip Miller) for *Ilex ambigua* (Michx.) Torr. or *Sericocarpus bifoliatus* (Walt.) Porter (a misapplication of a Linnaean binomial by Walter) for *Sericocarpus tortifolius* (Michx.) Nees. The recognition of *Sericocarpus* as a genus distinct from *Aster* is often questioned. Closer attention to the literature and to the plants themselves would have prevented misidentifying the annual *Sabatia stellaris* Pursh with the perennial *S. campanulata* (L.) Torr. The latter species although unknown from southern peninsular Florida is included while the former species, which is reasonably common in southern Florida, is not mentioned.

It is unfortunate that the exorbitant cost of printing makes it most unlikely that a revised new and improved edition will be forthcoming in the near future. But all this is nit-picking. The authors are well aware of the book's shortcomings. The fact remains that this book offers the most useful introduction to the flora of southern Florida. As the late Lloyd Shinners wrote, "Blessed are they that write state and local floras. They discharge the taxonomist's elementary duty to the general public."
—ROBERT L. WILBUR, Department of Botany, Duke University, Durham, North Carolina 27706.

INDEX TO VOLUME XXI

Classified entries: botanical names (new names are in **boldface**); major subject headings, including key words from titles; reviews. Incidental references to taxa and taxa merely enumerated in floristic lists or tables are not indexed. Names of authors followed by titles of contributed articles are listed alphabetically in Table of Contents, pp. iv–vii. NOTE: Number 5, Part Two (The Plants of Santa Barbara Island, California) is indexed separately, pp. 391–393.

A WEST AMERICAN JOURNAL OF BOTANY

A quarterly journal devoted to the publication of botanical research, observation and history. Back volumes may be obtained from the Secretary at $12.00 per volume. Single numbers of Volumes 1 and 2 may be obtained at $1.00 and of Volumes 3 through 20 at $2.00. Some numbers are in short supply and are not available separately.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication should not exceed an estimated 15 pages when printed unless the author agrees to bear the cost of the additional pages at the rate of $20 per page. Illustrative materials (including "typographically difficult" matter) in excess of 30 per cent for papers up to 10 pages and 20 per cent for longer papers are chargeable to the author. Subject to the approval of the Editorial Board, manuscripts may be published ahead of schedule, as additional pages to an issue, provided the author assumes the complete cost of publication.

Shorter items, such as range extensions and other biological notes, will be published in condensed form with a suitable title under the general heading "Notes and News."

Manuscripts and accompanying illustrative materials must be submitted in duplicate; the author should retain a third copy. The manuscript MUST be double spaced throughout, including the title, text, references, tables, legends for figures, literature cited, etc. Footnotes (which should be avoided wherever possible), figure captions, and tables should be typed on sheets separate from the text. Addresses of authors should include ZIP.

Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum, Part 1. The Herbaria of the World*. Utrecht, Fifth Edition, 1964).

Abbreviations of botanical journals should follow those in *Botanico-Periodicum-Huntianum* (Hunt Institute, Carnegie-Mellon University, Pittsburgh, Pennsylvania, 1968). In cases where the author is unable to determine the correct abbreviation for a journal title, he should write it in full. Titles of books should be given in full, together with the place and date of publication, name of publisher, and an indication of the edition if other than the first. Do not underline any words in the literature cited, including binomials.

Membership in the California Botanical Society is normally considered a requisite for publication in MADROÑO.

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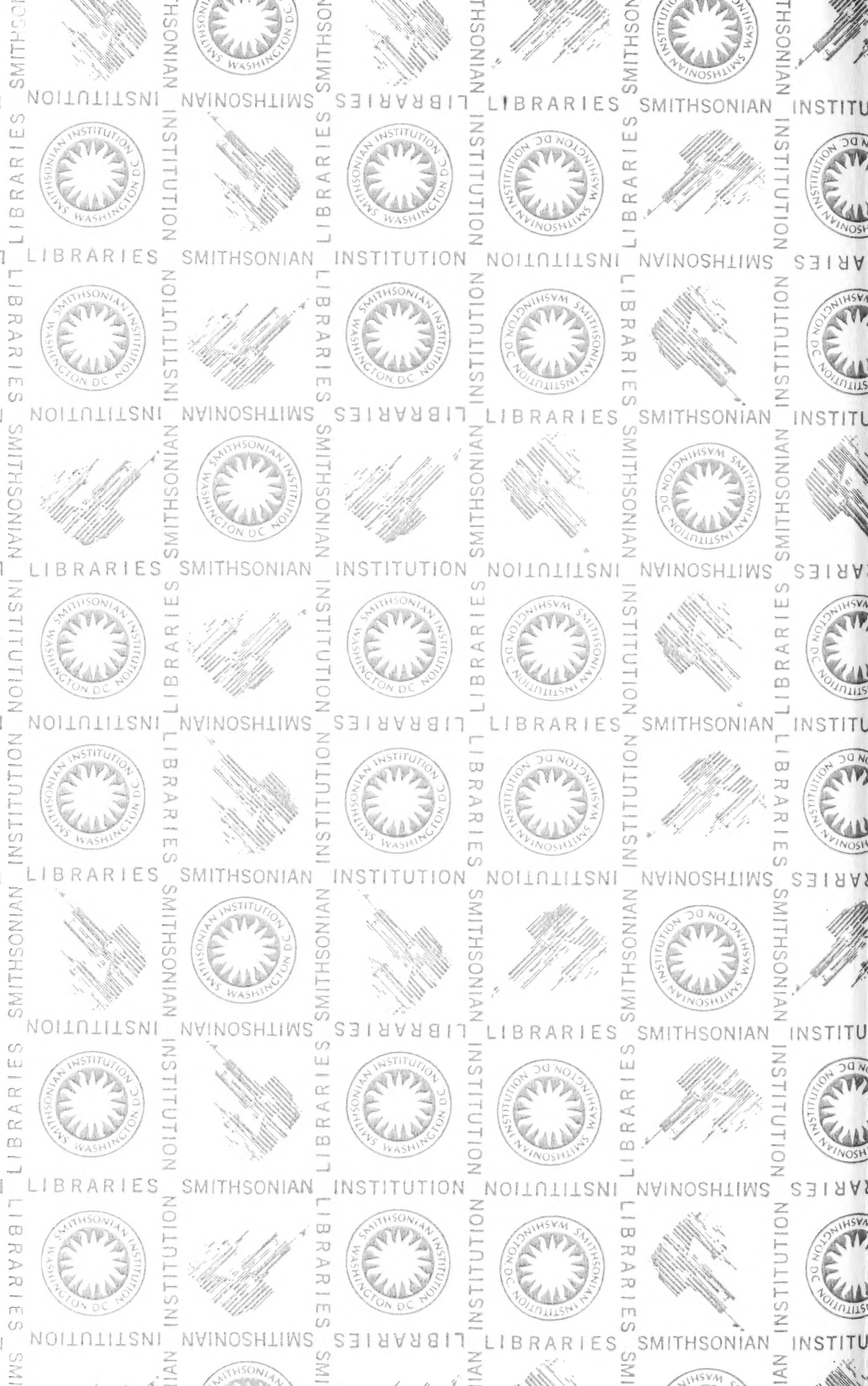I certify that the statements made by me above are correct and complete.
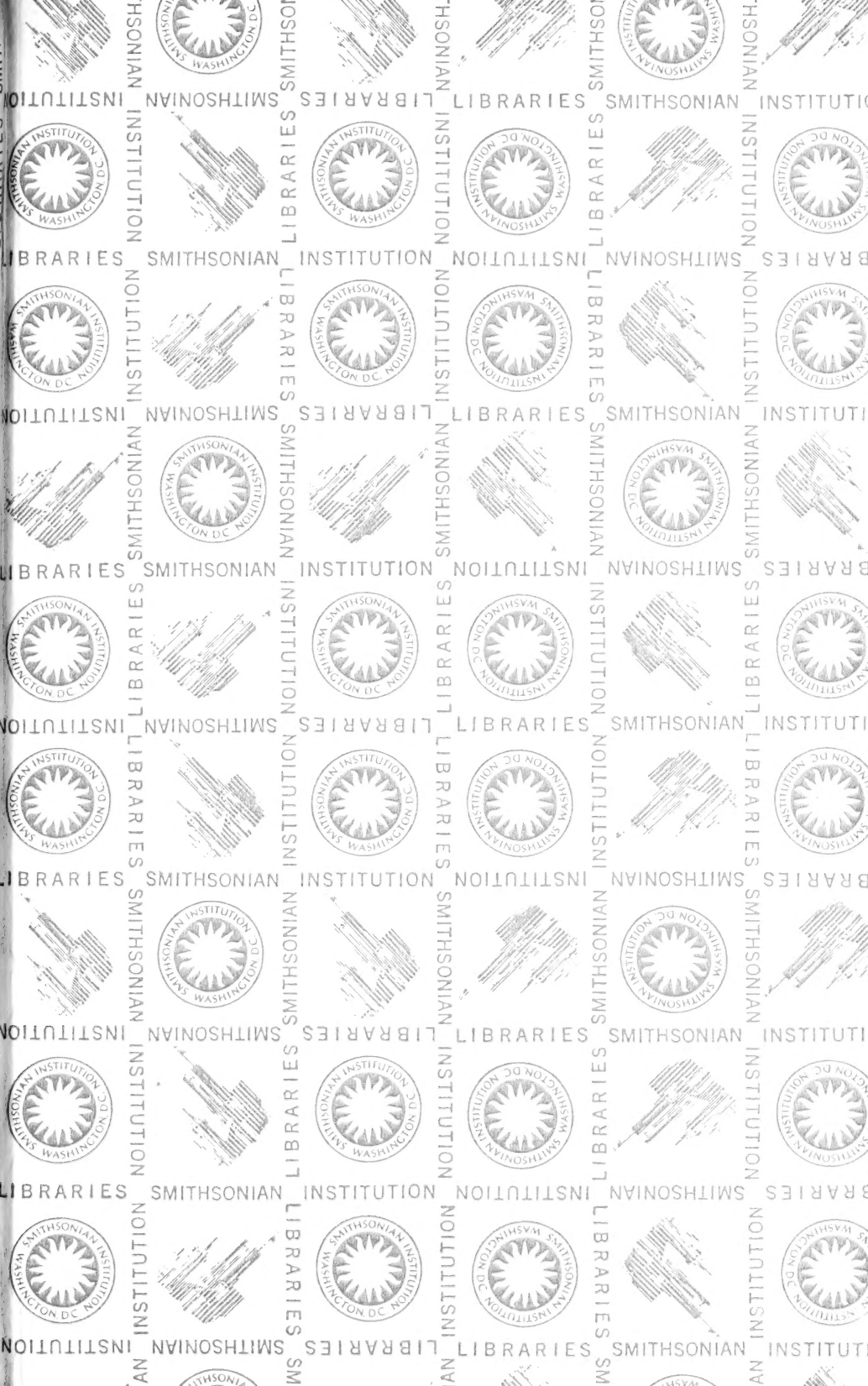
ROBERT ORNDUFF, Editor

September 1, 1972