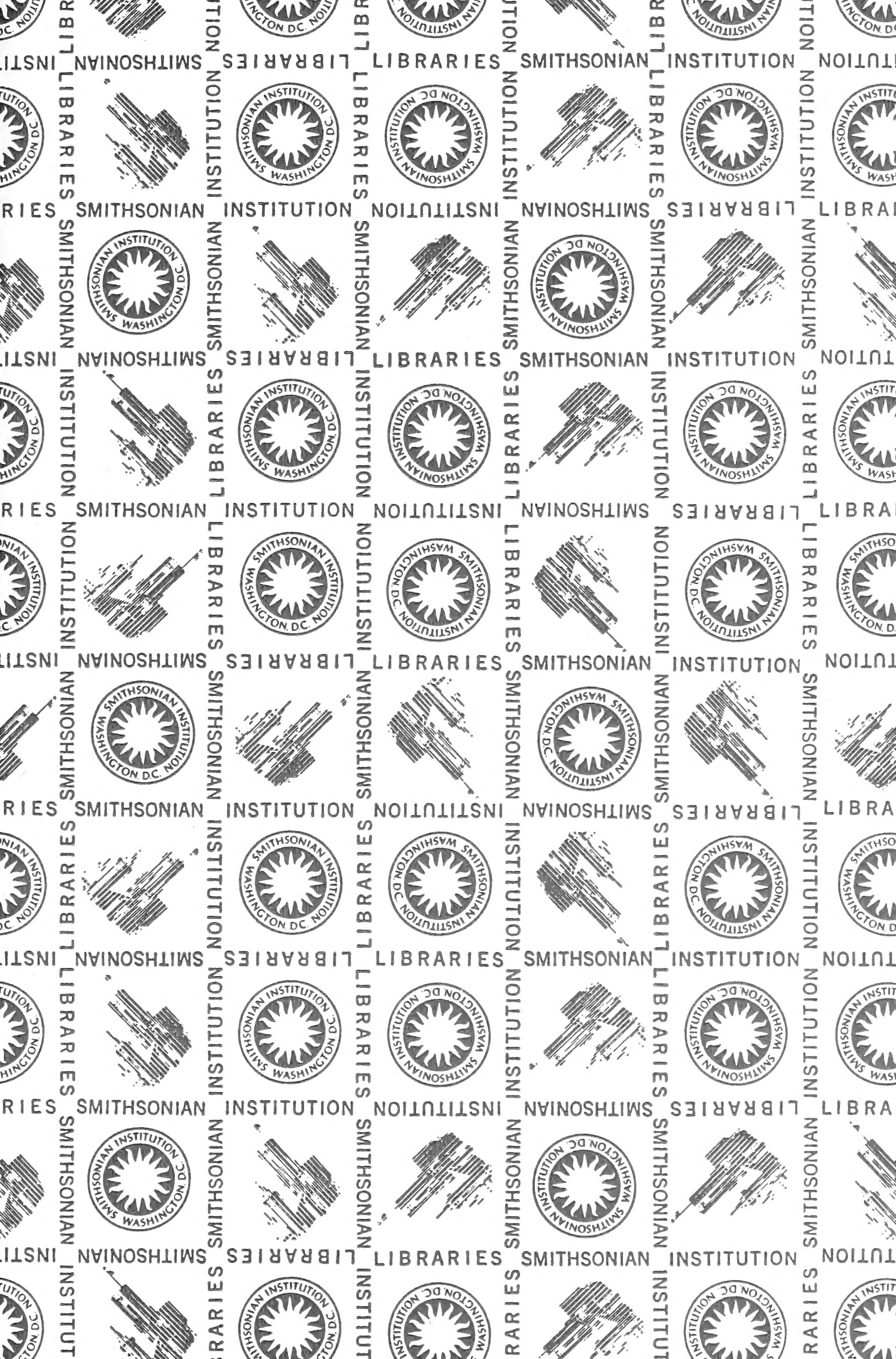
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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME XXX

1983

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Reid Moran began botanizing the world when he was very young and had a back-yard *Dudleya* collection when no more than ten years old. He did his undergraduate work at Stanford and then went on to Cornell to work on *Dudleya* with Jens Clausen. This was in the early 40s, when some war or another broke out, and Reid joined two of his cohorts as enlistees in the airforce. They ended up in the 15th Airforce flying raids over Jugoslavia. In a stroke of luck, neither good nor bad, Reid got zapped in mission no. 1 and was found by some of Tito's partisans tangled in the top of a tree he was trying to identify. After a lengthy walk he made his way back to safety in Italy and finally flew back to the USA. It should be noted, though, that the return flight was mysteriously routed through a number of North African bases, at each of which Reid managed to nab a few specimens. When discovered back at Cornell, he was in the herbarium pressing some of his acquisitions—in full uniform. His well-known, unique sense of humor has affected many of his colleagues, and the noteworthy collection section of this journal has never fully recovered from his famous "I found it there then" contribution.

He finished his PhD at Berkeley with Lincoln Constance and after a brief time as a UC extension instructor, moved to the San Diego Museum of Natural History.

Reid is certainly one of the finest field botanists in the West (sensu lato), and his knowledge of the northwest Baja California flora and that of the islands is unparalleled. We take great pleasure in dedicating volume 30 to him.

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POLLEN ANALYSIS OF PAST VEGETATION AT POINT REYES NATIONAL SEASHORE, CALIFORNIA

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Department of Geology, Rutgers University,
Newark, NJ 07102

ABSTRACT

Pollen analysis indicates major vegetational changes near Wildcat Lake, Point Reyes National Seashore, California, in the last millennium. Changes in the relative proportions of grass and shrub pollen both before and after colonization imply that the proportions of grassland and scrub vegetation were not constant even before European colonization. Near the top of the sediment core the ratio of grass to shrub pollen increases. The simultaneous appearance of pollen of introduced plant species allows this level of the diagram to be dated historically at about 1850 A.D. Thus this increase in grasses may be correlated with increased grazing. A shift from abundant *Alnus* pollen to *Myrica* and *Salix* near the bottom of the core is interpreted as the result of a landslide that changed local drainage.

Agricultural and logging practices obscure precolonial vegetational patterns in the New World. Because the patterns are probably caused primarily by interactions of climate, soil and topography, their reconstruction is of considerable interest to ecologists. For example, the Mediterranean type of vegetation that characterizes western California has a fairly short history of active exploitation, generally less than 150 years. Near the coast, extensive short grass pastures are interspersed with shrubby vegetation, occasional small, bunch-grass prairies, and deciduous or coniferous woodlands. The mountain ridges parallel to the coast are mainly forested with *Pinus* spp. or *Pseudotsuga menziesii,* and many valleys east of these ridges in the northern and north-central parts of the state contain *Sequoia sempervirens* (Munz and Keck 1959, Ornduff 1974).

Probably the most active cultural exploitations are grazing and urbanization, which have nearly obliterated the natural vegetation of coastal prairie, dominated by grasses such as *Deschampsia holciformis, Calamagrostis nutkaensis* and *Festuca californica.* Grazing has also modified coastal scrub, dominated by shrubs such as *Rhus diversiloba, Rubus ursinus, Artemisia californica, Baccharis pilularis, Lupinus* spp., and members of the Rhamnaceae (Howell 1949, Munz and Keck 1959, Barbour et al. 1973, Ornduff 1974, Heady et al. 1977, Grams et al. 1977). The present study concerns the history of an area north of San Francisco, Point Reyes National Seashore.

Previous studies of the past and present coastal vegetation have reached conflicting conclusions about its history, as well as its present

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composition. North of Point Reyes to the Oregon border, Burtt-Davy (1902) found a variety of species, e.g., *Erodium moschatum, Bromus rigidus, Hordeum leporinum* and *Centaurea melitensis,* invading pasture land in 1900. Based on observations of fenced-off areas, he deduced that the original forage plants had been perennial bunch grasses, chiefly *Danthonia, Stipa* and *Melica.* Wild oats (*Avena fatua*) and *Erodium* displaced these very palatable species in the 19th century as grazing pressure increased. Continued grazing led to dominance by *Hordeum jubatum, Sitanion hystrix* and *Bromus mollis* by 1900. He saw the presettlement landscape as consisting of prairies and "hard" chaparral of *Adenostema fasciculatum, Ceanothus cuneatus* and other chaparral species (Burtt-Davy 1902).

At Point Reyes, *Baccharis pilularis* dominates the coastal scrub, with at least 25% cover (Grams et al. 1977). Floristic differences in the scrub correspond with differences in exposure: on north-facing slopes *Polystichum munitum* is second in importance, whereas on south-facing slopes *Rhamnus californica* is second. Grams considered all but one of the sites to be "undisturbed" because they were not being grazed, but he did not outline the history of prior disturbance.

Also at Point Reyes, Elliott and Wehausen (1974) studied disturbance effects on deep, sandy soil in level, grazed sites. The native bunch-grass *Deschampsia caespitosa* formed denser cover in a plot ungrazed for six years than in plots continuously grazed by cattle. The growth difference may suggest a shift to prairie vegetation and is interpreted by Elliott and Wehausen as indicating that prairie was the dominant type of vegetation prior to grazing. However, *Baccharis pilularis* had the second highest cover on the plot, and *Rumex acetosella,* an introduced perennial, ranked fourth. The less heavily grazed plot had more *Deschampsia caespitosa* than the other, but also more *Baccharis pilularis.* Their study thus does not give a clear indication of the pre-grazing vegetation, whether it was grassland or scrub.

One hypothesis suggested by these earlier studies (e.g., Burtt-Davy 1902, Elliott and Wehausen 1974, Grams et al. 1977), which is tested here, is that there were major shifts in the proportion of grassland to coastal scrub taxa in the vegetation from pre-Columbian time to the present. This hypothesis would be supported by pollen records indicating changes in the ratio of grass to scrub pollen, representing a change in the ratio of prairie to scrub vegetation. The main shrubs to be considered are members of the Asteraceae, e.g., *Baccharis pilularis* and *Artemisia* spp., members of the Rhamnaceae, and *Rhus diversiloba.* The direction and timing of changes in the pollen record would suggest patterns of succession in the past.

STUDY AREA AND METHODS

Point Reyes Peninsula, located at 38°N, 123°W, is separated from the mainland by the San Andreas rift zone. The base rock of Cretaceous granodiorite crops out in the northeastern part of the Peninsula and on the western tip. In most of the area the Miocene Monterey Formation, mainly bentonitic shale, overlies the granodiorite (Galloway 1977, Howard 1979). The dip of the Monterey Formation parallels the slope of the terrain, resulting in extreme landslide susceptibility in view of the bentonitic shale, high rainfall on the seaward slopes, and earthquakes (Clague 1969). These landslides have produced a landscape of steep breakaway scarps, large hummocks, and frequent lakes where slumps have dammed stream valleys (see Galloway 1977).

The climate is Mediterranean, with wet, cool winters and cool, foggy summers with little precipitation. The mean maximum temperature in July is about 16–18°C, whereas the mean minimum temperature for the same month is 11°C. Mean maximum temperature in January is 13°C, and the mean minimum is 5–7°C. Mean annual precipitation is 58–67 cm, with almost no rain falling in July–August and the maximum falling in December–February (Elford 1970). Fires in the coastal scrub are common and may alter the vegetation (Wells 1962).

Soil type maps of the Point Reyes Peninsula are not available, but generally the soil in the study area appears to be shaley clay loam over shaley clay, about 50–100 cm deep (Grams et al. 1977). There are also local shale outcrops with very shallow soil.

Wildcat Lake is located near the southwest tip of the Point Reyes National Seashore. A landslide estimated at 70,000–100,000 years B.P. blocked a valley drainage, created the lake, and left a scarp on the lake's northeast side (Fig. 1) (Clague 1969). Later slides of lesser extent left piles of debris, especially on the southeast side of the lake. The ages of these slides have not been determined.

Two sediment cores were taken in 1978 by Roger Byrne and Jeffrey Loux. One, about 50 cm long, was obtained with a 10 cm diameter plastic tube for retrieval of relatively undisturbed shallow samples. The second, 300 cm long, was obtained with a 5 cm diameter Livingstone piston corer, near the site of the first. The coring site was located in a deep part of the lake away from the inlet and outlet at the northeast end (Fig. 1).

Samples were taken from the short core at 1, 20, 30, 35, 40, 45, and 50 cm. From the long core, samples were taken at 25 cm intervals from 50 cm below the surface to 275 cm, plus one at 55 cm. All samples were prepared according to standard procedures for concentrating pollen and were mounted in silicon oil (Faegri and Iversen 1975). An average of 11,850 *Lycopodium* spores added to each sample served as a control for comparing relative concentrations of taxa in the sediment. For each sample at least 200 pollen grains were counted at 430×.

Pollen of species locally associated with wet conditions, *Alnus, Salix, Myrica,* and *Typha,* constituted a large proportion of the fossil assemblage in many samples. Changes in these obscured changes in

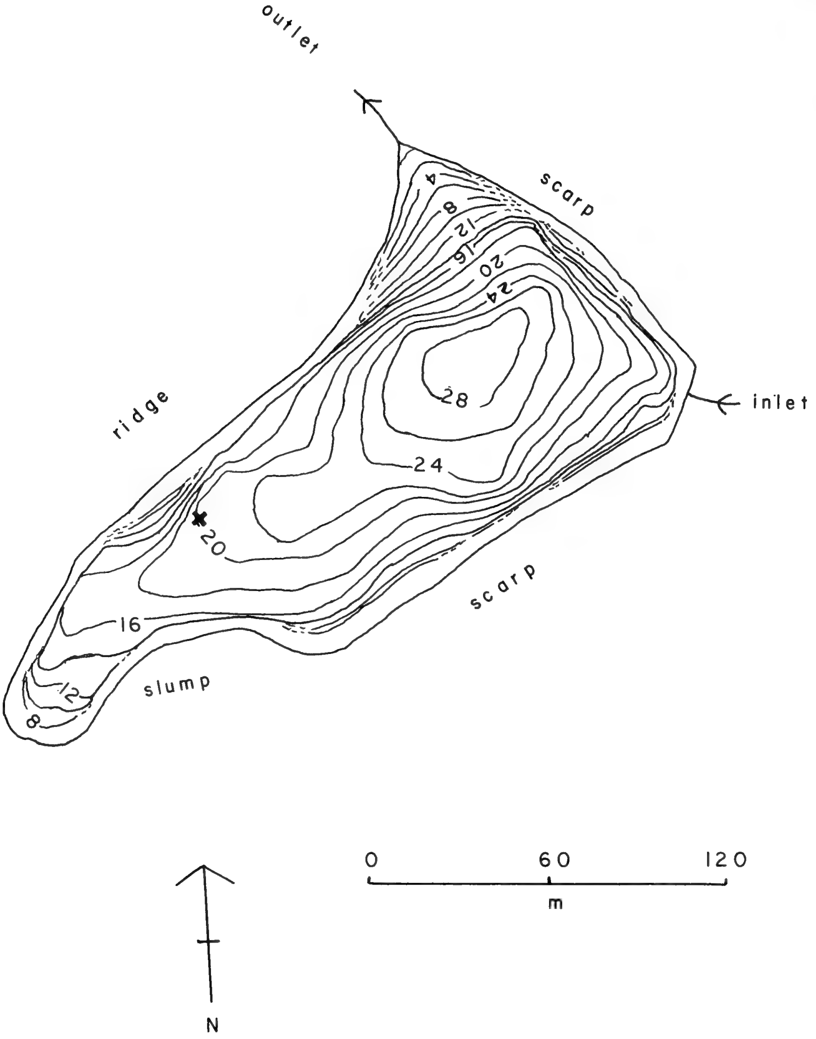

FIG. 1. Bathymetric map of Wildcat Lake, including coring site (X) (modified from Clague 1969).

the less common grass and shrub taxa. Lack of radiometric dates for the sediment and major changes in pollen influx made the use of "absolute" pollen diagrams inappropriate. Therefore pollen percents were calculated on two totals, that of the wetland species as a percent of the total and that of the remaining taxa as a percent of these taxa. This differentiation distinguished changes in local drainage patterns from changes in upland vegetation. Pollen of the wetland species was generally 30% or more of the total, indicating that it was largely locally produced. Upland pollen was blown in from varying distances (Erdtman 1969, Faegri and Iversen 1975).

To study fire history, the area covered by charcoal particles was determined on the same slides that were used for pollen counts. Only black charcoal in which cellular structure (e.g., spiral wall thickenings or bordered pits) was visible was tallied. The area covered by such a piece was determined using a reticle with unit area = 150 μm^2. The total area of charcoal for each sample was divided by the number of control grains (*Lycopodium* spores) counted on the same traverses to estimate charcoal concentration. A minimum of 10 control grains, or 10 traverses (at 430×), was counted at each level.

On 8 April and 2 June 1979, the most obvious taxa with the greatest apparent cover were noted along 12 and 17 km of trails, respectively. On 8 April, the most conspicuous members of the scrub community were *Artemisia californica, Lupinus* spp., *Rhus diversiloba, Pteridium aquilinum* and *Polystichum munitum.* Common species noticed blooming were *Lupinus* spp., *Sanicula arctopoides* on shallow soil, *Eschscholzia californica, Iris douglasii, Ranunculus* sp., *Heracleum lanatum* and *Rumex acetosella.* In the canyons where streams flowed to the ocean there were small, salt-stunted *Pseudotsuga menziesii* and some *Quercus agrifolia.* Higher up above the first range of hills *Pseudotsuga* grew much larger. Near Bass Lake and Lake Ranch, south of Wildcat Lake, were *Salix* sp., *Pseudotsuga menziesii* and *Alnus rubra.*

Near Wildcat Lake, *Baccharis pilularis* and *Rhamnus californica* were common. *Rumex acetosella* and *Plantago lanceolata* formed most of the vegetation on small paths. *Alnus rubra* grew thickly along the inlet stream, and *Salix* sp. at the outlet. *Salix* also provided dense cover in a gully at the south end of the lake. Trees on the uplands in the vicinity of the lake were *Umbellularia californica, Quercus agrifolia* and *Pseudotsuga menziesii.* The only area covered mainly with grasses in the valley around Wildcat Lake was southeast of the large slump southeast of the lake.

RESULTS

Pollen data are given in Fig. 2. Major changes occur between levels 225 and 150 cm in the wetland species. The most salient changes are the decline in *Alnus* and *Typha* pollen from 200 cm to 150 cm and the concomitant increase of *Myrica* and *Salix.* Notable changes in "non-aquatic" pollen occur at 150–125 cm and around 50–55 cm. Near 150 cm, aquatics appear to stabilize, whereas *Sequoia* and *Artemisia* pollen percentages decline and grass pollen percentage increases. Slightly higher in the core, percent pollen of the Rhamnaceae decreases as that

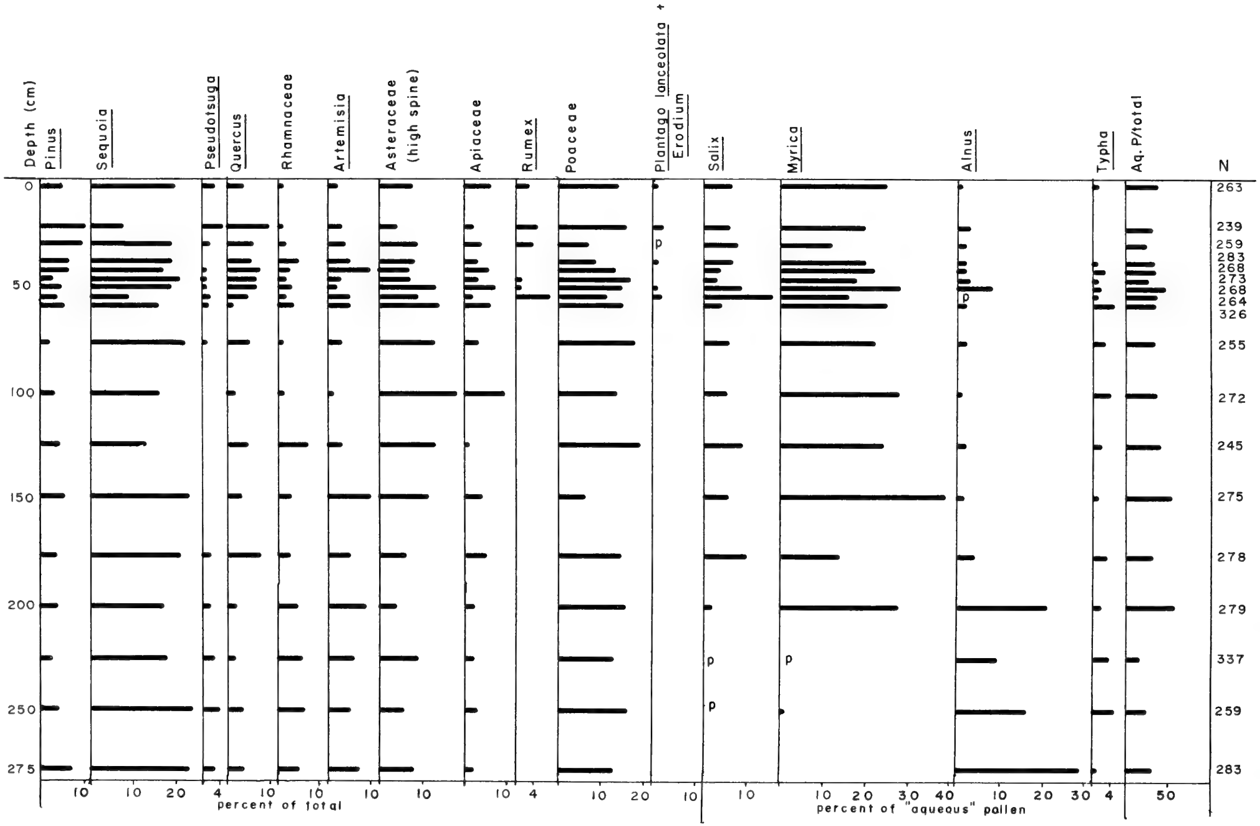

FIG. 2. Wildcat Lake pollen percentages. At the bottom of the diagram, for "percent of total" read "percent of total minus 'aqueous' pollen."

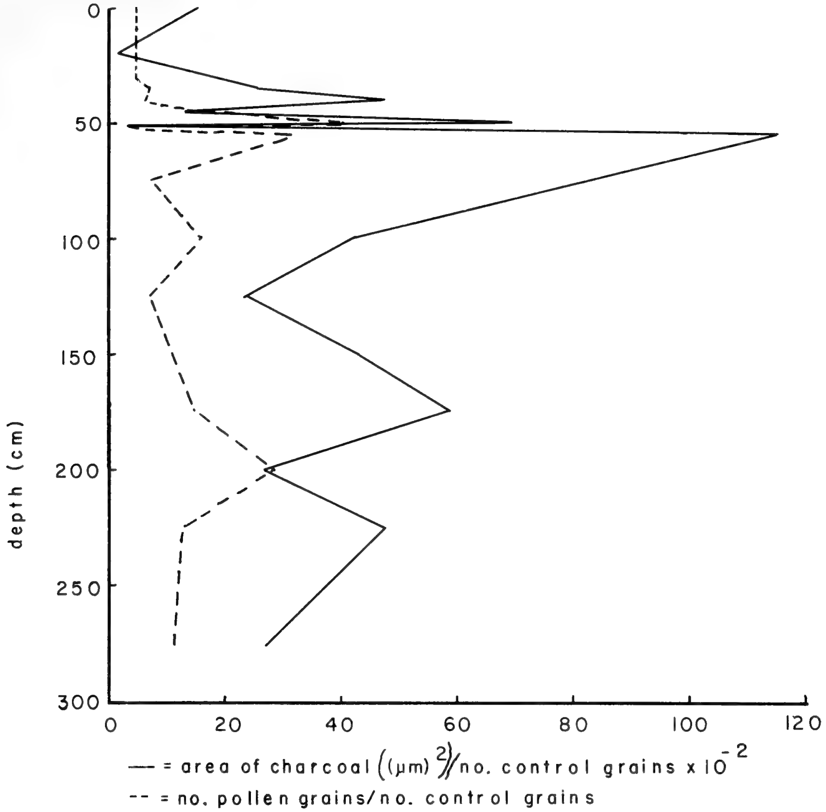

FIG. 3. Charcoal concentration in samples compared with pollen concentration in the same samples.

of the Apiaceae increases. Above about 50 cm a general increase in *Pinus* and *Quercus* pollen is accompanied by a decrease in Asteraceae and possibly in Poaceae. The 50 cm level is also marked by the appearance of the introduced European pasture weeds *Plantago lanceolata* and *Rumex acetosella* and an occasional grain of *Erodium*.

The concentration of charcoal is compared with concentration of pollen in Fig. 3. An increase in the concentration of charcoal where a similar increase does not occur in the concentration of pollen probably indicates the occurrence of a fire or fire period. Concomitant increases of pollen and charcoal are caused by changes in sedimentation, which would affect both similarly. Fires are thus indicated at 0, 40, 175, and 225 cm.

The ratio of grass pollen to shrub pollen (Fig. 4) ranges from 1.2:1 to 0.3:1, with a mean of about 0.8:1. The low corresponds with a peak

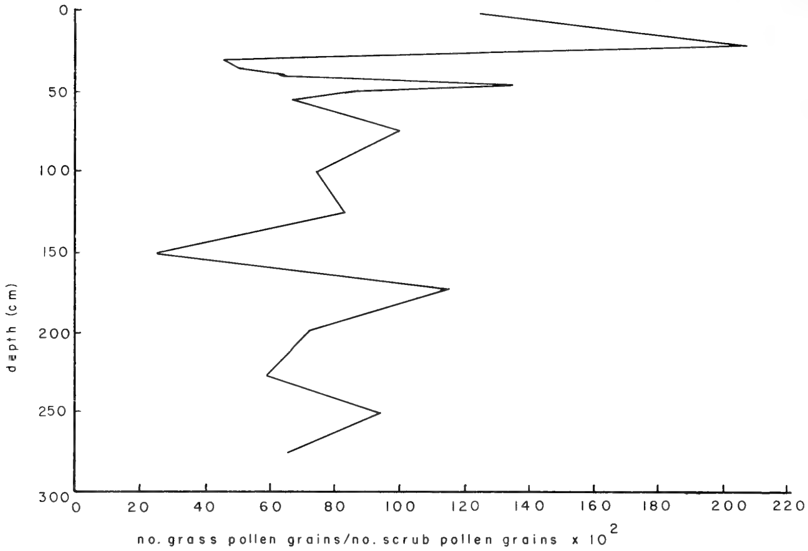

FIG. 4. Ratio of grass (Poaceae) pollen to scrub (Asteraceae, including *Artemisia,* Rhamnaceae, *Rhus*) pollen.

in *Myrica* pollen at 150 cm. This fluctuating ratio becomes slightly higher (1.0:1) and fluctuates more above 50 cm.

DISCUSSION

The most precise date in the pollen core is the first appearance of pollen of introduced taxa, *Rumex acetosella* and *Plantago lanceolata,* at 50 cm (Fig. 2). Historical data place this near 1850 A.D. The core was taken in 1978, indicating a sedimentation rate of 50 cm/128 yr, or 0.39 cm/yr. Extrapolation of this rate to sediment below this point gives a minimum estimate of 1275 A.D. for the age of the sediment. Erosion accelerated by grazing, which increased the input of sediment to the lake, plus compaction at lower levels make this a very conservative estimate of the age of the bottom of the core.

The variations in the ratio of grass pollen to shrub pollen (Fig. 4) support the hypothesis that the ratio of grassland to scrub has changed in the past. Fluctuations in the proportion of grassland seem to have occurred before European settlement of the area. It appears likely that the precolonial landscape contained a mixture of prairie and chaparral vegetation, as suggested by Burtt-Davy (1902). The areas studied by Elliott and Wehausen (1974) and Grams et al. (1977) may represent naturally occurring temporal and spatial variation in the mosaic of vegetation.

The low ratio of grass to shrub pollen at 150 cm, which corresponds with a peak in *Myrica* pollen, may be associated with a fire, because *Myrica* spreads rapidly after fires (Howell 1949). Very high charcoal counts at about 175 cm (Fig. 3) show the possibility of a fire at that level. The fire may have been followed by the spread of *Myrica* and fire-stimulated scrub species, and a temporary low period of grass growth.

That grass pollen is generally less common than the scrub species cannot, by itself, be taken as evidence that scrub was more common than prairie. Differential production and dispersal of pollen alone may have caused this difference if the scrub species produce more pollen per unit area than the grasses. However, the increased fluctuations in the ratio after European settlement, and the higher grass pollen in some samples, suggest that increased exploitation of the land by grazing increased grassland at the expense of shrubs.

The pollen evidence of wetland species (Fig. 2) raises another issue. It appears that sudden changes have occurred in local drainage over the period sampled by this core. These changes, probably associated with landslides, have occurred since the formation of the lake. Above 200 cm the dramatic decrease in alder pollen strongly indicates a reduction in the habitat of alder, which in this area is generally along streambanks. One may surmise that at this time there was a local landslide or slump that slowed the flow of water in a nearby stream such that the alder no longer had a suitable habitat locally. Then the increased swampy area was invaded by *Salix,* which presently forms a nearly impenetrable thicket at the outlet of the lake near the north end. The simultaneous decline of *Typha* pollen could be related to slump filling of the shallow littoral site formerly occupied by *Typha. Myrica* may have invaded the disturbed habitat formed by the slump debris.

Pseudotsuga, which grows on the ridge east of the lake, is represented in the pollen record with a maximum of six percent. This confirms Erdtman's (1969) statement that *Pseudotsuga* pollen has very low powers of dispersal.

After European settlement, the relative amounts of *Pinus* and *Quercus* pollen increased and, at least at one point, the amount of *Sequoia* pollen declined sharply. A decline in Asteraceae and Poaceae pollen is associated with the increases in *Pinus* and *Quercus* pollen. This might correspond with the type of grazing landscape described by Lapérousse in 1786, in which a few trees were left in cattle pastures for shade (Lapérousse 1937). The grazed Poaceae and Asteraceae produced little pollen, whereas the trees may have produced more copiously than when in a thicker stand. Scrub, consisting largely of *Artemisia* and Rhamnaceae, persisted outside the pastures (Lapérousse 1937, Beechey n.d.). The sudden drop in *Sequoia* pollen and subsequent recovery above 30 cm probably indicates the heavy logging of this species in the early 20th century. The peak of *Salix* pollen at 50 cm may suggest that Judge Shafter, who owned this land in the late 19th century, tried to use *Salix* as a living fence in places, as did ranchers in the southern part of the state (Fabian 1869).

The vegetation in this area presents a basic pattern in which the non-arboreal pollen remains near 40% of the total. The most important upland taxa are Poaceae, Asteraceae (including *Artemisia*) and *Sequoia,* the latter blown in from a distance. However, shifts in the relative abundances of these pollen taxa indicate changes in the vegetation during the centuries preceding European settlement in addition to changes caused by European settlement. Causes of the pre-Columbian changes are unknown, but topographic disturbances in the area are indicated by sudden shifts in taxa whose distribution is related to changes in local drainage. We may thus see a superposition of topographic disturbance on a system adapted to the local climate, soils and topography.

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The research for this paper was carried out at the University of California, Berkeley, in 1979, while I was a Research Fellow in the Department of Geography. Roger Byrne suggested the topic and provided invaluable logistical assistance, as well as discussion of ideas. Jeffrey Loux collected and processed the sediment as part of term paper research in 1978. Richard T. T. Forman, T. Webb III and G. Batchelder provided helpful comments on earlier versions of this paper.

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HYBRIDIZATION AND GENETIC RECOMBINATION OF CIRSIUM CALIFORNICUM AND C. OCCIDENTALE (ASTERACEAE: CARDUCEAE)

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ABSTRACT

Sympatric populations of *Cirsium californicum* (series *Neomexicana*) and *Cirsium occidentale* (series *Occidentalia*) were studied. The populations occurred as a set of colonies along Happy Canyon Road, Santa Barbara County, California. Morphological data, pollen fertilities, and controlled crosses all support the conclusion that the two taxonomic species studied are one biological species at the Happy Canyon site, that no sterility barriers exist to prevent gene recombination, and that hybrid and recombinant forms compose almost the entire Happy Canyon *Cirsium* population. However, microgeographic differentiation of recombinant morphological types was observed to be correlated to ecological habitats. Protein electrophoretic data support the conclusion that habitat-correlated electrophoretic and morphological phenotypes have a genetic basis rather than having been environmentally induced. The data suggest that the two species have hybridized in the studied population and that differentiation may be occurring along new lines.

The genus *Cirsium* is in the family Asteraceae, tribe Carduceae (Thistle). Taxonomically, there are between 200 and 250 described species in the genus, of which 34 occur in Washington, Oregon, and California (Howell 1968). Approximately 30 of the West Coast species occur in California (Munz and Keck 1959). The classification of the California species of *Cirsium* has been changed several times in this century (Jepson 1925, Munz and Keck 1959, Howell 1968, Munz 1974). All of these authors have suggested that the taxon *Cirsium* is evolutionarily complex and in need of further study before its evolutionary dynamics can be completely understood.

Taxonomic division of *Cirsium* into species is made difficult in part by the presence of morphologically intermediate individuals. Hybridization of Pacific Coast species has been suggested between approximately 23 species pairs involving 19 species (Howell 1968). Hybridization occurs not only between closely related species, but also between some morphologically dissimilar species (*C. fontinale* and *C. quercetorum,* and *C. brevifolium* and *C. utahense*). It appears that the genus is taxonomically complex and that the difficulty of species delimitation may result from rapid, present-day evolution.

Despite the several revisions of the genus, *C. californicum* and *C. occidentale* have always been considered distinct; they have always been placed in separate series and have never been reported to hy-

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bridize. Acceptance of the current ranking of *C. californicum* and *C. occidentale* is based on the apparent historical continuity of classifications and agreement of taxonomists (Jepson 1925, Munz and Keck 1959, Howell 1968, Munz 1974).

This study presents data on the interactions of *C. californicum* and *C. occidentale* occurring sympatrically in a single well-defined geographic population. Two questions are addressed. First, what degree of biological distinctness has been reached between the species *C. californicum* and *C. occidentale* in the study area? Second, what, if any, geographically related genetic differentiation exists in the studied population? Answers to these questions may lead to a greater understanding of the processes of evolution in nature and ultimately of the phylogeny of *Cirsium*.

Materials and Methods

Species description. C. californicum branches from the base upwards. The plants have a strong taproot. Basal leaves develop in a rosette and can be up to 3 dm long and 1 dm wide. They are oblanceolate, deeply lobed, and have slender spines. Caulescent leaves are shorter, and have reduced lobes and spininess distally. Leaf blades are glabrescent and green above, and white arachnoid-wooly below. The capitula of *C. californicum* usually occur solitarily on the ends of long slender peduncles. The heads are up to 6 cm in diameter, and up to 4.5 cm long. The involucre is bowl shaped, making the capitulum hemispheric. Phyllaries are spine tipped and spreading above. Flowers are tubular and white, sometimes pink (Table 1).

C. occidentale is an herbaceous, taprooted plant up to 3 m tall. Basal leaves form a rosette up to 8 dm in diameter from which a single thick stem arises. Branching occurs only on the upper stem and forms the inflorescence. Leaves are purple to reddish with light cottony pubescence, deeply lobed, and very spiny. Deep lobing and spininess occur from the leaf base to the distal tip. The branching pattern forms a panicle. Flowers in the heads are compressed into a vertical cylinder by the phyllaries. Phyllaries are constricted to form a narrow neck, are spine tipped, and have cottony webbing. Flowers are all tubular, perfect, and red (Table 1).

The population. The population studied was composed of *C. californicum* and *C. occidentale* individuals in an essentially linear array of 42 disjunct colonies along Happy Canyon Road to the summit of Figueroa Mountain, Santa Barbara County, California. In this respect it resembled the linear stepping stone model of population structure (Kimura 1953). The population was dispersed over approximately 19 km and elevation ranged from approximately 600 to 1100 m. Four habitat types were traversed by the Happy Canyon roadway with its associated *Cirsium* population: chaparral, valley grassland, southern

TABLE 1. MEAN AND STANDARD ERROR FOR EACH OF THE 35 MORPHOLOGICAL CHARACTERS. Key: [1] Includes reference specimens and individuals fitting species description which were used in the experimental crosses. [2] n = 4, n = 1, n = 34, and n = 105, respectively (not all specimens had mature seeds). * Denotes characters whose means are significantly different in *C. occidentale* and *C. californicum* (±2 S.E. do not overlap).

					Principal coordinate axis III			
	Cirsium occidentale[1]		*Cirsium californicum*[1]		+ cluster		− cluster	
Character in cm except ±0/1 and #	$\bar{x}$ n = 16	S.E.	$\bar{x}$ n = 17	S.E.	$\bar{x}$ n = 66	S.E.	$\bar{x}$ n = 206	S.E.
Stem leaf:								
Length	12.86	0.74	12.05	1.00	10.07	0.68	10.72	0.41
Width*	1.34	0.14	0.86	0.08	1.00	0.09	0.80	0.03
No. lobes	15.88	0.52	13.24	1.15	13.64	0.50	15.19	0.26
Spine length*	0.49	0.04	0.28	0.02	0.42	0.02	0.40	0.01
Lobe depth	0.95	0.12	0.89	0.14	0.67	0.05	0.69	0.03
Color ±*	0.94	0.06	0.00	0.00	0.49	0.06	0.30	0.03
Pubescence ±*	0.94	0.06	0.18	0.10	0.05	0.03	0.98	0.01
Peduncle leaf:								
Length*	2.51	0.30	1.38	0.16	1.54	0.08	1.87	0.05
Width*	0.36	0.06	0.14	0.02	0.17	0.01	0.18	0.01
No. lobes*	8.00	1.03	3.65	0.43	6.38	0.44	5.48	0.20
Spine length*	0.37	0.03	0.23	0.02	0.32	0.02	0.29	0.01
Lobe depth	0.16	0.02	0.09	0.02	0.10	0.01	0.12	0.01
Color ±*	0.88	0.09	0.00	0.00	0.47	0.06	0.31	0.03
Pubescence ±*	0.94	0.06	0.18	0.10	0.39	0.06	0.88	0.03
Peduncle:								
Length	16.15	2.85	23.94	4.13	17.85	1.34	17.68	0.68
Diameter*	0.33	0.02	0.21	0.02	0.22	0.01	0.23	0.01

TABLE 1. CONTINUED.

					Principal coordinate axis III			
	Cirsium occidentale[1]		*Cirsium californicum*[1]		+ cluster		− cluster	
Character in cm except ±0/1 and #	$\bar{x}$ n = 16	S.E.	$\bar{x}$ n = 17	S.E.	$\bar{x}$ n = 66	S.E.	$\bar{x}$ n = 206	S.E.
Capitula:								
Bract length*	1.72	0.23	1.00	0.10	1.29	0.05	1.49	0.03
Bract width	0.28	0.02	0.24	0.02	0.29	0.01	0.31	0.01
Total height*	4.38	0.21	3.31	0.10	3.68	0.09	3.60	0.04
Bract pubescence ±*	0.81	0.10	0.00	0.00	0.41	0.06	0.20	0.03
Involucre:								
Width*	2.61	0.16	1.88	0.13	2.10	0.06	2.30	0.04
Height*	2.96	0.20	1.94	0.10	2.30	0.07	2.19	0.04
Corolla:								
Tube length*	2.06	0.13	1.53	0.09	1.65	0.04	1.72	0.02
Throat width	0.11	0.01	0.11	0.01	0.10	0.00	0.10	0.00
Lobe length*	1.01	0.10	0.65	0.02	0.79	0.03	0.74	0.01
Lobe shape ±*	0.81	0.10	0.00	0.00	0.38	0.06	0.27	0.03
Anther:								
Length	0.99	0.06	0.86	0.05	0.92	0.03	0.95	0.04
Tail length	0.11	0.01	0.07	0.01	0.11	0.01	0.11	0.01
Length past corolla	0.87	0.09	0.59	0.06	0.79	0.04	0.72	0.02
Stem diameter*	0.95	0.07	0.62	0.05	0.86	0.04	0.79	0.03
Pappus length*	2.18	0.09	1.55	0.06	1.88	0.06	1.84	0.02
Seed length[2]	0.61	0.01	0.50	—	0.64	0.01	0.65	0.01
Seed width[2]	0.29	0.01	0.20	—	0.26	0.01	0.27	0.00
Stem color ±*	0.81	0.10	0.00	0.00	0.49	0.06	0.32	0.03
Stigma length	0.56	0.06	0.48	0.04	0.46	0.02	0.48	0.01

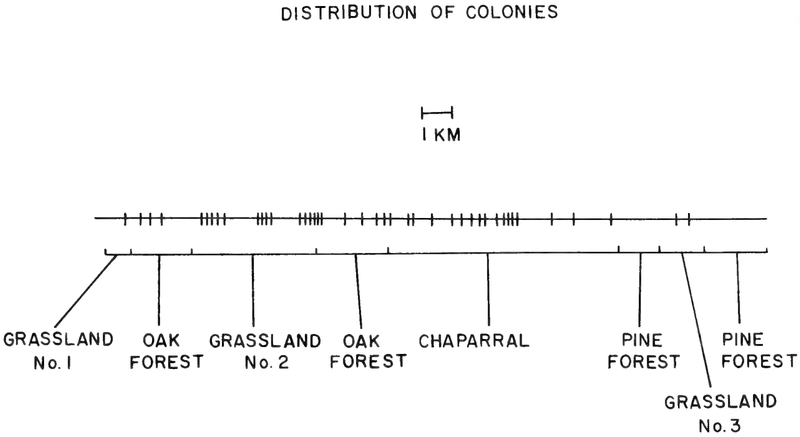

FIG. 1. Map of colony and habitat distribution for Happy Canyon *Cirsium* population.

oak woodland, and yellow pine forest (Munz and Keck 1959). Colonies of the Happy Canyon *Cirsium* population were distributed such that 41% were in the chaparral region; 38% in the grassland areas; 21% in the oak woodland, and none in the pine forest (Fig. 1). A survey of the terrain away from the road revealed that Happy Canyon *Cirsium* occurred only in roadside colonies.

Elevation increased most rapidly in the chaparral area (400 m) and least in the nearly level grassland regions. Three separate grassland areas existed, isolated from one another by large areas of other habitat types. Grasslands No. 1 and No. 2 were spatially close and at approximately the same elevation, whereas grassland No. 3 was isolated from both grasslands No. 1 and No. 2 by large areas of other habitat types and was at a significantly higher elevation.

Even though *Cirsium* colonies do not extend into the native, undisturbed vegetation in the study region, habitat type is an indicator of and modifies, the overall environment. That is, the species composing the surrounding community are a result of the environment of a region, and may be a better measure of the environment than can be obtained through direct measurements, because even if many environmental parameters are measured at many locations, one still does not know the relative weighting of the factors (Unger 1836, Schimper 1898, Warming 1909, Drude 1913, Odum 1959, Ovington 1962, Daubenmire 1968, Krajina 1969, Mueller-Dombois and Ellenberg 1974). Thus, it is as a reflection of the environment, rather than extensive interaction of *Cirsium* with species in the community, that I refer to habitat type.

Colonies of *Cirsium* consisted of discrete patches of individuals occurring at densities between 1 and 4 plants per m^2. When *Cirsium* occurred on both sides of the road at a location they were considered a single colony. Approximately 200 flowering individuals occurred in each colony, except the grassland colonies, which ranged between 500 and 1000 flowering individuals. The only colonies with fewer individuals were the three chaparral colonies adjacent to the pine forest habitat, and the isolated grassland colony No. 1 in Fig. 1. The study was carried out from 1976 to 1979, and collections were made in 1977.

Morphological data and analysis. A random sample of each colony was obtained by collecting plants along a line transect. Two hundred thirty-two plants from the Happy Canyon population (an average of 5.5 plants per colony) were chosen from the collections, using a random numbers table, for numerical taxonomic analysis. In addition, 15 plants used in crosses and chosen for their similarity to *C. californicum, C. occidentale,* or for their intermediacy, were included in the morphological analysis. Finally, included were 12 herbarium specimens of *C. californicum,* 11 of *C. occidentale,* 2 of apparent hybrid identity (Santa Cruz Island and Tule River), a specimen of *C. vulgare,* and a specimen of *C. tioganum,* all identified previously by other collectors. Specimens were all from the University of California at Santa Barbara Herbarium (UCSB 7229–7235, 7239–7244, 6454, 6456, 6459, 8440, 15330, 18245, 22061, 22291, 24011, 24291, 24320, 28865, 31527, 32531). The *C. californicum* and *C. occidentale* herbarium specimens were used as references for species phenotypes. By using specimens identified and reviewed by other systematists, personal biases were eliminated in establishing references.

Thirty-five morphological characters were used in the numerical taxonomic analysis (Table 1): 28 metric and 7 plus-minus (+ pubescence = dense; + color = red; + corolla lobe shape = spatulate). Characters were chosen that showed variability in the population and that were obtainable from herbarium specimens as well as living material. Characters were measured on plants of similar age, and on organs of comparable development.

All characters were ranged between values of 0 and 1 before Q matrix numerical analyses, so that they all had equal weight (Sneath and Sokal 1973). Morphological data analysis was performed by the distance diagram technique (Wells 1979), cluster analysis (NTSYS Program), and principal coordinate analysis (Gower 1966), all of which operate on Q type matrices. Principal component analysis (SPSS Program) and means and their standard errors were obtained from R type matrices. Analyses were performed on an IBM 360/75 computer. The generalized n row by m column hypergeometric version of the general exact test (Wells and King 1980) and the chi-square test were used to test for a relationship between habitat type and morphological form, as defined by the principal coordinate analysis. The spatial (11.5 km) and elevational (400 m) isolation between *Cirsium* of grassland No. 3 and No. 1 & 2 allowed testing of the hypothesis that habitat correlated selection had occurred, rather than formation of a cline or selection by an environmental factor not related to habitat.

The alternative hypotheses were considered by testing for differences between the *Cirsium* of grassland areas 1 & 2 and 3, between the *Cirsium* of grassland 1 & 2 and chaparral, and between grassland 3 and chaparral *Cirsium* using the chi-square and general exact test statistics. If a cline existed or selection by a factor actually uncorrelated to habitat occurred, then *Cirsium* in grassland areas 1 & 2 and 3 should be different because they are isolated and at different elevations. However, grassland *Cirsium* from areas 1 & 2 and 3 should not differ, but each should be different from chaparral *Cirsium,* if habitat determining factors are causing differentiation. Finally, silhouettes of stem leaves, inflorescences, and peduncle leaves provide a graphic display of the variation within the Happy Canyon population.

Sterility barriers. The presence of sterility barriers to gene recombination was tested by observing pollen fertility, and by ovule development in controlled crosses, as well as by morphological analysis. Ownby et al. (1975) have studied *C. californicum* and *C. occidentale* cytologically and demonstrated that both have $2n = 30$ chromosomes throughout their range. Percent pollen fertility was tested on the 274 plants used for morphological analysis. A flower was removed from each of the dried specimens, 200 grains sampled and stained with lactophenol blue to determine percent fertility (Radford et al. 1975). Fertility barriers were also tested by crosses between species, within species but between individuals, between species types and hybrid types, and by bagging. An analysis of variance on the arcsine $\sqrt{\text{frequency}}$ of developed ovules was used to determine significance of differences. Finally, 1160 capitula, each from a separate plant (a sample independent of those used for morphological analysis), were dissected and the percentages of developed ovules recorded.

Protein electrophoretic data and analysis. Seeds removed from the inflorescences collected to determine the field ovule development of heads were germinated and grown to small rosettes. Leaves of the rosettes were removed and used (while still fresh) for electrophoresis in the isozyme analysis. Slab acrylamide gel electrophoresis was used to separate isozymes following the techniques described by Wells and Wells (1980). The enzyme loci studied include leucine aminopeptidase (LAP), alkaline phosphatase, acid phosphatase, malate dehydrogenase, lactate dehydrogenase, and "general protein." Isozyme stain formulas are those of Shaw and Prasad (1970) and Johnson (1975). Results were grouped according to habitat type. The hypergeometric version of the general exact test (G.E.T.) and the chi-square test were used to determine whether significant differences occurred in genotype fre-

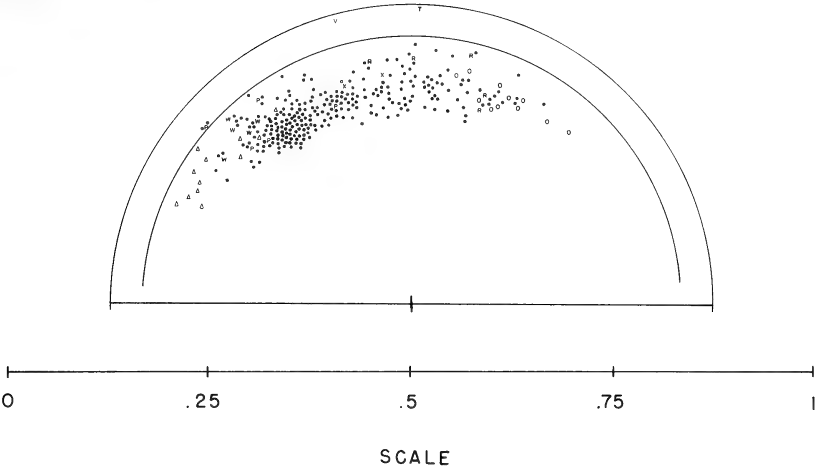

FIG. 2. Distance diagram of Happy Canyon and herbarium reference individuals. *Cirsium occidentale* and *C. californicum* reference specimens fall into two distant clusters according to species. *Cirsium vulgare* and *C. tioganum* are depicted as distinct species by their position. Happy Canyon individuals exist as a continuum of points from the *C. occidentale* to the *C. californicum* herbarium specimens as would be expected if hybridization and backcrossing are occurring. △ = *C. californicum,* ○ = *C. occidentale,* ● = Happy Canyon *Cirsium* individuals, V = *C. vulgare,* T = *C. tioganum,* and X = *Cirsium* herbarium specimens of questioned species identity. Individuals used in crossing experiments: R = red flowered plants resembling *C. occidentale,* W = white flowered plants resembling *C. californicum,* and P = pink flowered plants intermediate in floral characteristics.

quencies between colonies grouped by habitat type. Both the general exact and chi-square tests were also used to test whether habitat related selection was actually occurring by comparing grasslands 1 & 2 and 3, and to chaparral *Cirsium,* as was done with the morphological data. Genotype frequencies rather than allele frequencies were used because random mating could not be assumed, and because they are more conservative (sample size ½) than inferred allele frequencies (Spiess 1977).

RESULTS AND DISCUSSION

One biological species or two? Morphological variation in the population, pollen fertility within the population, and seed set in experimental crosses were examined to determine whether *C. californicum* and *C. occidentale* are true biological species in the Happy Canyon population. Morphological data are displayed in a distance diagram (Wells 1979) in Fig. 2; a phenogram from a cluster analysis is given as Fig. 3; scatter diagrams of the first three axes of a principal coordinate analysis (Gower 1966) in Figs. 4, 5; as means and their standard

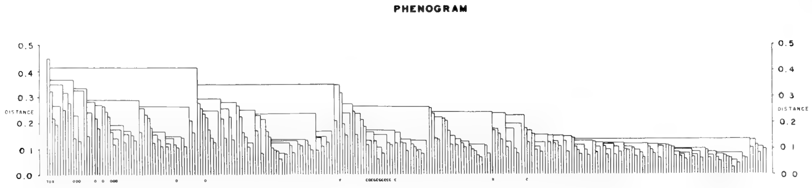

FIG. 3. Phenogram from unweighted pair group method using arithmetic average linkage cluster analysis. The lack of large differences in the cluster levels indicates a gradation of morphological forms, as would be expected through hybridization and backcrossing. Herbarium specimens: O = *C. occidentale,* C = *C. californicum,* T = *C. tioganum,* V = *C. vulgare,* and X = *Cirsium* herbarium specimens of questioned species identity.

errors in Table 1; and as stem leaf, inflorescence, and peduncle leaf silhouettes in Figs. 6, 7, 8.

Distance diagram. The herbarium specimens identified as *C. californicum* and as *C. occidentale* fell into two distinct clusters along species lines (Fig. 2). *Cirsium vulgare* and *C. tioganum* herbarium specimens fell outside the inner semicircle and close to the outer semicircle centrally in the diagram, as should distinct species. Also note that two herbarium specimens of hybrid identity (Santa Cruz Island; and Tule River, Tulare County, California) fell at an intermediate "hybrid" position on the distance diagram.

The study population was a continuum of forms, ranging from *C. californicum* to *C. occidentale* within both circles (Fig. 2). Of 247 plants of the Happy Canyon sample, only two fell outside the inner semicircle of the distance diagram, as might be expected if backcrosses frequently occur and neither parental line contains all alleles of some genes for extreme character values (Grant 1964). All evidence from the distance diagram is consistent with the hypotheses that only one biological species was being studied in Happy Canyon, that no sterility barriers existed, that hybridization and backcrossing are common, and that Happy Canyon *Cirsium* may be treated as one genetic population.

The distance diagram also includes the individuals used in crosses that will be analyzed later. Some *C. occidentale* individuals used in crosses appear to be backcrosses, but as Fig. 2 depicts, examples of *C. californicum* and *C. occidentale* as defined by the reference individuals were difficult to find.

Cluster analysis. One sees no distinct clusters, but rather a gradation of cluster levels in Fig. 3. If there had been a barrier to initial hybridization and subsequent backcrossing, two distinct clusters should have been produced by the cluster analysis, corresponding to *C. californicum* and *C. occidentale,* respectively. The cluster analysis, like the distance diagram, supports the interpretation that a single genetic

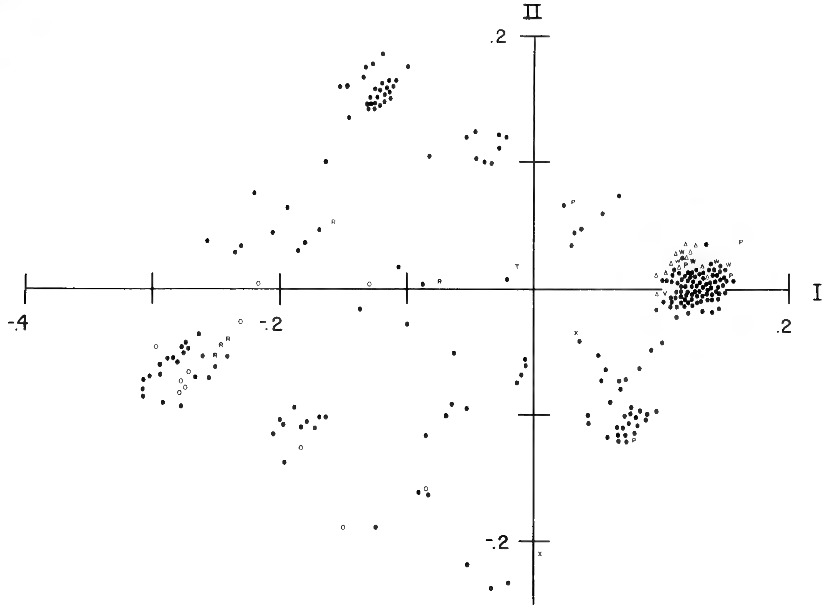

FIG. 4. Principal coordinate analysis axes I and II. No distinct clusters occur as expected when hybridization and backcrossing occurs. Herbarium specimens: O = *C. occidentale*, △ = *C. californicum*, T = *C. tioganum*, V = *C. vulgare*, and X = *Cirsium* herbarium specimens of questioned species identity. Individuals used in crosses: R = *C. occidentale*, W = *C. californicum*, and P = intermediate. ● = Happy Canyon *Cirsium* individuals.

population was being studied with no sterility barriers between morphological types.

Principal coordinate analysis. Next, individual morphological variation was studied through principal coordinate analysis. The first three axes account for 64% of the total variance; the first 13, for 93% of the total variance. Depicted as Fig. 4 are axes I and II, and as Fig. 5 are axes I and III. If barriers exist to gene exchange and recombination, the principal coordinate analysis should depict just two isolated clusters of points: one containing all of the *C. californicum* reference individuals, and the other all of the *C. occidentale* reference individuals. Axes I and II reveal no isolated cluster of points; a continuum exists between *C. occidentale* grouped reference points and those of *C. californicum*. Figure 4, therefore, gives evidence that only one genetic population exists.

Figure 5, which displays axes I and III of the principal coordinate analysis has new information, but still supports the conclusion that one biological species was being studied and that there were no bar-

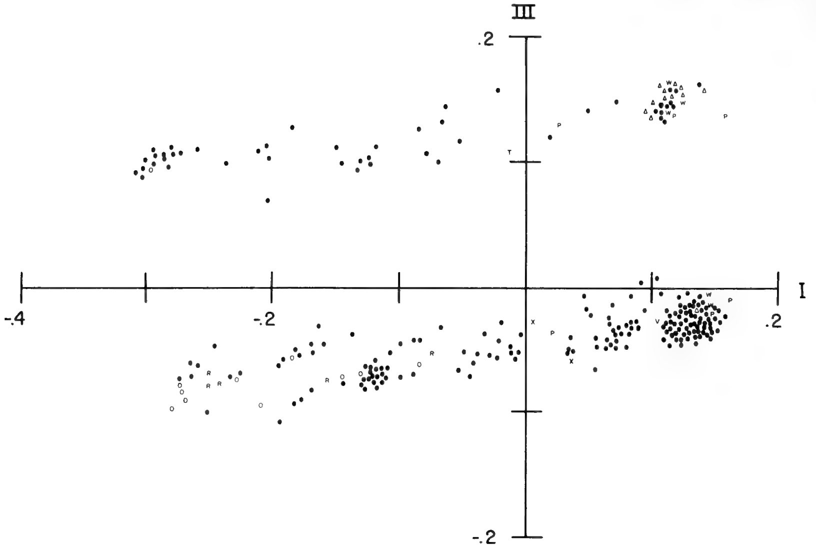

FIG. 5. Principal coordinate analysis axes I and III. Two distinct clusters occurred corresponding to the positive and negative poles of axis III. However, reference individuals of both *C. californicum* and *C. occidentale* occurred in both clusters, and within a cluster a continuum of forms exists between the species types. Therefore, some factor (e.g., environmental selection) other than species has caused differentiation of two recombinant forms. Herbarium specimens: O = *C. occidentale,* △ = *C. californicum,* T = *C. tioganum,* V = *C. vulgare,* and X = *Cirsium* herbarium specimens of questioned species identity. Individuals used in crosses: R = *C. occidentale,* W = *C. californicum,* and P = intermediate, ● = Happy Canyon *Cirsium* individuals.

riers to hybridization. Clearly, two clusters occur in Fig. 5, one on the positive side of axis III and the other on the negative. However, reference individuals of both species, and of both species types used for crosses, occur in both clusters. Also, in both the positive and negative clusters there is a continuum of forms spanning the space between the reference specimens of both species. Thus, the morphological evidence still supports the theory that there is but one biological species being studied, and that recombinant forms constitute the majority of the individuals of the studied population. However, there appears to be grouping of recombinant phenotypes into two clusters by some force (genetic or developmental response). Principal coordinate analysis of axes II and III (available from the author) gave results similar to axes I and III. Axis three still caused separation into two clusters, and each cluster still had both reference species included.

Principal component analysis. A principal component analysis (R matrix) was performed in an attempt to describe the characteristics that separate individuals into the two clusters in the principal coordinate analysis (Q matrix). Unfortunately, the component analysis (available from the author) did not greatly simplify the data space. The first eight principal component axes (64% of the variance) were studied. Only one cluster was produced in the analysis, a result that is consistent with hybridization but does not characterize individuals in the two principal coordinate clusters.

Means and standard errors. The means and their standard errors of each of the 35 characters for individuals classified as *C. californicum, C. occidentale,* and for individuals of each of the principal coordinate clusters were examined next for differences and relations in characteristics between members of the two coordinate clusters (Table 1). In the positive cluster, 34% of the character means are not significantly different from *C. occidentale* (within 2 standard errors) but are significantly different from *C. californicum,* and 26 percent do not differ from *C. californicum* but do differ from *C. occidentale.* The negative cluster has 31% of the character means non-differentiable statistically from *C. occidentale* but different from *C. californicum,* and 23% not different from *C. californicum* but different from *C. occidentale.* Forty-three percent of the characters have means significantly different between the plus and minus clusters. Individuals of the plus cluster have arachnoid pubescence on both peduncle and stem leaves, have long peduncle leaves, and wider inflorescence bracts, as does *C. californicum,* while having the number of leaf lobes, spine lengths on leaves, stem diameter, pappus length, and corolla lobe shape similar to *C. occidentale.* The negative cluster has these characters similar to the opposite parent, though not always as extreme. The minus cluster also has involucre shape like *C. occidentale,* but the plus cluster is quite variable in this character. Thus, the principal coordinate clusters are hybrid individuals composed of recombinant characteristics.

Silhouettes. Gestalt description of morphological variation of *Cirsium* in Happy Canyon is supplied by the silhouettes of stem leaves, inflorescence, and peduncle leaves (Figs. 6, 7, and 8). Recombinant types exist in the leaf silhouettes (Fig. 6). Again, a complete gradation of forms is seen in capitula (Fig. 7), and in the peduncle leaves (Fig. 8).

In the morphological analysis of the Happy Canyon population, organ silhouettes and a wide variety of numerical methods all suggest that, although the population includes two recognized taxonomic species, it is composed primarily of hybrids and backcross forms.

Pollen fertility. Sixty-seven percent of the individuals sampled had pollen fertility higher than 90%, and 85% of the population had pollen fertility higher than 80%. Unless the individuals with low fertility are all F_1 or some other specific type hybrid, no evidence emerged to indicate a sterility barrier. Apparently only one genetic population exists.

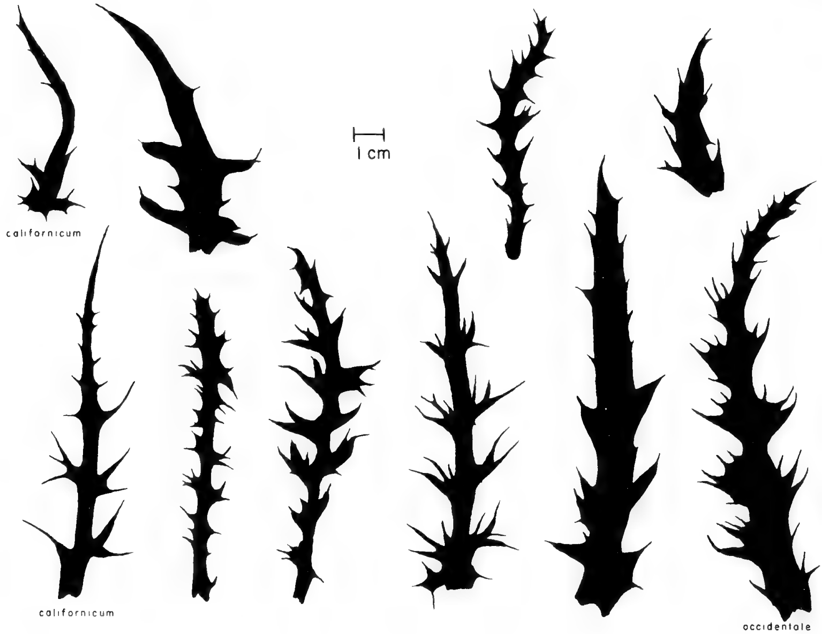

FIG. 6. Stem leaf silhouettes. Typical *C. occidentale* leaf is depicted lower right, and typical *C. californicum* leaf upper and lower left. A gradation of forms existed from one species to the other species.

A distance diagram (Fig. 9) may reveal a clustering of infertile hybrid individuals. If found, such clustering would suggest that two biological species, rather than one, were being studied. Individuals with low fertility were uniformly distributed across the morphological spectrum. Thus, pollen sterility does not restrict gene migration and recombination in the *Cirsium* population studied.

Ovule development. Another test for sterility barriers was that of ovule development per head in experimental crosses (Table 2). Those capitula that were bagged rarely produced any developed ovules. All cross-pollinated inflorescences produced a markedly greater proportion of developed ovules than did bagged plants. There are two hypotheses about out-crossing ovule development that should be tested. The first is that one or more types of crosses between different individuals (*occidentale* × *occidentale, californicum* × *californicum, occidentale* × *californicum, occidentale* × hybrid, *californicum* × hybrid, or hybrid × hybrid) will have significantly higher or lower percent ovule development than the other crosses. The other hypothesis is that crosses between individuals of the same species (*occidentale* × *occidentale,* and *californicum* × *californicum*) will have significantly higher or lower

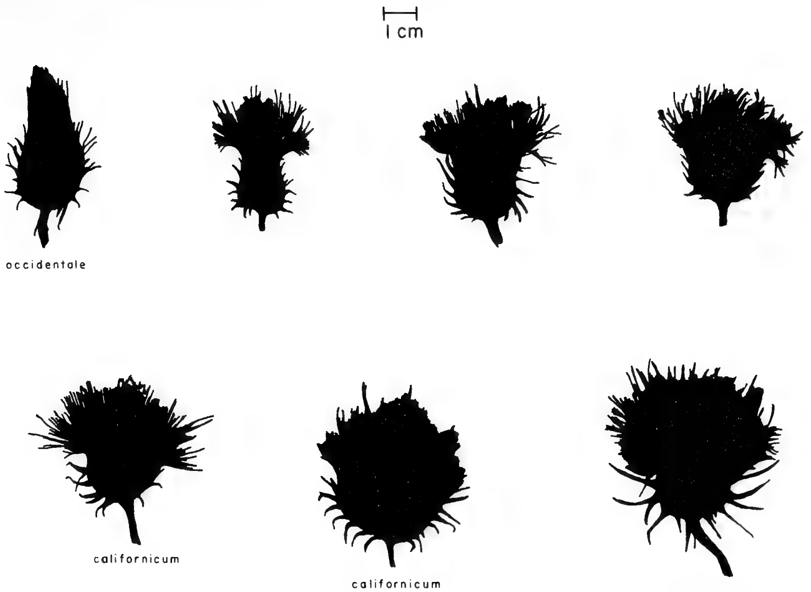

FIG. 7. Inflorescence silhouettes. Typical *C. occidentale* form is shown by the upper left inflorescence, and typical *C. californicum* forms by the lower left and center silhouettes. A gradation of forms existed from one species to the other.

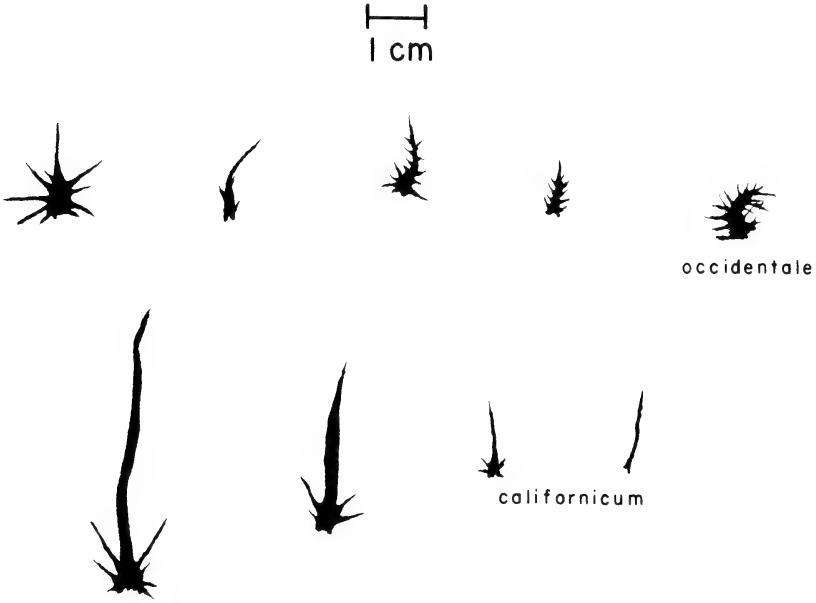

FIG. 8. Peduncle leaf silhouettes. Typical *C. occidentale* form is depicted by the upper right silhouette and typical *C. californicum* forms by the lower right two leaves. A wide variety of recombinant forms existed, a few of which are shown.

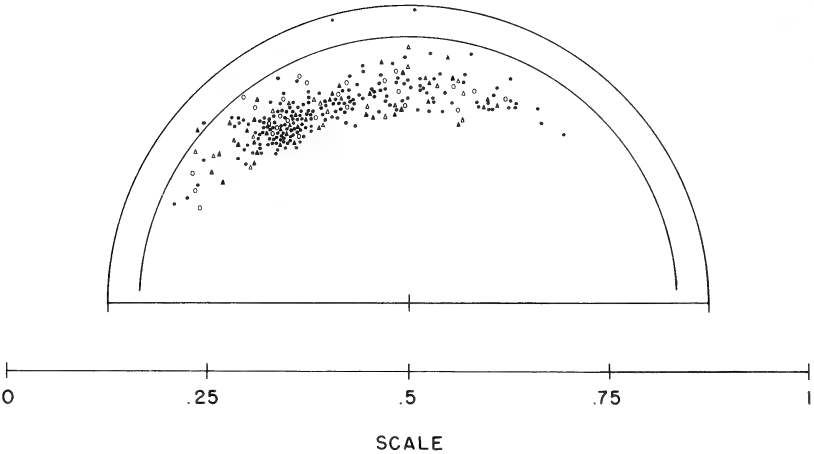

FIG. 9. Distance diagram of reference and Happy Canyon individuals. Symbols refer to percent pollen fertility of the individuals. Sterility was randomly distributed throughout the scatter. Thus, there was no evidence of a sterility barrier to gene recombination. ● = pollen fertility >95%, ▲ = pollen fertility between 90% and 95%, ○ = pollen fertility 80% to 90%, and △ = pollen fertility below 80%.

percent ovule development than crosses between species, species × hybrid, or hybrid × hybrid. These two hypotheses were tested by use of a one-way analysis of variance on the arcsine transformed data (arcsine $\sqrt{\text{frequency}}$ developed ovules per head). Neither test showed a significant difference (Table 2), so the null hypothesis that all types of crosses are equally fertile cannot be rejected.

Finally, developed ovule frequency in capitula of controlled lath house crosses was compared to the frequency of developed ovules per head in the field. In nature, mean percent developed ovules was 20.1 (S.D. = 25.9 n = 1160 flowers dissected). The non-developed ovaries were small and shriveled as if fertilization had not occurred. It may be that the efficiency of the pollen vectors in transporting pollen limits ovule development, as shown by Levin (1968) for *Lithospermum*. Developed ovules of capitula in experimental crosses were also about 20%.

The principal coordinate analysis separated *Cirsium* individuals into two distinct groups based on morphological characters. These clusters do not correspond to the taxonomic species. Could different environments have caused the observed phenotypic variation? This possibility was examined by asking whether a correlation exists between the defined habitat types and morphological phenotypes (Table 3). The null hypothesis is that the number of individuals in a cell is dependent only on the frequency of individuals sampled from a habitat and that the distribution of phenotypes is identical in each habitat. The null hy-

TABLE 2. OVULE DEVELOPMENT FREQUENCY IN EXPERIMENTAL CROSSES.

Bagged plants: $\bar{x} = 0.00097$; $n = 18$. (Mean frequency)
Cross pollinated: Frequency developed ovules, $\bar{x} = 0.2117$; $n = 18$

	Cross (group)					
Cross #	1 *californicum* *californicum*	2 hybrid hybrid	3 *occidentale* *occidentale*	4 *californicum* Hybrid	5 *occidentale* Hybrid	6 *californicum* *occidentale*
1	0.1875	0.1739	0.1250	0.2127	0.5650	0.1429
2	0.2698	0.1633	0.2500	0.2000	0.2222	0.1020
3	0.2500	0.2413	0.1515	0.1875	0.1892	0.1765

Analysis of variance on: Arcsine transformed $\sqrt{\text{frequency}}$ developed ovules.

	Anova				
Source of variation	df	SS	MS	F	
Among groups	5	267.96	53.59	1.52	Not significant
Within groups	12	422.89	35.24		
Total	17	690.85			
Groups 1 + 3 vs. 2 + 4 + 5 + 6	1	0.639	0.639	0.018	Not significant

TABLE 3. RELATION BETWEEN OCCURRENCE OF INDIVIDUALS IN THE CLUSTER DEFINED BY THE 3RD PRINCIPAL COORDINATE ANALYSIS AXIS AND HABITAT TYPE.

Principal coordinate axis III	Habitat			
	Grassland	Oak forest	Chaparral	Total
+ Cluster	15	3	31	49
− Cluster	93	51	39	183
Total	108	54	70	232

$\chi^2 = 33.8$ df $= 2$; $p \ll 0.001$; G.E.T. $p = 5.7 \times 10^{-8}$.

TABLE 4. RELATION BETWEEN OCCURRENCE OF INDIVIDUALS OF ELECTROPHORESIS LEUCINE AMINOPEPTIDASE PHENOTYPES AND HABITAT TYPE.

	LAP phenotype		
Habitat	Fast band only	Fast and slow bands	Total
Oak forest	11	27	38
Grassland	35	114	149
Chaparral	46	54	100
Total	92	195	287

$\chi^2 = 14.1$ df $= 2$; $p < 0.001$; G.E.T. $p = 0.000757$.

pothesis must be rejected (G.E.T. $p = 5.7 \cdot 10^{-8}$; $\chi^2 = 33.8$, df = 2, $p < 0.001$) based on the data of Table 3. Thus, it appears that habitat type is associated with phenotype.

Individual genetic traits were examined by isozyme analysis in 287 offspring rosettes via slab acrylamide gel electrophoresis. The malate dehydrogenase, lactate dehydrogenase, and "general protein" stains were monomorphic and will not be discussed further.

The leucine aminopeptidase (LAP) results are presented in Table 4, which relates the results to habitat type. The differences are denoted slow and fast, where slow bands remained closer to the origin than the fast bands. LAP electrophoretic phenotypes all contained the fast band, but some contained a slow band while others did not. Both the chi-square and generalized exact test were performed (G.E.T. $p = 0.000757$; $\chi^2 = 14.1$, df = 2, $p < 0.001$). Thus, LAP genotype distribution was correlated to habitat type, which suggests that morphs correlated to habitat may also have a genetically based component. The alkaline phosphatase and acid phosphatase data are published elsewhere (Wells and King 1980). The alkaline phosphatase genotypes resembled those of LAP in being correlated with habitat type (G.E.T. $p = 0.023$) whereas those of acid phosphatase were uniformly distributed (G.E.T. $p = 0.412$).

The correlation between habitat and both morphological and electrophoretic phenotypes presents an additional question. Is micro-habitat selection actually occurring, rather than an elevationally related cline, or even selection by some environmental factor(s) not determining habitat?

Hypotheses generated by these questions can be tested because of the population structure of *Cirsium* in Happy Canyon, i.e., the spatial and elevational isolation of grassland region 3 from 1 & 2. Morphologically, 9.1% of the *Cirsium* of grassland No. 3 are from the + cluster (n = 11), in comparison to 14.4% of grassland *Cirsium* 1 & 2 (n = 97). LAP electrophoretic data had 13.0% of grassland region 3 *Cirsium* with only the fast band (n = 23), while 25.4% of area No. 1 & 2 *Cirsium* had only the fast band (n = 126).

If a cline or a nonhabitat-related environmental factor were operative, then, grassland *Cirsium* colonies 1 & 2 should differ from No. 3, and both grassland *Cirsium* No. 3 and No. 1 & 2 should differ from the intervening chaparral *Cirsium*. However, if habitat-related selection is occurring then one would expect *Cirsium* in grassland habitats 1 & 2 and 3 not to be significantly different, but that they would differ from those *Cirsium* found in the chaparral.

Grassland *Cirsium* in regions 1 & 2, as defined morphologically by the principal coordinate analysis, did not differ significantly from those in region 3 (G.E.T. $p = 0.72$, $\chi^2 = 0.21$, df = 1, $p > 0.6$), but each did differ significantly from the chaparral *Cirsium* (grassland 1 & 2 vs. chaparral: G.E.T. $p = 2.19 \times 10^{-5}$; $\chi^2 = 18.29$, df = 1, $p <$

0.005; grassland 3 vs. chaparral: G.E.T. $p = 0.0431$; $\chi^2 = 4.93$, df = 1, $p < 0.05$). The LAP isozyme data showed the same pattern of differences as morphology (grassland 1 & 2 vs. 3: $\chi^2 = 1.65$, df = 1, $p > 0.2$; grassland 1 & 2 vs. chaparral: $\chi^2 = 10.50$, df = 1, $p < 0.005$; grassland 3 vs. chaparral: $\chi^2 = 8.47$, df = 1, $p < 0.005$). Alkaline phosphatase data (Wells and King 1980), however, showed significant differences only between grassland 1 & 2 and chaparral *Cirsium* (G.E.T. $p = 0.0265$), but not between the grassland 1 & 2 and 3 *Cirsium* (G.E.T. $p = 0.84$), or between grassland 3 and chaparral *Cirsium* (G.E.T. $p = 0.0682$).

CONCLUSIONS

1. The Happy Canyon *Cirsium* population consists of one biological species with no sterility barriers.
2. Morphological and electrophoretic phenotypes correlated with habitat type appear to have a genetic basis.
3. The differentiation corresponding to habitat types suggests that several phenotypic traits may be subject to selection and that differentiation along new lines may have resulted after hybridization of *C. californicum* and *C. occidentale* in the Happy Canyon population.

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A NEW GYPSOPHILIC SPECIES OF GALIUM (RUBIACEAE) FROM NORTH-CENTRAL MEXICO

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Abstract

A new species, **Galium dempsterae,** is described from gypseous deposits in north-central Mexico. It is known from only two collections, both obtained from Cerro Peña in southern Nuevo Leon. The taxon is related to yet another gypsophile, *G. juniperinum,* from areas about Cerro Potosi, Nuevo Leon; both of these taxa relate to *G. lacrimiforme,* a suspected gypsophile of the same broad region.

Explorations, both past and recent, of the numerous and often locally large gypseous outcrops in north-central Mexico have yielded a number of interesting endemics, some of them quite bizarre (Turner 1973, Turner and Powell 1979, Higgins and Turner 1982). Detection of the species of *Galium* described below is surprising because the genus recently received a thorough taxonomic treatment by Dempster (1977).

Galium dempsterae B. L. Turner, sp. nov.

G. juniperino Standley simulans sed foliis nonadpressis glabris, pedicellis longioribus, pilis fructuum brevibus valde incuratis (Fig. 1).

Polygamous suffrutescent rhizomatous coarse perennials, 10–12 cm tall; stems costate, divaricately branched, glabrous except for a circle of hairs ca. 0.1 mm long below each node; leaves in 4's, longer than the nodes except in inflorescence, glabrous, (2.5–)3–4(–5.2) mm long, 0.7–1.0 mm wide, subulate, pungent, spreading, thickish, faintly 1-nerved, sessile; glandular cells absent; inflorescence strict, the flowers in axillary 3(–5)-flowered dichasia in the upper leaf axils; peduncles 1.0–4.2 mm long, leafy bracts 2, 2–4 mm long, pedicels 1.7–4.0 mm long; corollas rotate, glabrous, yellowish-green, 2.0–3.3 mm wide, lobes 4, ovate, apices acute to acuminate; filaments 0.2–0.3 mm long; anthers yellow, 0.2–0.3 mm long; style 0.6–0.7 mm long (wet), divided ca. halfway to base; fruits dry (immature), set with very short, upwardly directed strongly incurved hairs, 0.1–0.2 mm long.

Type: Mexico, Nuevo Leon; gypsum outcrops on nw. slope of Cerro Peña Nevada, ca. 7 km ne. of San Antonio Peña Nevada (ca. 30 km nw. of Doctor Arroyo), Jul 1977, *C. Wells & G. Nesom 514* (Holotype LL).

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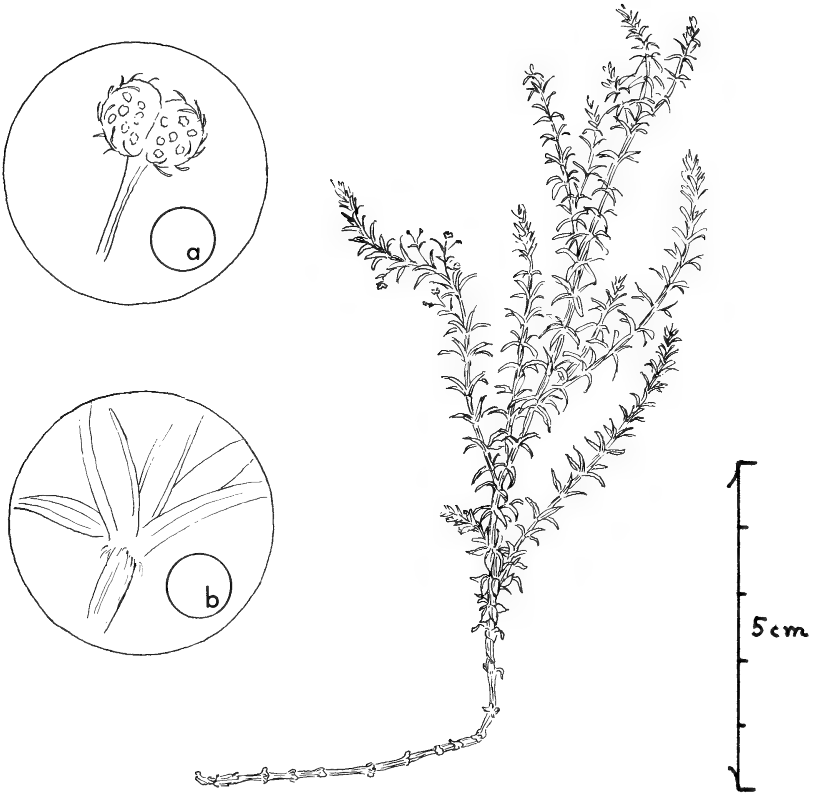

FIG. 1. Habit sketch of *Galium dempsterae* (×1). Inserts: a, fruit (×10); b, node, showing hairs (×6).

PARATYPE: Nuevo Leon: ca. 30 km ene. of San Antonio de Peña Nevada, base of Cerro Peña Nevada, "large area of gypsum outcrops," 6600 ft, 3–5 Aug 1981, *G. Nesom 4262* (TEX).

The species is apparently most closely related to yet another gypsophile, *Galium juniperinum* Standl., which occurs as a local dominant on the largely barren white gypseous soils about the village of Galeana some 120 km due north of the present site. Dempster (1977) in her critical, delightful, treatment of *Galium* for Mexico and Central America notes only a single collection (the type) of *G. juniperinum.* We have noted the species several times on gypseous outcrops near Galeana and have collected it on gypsum substrates on the northeastern lower slopes of Cerro Potosi, ca. 7.5 km northwest of Galeana (*Turner & Davies A-10,* TEX).

The fruit of *Galium dempsterae* is presumably similar to what we suspect is yet another gypseous endemic, *G. lacrimiforme* Dempster, known only from a single collection, ca. 13 km east of Dulces Nombres, Nuevo Leon, a region where gypseous outcrops are known to occur. Additional new taxa are likely to be found upon the various isolated, largely unexplored, gypseous outcroppings in north-central Mexico (Turner and Powell 1979).

It is a pleasure to name this species for Lauramay T. Dempster, whose very sound treatment of this difficult genus made easy our assessment of the present contribution. We are grateful to Dr. M. C. Johnston for providing the Latin diagnosis and to Dr. J. Henrickson for helpful suggestions.

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PIONOCARPUS BECOMES IOSTEPHANE (COMPOSITAE: HELIANTHEAE): A SYNOPSIS

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Abstract

Iostephane comprises four Mexican species, including **Iostephane madrensis** (S. Wats.) Strother (≡*Helianthella madrensis,* the type of *Pionocarpus* S. F. Blake). The species are clearly allied with members of Heliantheae but without an obvious nearest relative.

Perpetuation of *Pionocarpus* (a pappose monotype) is no longer tenable, in view of overall agreement in habitat preference, habit, and details of vegetative and floral morphology among members of *Iostephane* (originally characterized as epappose) and *P. madrensis,* which is here transferred to *Iostephane.* Indeed, some plants of *I. madrensis* from Durango and Zacatecas very closely approach, in vegetative and floral detail, plants of *I. papposa* from Oaxaca. One robust specimen from Durango (see discussion of *I. madrensis*) may be a hybrid between *I. madrensis* and *I. heterophylla.* Rather than make a bald transfer, I append a taxonomic synopsis of the now four species of *Iostephane.*

Members of *Iostephane* are all subscapiform, heavy-rooted perennials that inhabit pine, oak, or pine-oak forests between 1500 and 3000 m in Mexico, ranging from Sinaloa, Chihuahua, and Durango east and south to western Veracruz and central Chiapas. With regard to floral characteristics, the plants are clearly allied with members of Helianthinae s.str., near to but isolated from plants now assigned to *Viguiera* H.B.K. s.l.

IOSTEPHANE Benth. in Benth. & Hook., Gen. Pl. 2:368. 1873.—TYPE: IOSTEPHANE HETEROPHYLLA (Cav.) Benth. ex Hemsl. ≡ *Coreopsis heterophylla* Cav.
Pionocarpus S. F. Blake, Proc. Amer. Acad. Arts 51:521. 1916.—TYPE: *Pionocarpus madrensis* (S. Wats.) S. F. Blake ≡ *Helianthella madrensis* S. Wats. ≡ IOSTEPHANE MADRENSIS (S. Wats.) Strother.

Scapiform perennial herbs to 15 dm high, rhizomatous from tuberiform rootstocks; leaves mostly in basal rosettes, very variable among plants, less so within plants, petioles winged, at least distally, blades membranous to coriaceous, lanceolate to broadly ovate or deltoid,

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often with a deep, rounded sinus on each side, thus pandurate to 3-lobed, cuneate to subtruncate or subcordate basally, obtuse to acute or acuminate apically, entire to subentire to coarsely dentate with callous teeth, coarsely scabrous to nearly glabrous; heads solitary or 2–5(–12) in very loose associations; peduncles scapiform, bracteate, often swollen and fistulose distally; involucres turbinate to hemispheric, 1–2 cm high; phyllaries 12–26 in 2(–3) series, herbaceous, subequal, lance-linear to broadly lanceolate or lance-ovate, acute to acuminate, strigo-pilose; paleae scario-cartilaginous, navicular, keeled or not, acuminate, pungent, closely strigose; receptacles convex to conical; ray florets 8–21, neutral or styliferous but infertile, corollas purplish to pink (sometimes white) or yellow to orange, tube stout, lamina oblong to ovate, showy; disc florets 15–110+, perfect, corollas yellow (sometimes with purplish lobes), tube usually glabrous, length ≤⅓ that of the abruptly ampliate, cylindric, sparsely pubescent to densely hispidulous throat, lobes 5, equal, narrowly deltoid, abaxially pubescent; anthers blackish, very slender, minutely sagittate; style branches rather stout, abruptly hispidulo-penicillate; achenes purplish black, slightly laterally compressed, oblong-obovate in profile, typically quadrate in cross-section, glabrous to strigose; pappus none or of 0–2 fragile or deciduous, setose squamellae 1–3 mm long plus 0–4(–18) erose-lacerate, free or connate squamellae 0.5–1 mm long; chromosome number, $x = 17$.

Key to species of *Iostephane*

Phyllaries mostly lanceolate to lance-ovate, (3–)4–7 mm wide; ray corollas purple to pink (rarely white), lamina 25–58 mm long . . . . *I. heterophylla*

Phyllaries mostly linear to lance-linear, 1.5–3(–4) mm wide; ray corollas yellow to orange, lamina 9–31 mm long.

  Ray florets mostly 5–9; disc florets mostly 15–40, corollas 5(4.2–6) mm long; achenes mostly 3.5–4.5 mm long, glabrous; epappose . . . . *I. trilobata*

  Ray florets mostly 13(8–16); disc florets mostly 35–60, corollas 6(5.5–8.5) mm long; achenes mostly 4.5–5.5 mm long, sparsely to prominently strigose; pappus of setose and/or erose-lacerate scales.

    Leaf blades typically linear to narrowly lanceolate, length mostly 5–8+ times width, none lobed; pappus of 0–2 setae plus 10–18 erose scales; nw. Mexico . . . . *I. madrensis*

    Leaf blades typically ovate to deltoid to broadly lanceolate, length mostly 1–3 times width, often some or all lyrate to pandurate; pappus of 0–2 setae plus 2–4 erose scales; se. Mexico . . . . *I. papposa*

IOSTEPHANE HETEROPHYLLA (Cav.) Benth. ex Hemsl., Biol. Cen. Amer. Bot. 2:168. 1881.—*Coreopsis heterophylla* Cav., Icon. Pl. 3:34, pl. 268. 1795.—*Simsia heterophylla* (Cav.) Pers., Synop. Pl. 2:478. 1807.—*Ximenesia cavanillesii* Spreng., Syst. Veg., 16th ed. 3:605. 1826, nom. nov.—*Echinacea heterophylla* (Cav.) D. Don in Sweet, Brit. Fl. Gard. ser. 2. 1: pl. 32. 1831 [1830].—TYPE: Grown in Madrid from Mexican seed; the plate fixes application of the name.

Rudbeckia napifolia H.B.K., Nov. Gen. Sp. 4:244. 1820.—TYPE: "Crescit juxta Santa Rosa de la Sierra, alt. 1300 hex (Nova Hispania). ♃ Floret Septembri," *Humboldt and Bonpland s.n.* (Holotype: P, microfiche!).

Echinacea dicksonii Lindl., Edward's Bot. Reg. 24: pl. 27. 1838.—*Iostephane heterophylla* (Cav.) Benth. ex Hemsl. var. *dicksonii* (Lindl.) W. M. Sharp, Ann. Missouri Bot. Gard. 22:82. 1935.—TYPE: Grown in England by the Horticultural Society from Mexican seed; the plate fixes application of the name.

Echinacea dubia Knowl. & Westc., Fl. Cab. 3:163, pl. 131. 1839.—TYPE: Grown by Birmingham Botanical and Horticultural Society from Mexican seed; the plate fixes application of the name.

Iostephane heterophylla (Cav.) Benth. ex Hemsl. var. *acutiloba* W. M. Sharp, Ann. Missouri Bot. Gard. 22:83. 1935.—TYPE: Mexico, Jalisco, near Guadalajara, Aug 1893, *C. G. Pringle 4480* (Holotype: MO!; isotypes: F!, GH!, MIN!, MO!, MSC!, NY!, UC!, US!).

Plants 3–9(–15) dm high; petioles 4–12(2–25) cm long, leaf blades 6–15(3–27) cm long, 5–12(2–18) cm wide; phyllaries 14–26, lance-ovate to lanceolate, 16(8–28) mm long, 3–7 mm wide; paleae 8.4–11.8 mm long; ray florets 8–21, corollas typically purple to magenta or pinkish, exceptionally white (e.g., Guerrero, *Moore 4534,* A, MICH), lamina 25–58 mm long; disc florets 50–100+, corollas 6.2–9.1 mm long; achenes 3.6–6.6 mm long, sparsely to moderately strigillose; pappus none or of 1–2 setose squamellae 1–2 mm long plus 0–4+ cuneate to lanceolate, erose to lacerate scales less than 1 mm long (e.g., Puebla, Aug 1908, *Purpus s.n.,* UC); chromosome number, $2n = 34$.

Known mostly from pine, oak, and pine-oak forests or adjacent clearings or meadows, sometimes drier forest with junipers, 1500–3000 m, in Mexican states: Chih., Sin., Dgo., S.L.P., Gto., Aguasc., Jal., Mich., Mex., D.F., Hgo., Pue., Mlos., Gro., Ver., and Oax.

Iostephane madrensis (S. Wats.) Strother, comb. nov.—*Helianthella madrensis* S. Wats., Proc. Amer. Acad. Art 23:278. 1888.—*Pionocarpus madrensis* (S. Wats.) S. F. Blake, Proc. Amer. Acad. Arts 51:522. 1916.—TYPE: Mexico, Chihuahua, "pine plains at the base of the Sierra Madre," Sep 1887, *C. G. Pringle 1302* (Holotype: GH!; isotypes: F!, NY-2!, US!).

Helianthella iostephanoides Greenm., Proc. Amer. Acad. Arts 40:41. 1904.—Type: Mexico, Zacatecas, "in the Sierra Madre," 18 Aug 1897, *J. N. Rose 2391* (Holotype: GH!; isotype: US!).

Plants mostly 3–7 dm high; petioles 6–12 cm long, leaf blades linear to lanceolate, 10–16(–25) cm long, 1–3(–6) cm wide; paleae 9–11 mm long; ray florets 9–16, corollas yellow, lamina 9–15(–30) mm long; disc florets 35–60, corollas 5.5–6 mm long; achenes 5–5.5 mm long, strigillose; pappus of 0–2 setose squamellae 2–3 mm long plus, typically, 10–18 free or connate, erose-lacerate scales 0.3–1 mm long; chromosome number unknown.

Known from pine and pine-oak forests between 2100 and 2650 m in Chih., Dgo., Gto., Jal., and Zac. *Breedlove 44199* (CAS) from 65–75 km sw. of Cd. Durango is exceptional in having leaf blades roughly 10–15 cm long by 4–6 cm wide and ray florets with laminas to 3 cm long. I first took the plant to be a yellow-rayed form of *I. heterophylla.* Now I think it may be a hybrid involving that taxon and *I. madrensis.* Pollen from the specimen appears to be normal and fertile (stained in lactophenol cotton-blue).

Iostephane papposa Fay, Brittonia 25:192. 1973.—Type: Mexico, Oaxaca, ca. 10 km s. of Suchix[s]tepec (ca. 95 km n. of Puerto Ángel), 2300 m, 8 Nov 1970, *A. Cronquist 10895* (Holotype: NY!; isotypes: ENCB!, MEXU, MICH!, UC!, UTC).

Plants 4–6 dm high; petioles 4–12(3–15) cm long, leaf blades 6–12 (–15) cm long, 3–6(–8) cm wide; phyllaries 18–22, lance-linear to linear, 8–15 mm long, 1.6–2.8 mm wide; paleae 8–10.5 mm long; ray florets 8–13, corollas yellow to orange, lamina 17–31 mm long; disc florets 30–50, corollas 5.9–8.5 mm long; achenes 4.2–4.5 mm long, sparsely strigillose; pappus of (1–)2 setose squamellae 1.5–3 mm long plus 2–6 cuneate to lanceolate, erose-lacerate scales ca. 0.5 mm long; chromosome number unknown.

Known only from six gatherings made in pine-oak forests in Oaxaca at 2200–2700 m: five from ca. 100 km s. of Oaxaca along route 175 from Oaxaca to Puerto Ángel (vicinity of type locality) and one from 2 km e. of Ixtan de Juarez, ca. 30 km ne. of Oaxaca (*Hill 1803,* NY).

Iostephane trilobata Hemsl., Biol. Cen. Amer. Bot. 2:169. 1881.—Type: Mexico, Chiapas, without locality or date, *Ghiesbreght 101* (Holotype: K; isotype: GH!).

Rudbeckia chrysantha Klatt, Leopoldina 23:143. 1887.—[*Echinacea chrysantha* Sch.-Bip., in sched. fide Klatt, loc. cit.]—Type: Mexico, "Cumbre de Estepa," *Liebmann "575"* (Holotype: C; leaf and drawing: GH!).

Gymnolomia scaposa Brandegee, Univ. Calif. Publ. Bot. 4:93. 1910.—Type: Mexico, Puebla, near Coaxcatlan, oak forests, 8000–9000 ft, Sep 1909, *C. A. Purpus 4120* (Holotype: UC!; isotypes: F!, GH!, MO!, NY!, US!).

Plants 2–6 dm high; petioles 6–10(3–15) cm long, leaf blades 6–8(3–12) cm long, 3–4(2–6) cm wide; phyllaries 12–21, lance-linear to linear, 6–12 mm long, 1.5–3.1 mm wide; paleae 5.8–9.8 mm long; ray florets 5–9, corollas yellow to orange, lamina 9–20 mm long; disc florets 15–40, corollas 4.2–6 mm long; achenes 3.2–4.8 mm long, glabrous; pappus none; chromosome number, $2n = 34$, ca. 68.

Known from pine-oak forests between 1500 and 2600 m, principally in Chiapas and Oaxaca; other collections: Mexico, Cumbre de Estepa, *Liebmann 575* (GH); Mexico, near Nanchitla (ca. 80 km wsw. of Mexico City), 7 Oct 1933, *Hinton 4965* (GH, MO, NY, US); same locality, 15–16 Sep 1958, *Matuda 32806* (CAS, ENCB); Mexico, Cerro de Jilotepec (ca. 65 km nnw. of Mexico City), 27 Sep 1953, *Matuda 29094* (NY); Puebla, Coaxcatlan (se. of Tehuacan, ca. 18°16′N, 97°09′W), Sep 1909, *Purpus 4120* (F, GH, MO, NY, UC, US). Specimens of this species labeled as coming from Durango (*Jackson 7190* in UC and *7191* in NY) are actually from Oaxaca (Jackson, pers. comm.).

ACKNOWLEDGMENTS

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CERATOZAMIA MICROSTROBILA (ZAMIACEAE), A NEW SPECIES FROM SAN LUIS POTOSÍ, MEXICO

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ABSTRACT

Ceratozamia microstrobila is described from southeastern San Luis Potosí, Mexico. It is compared with *C. zaragozae* Medellin-Leal and *C. hildae* Landry & Wilson, to which it is mostly closely related.

We believe the genus *Ceratozamia* is highly variable, and the possibility of natural hybrids exists. We have found differences within and between populations of the same species in leaflet width and length, as well as in mature cone sizes. However, we feel the genus seems to form two main groups: large plants with large trunks, many leaves, and large cones, of which *C. mexicana* Brogn. is typical; and a group of small plants with small, almost subterranean trunks, bearing few small leaves and small cones, to which belong *C. zaragozae* Medellin-Leal, *C. hildae* Landry & Wilson, and the species described below.

Ceratozamia microstrobila, Vovides & Rees, sp. nov.

Truncus ovoideus vel subcylindricus, usque ad 24 cm longus et usque ad 10 cm diametro; folia pinnata usque ad 70 cm longa; petiolus inermis, basi tomentosus; cataphylla triangula, tomentosa, cauli adnata, 3–5 mm longa; foliola lanceolata, 15–18 cm longa, 2.8–3.2 cm lata, ad marginem subrevoluta, apice acuta, strobilus masculinus, 17 cm longus, 2.3 cm diametro, brunneus, pedunculatus; pedunculus inermis, tomentosus, 5 cm longus; microsporophylla bicornia, 7 mm longa, 5 mm lata, cornua 2 mm longa, parte sterili inter cornua 2 mm longa; strobilus femineus pedunculatus, subcylindricus, viridi-brunneus, 6 cm longus, 4.4 cm diametro; megasporophylla peltata, 1.7–2.1 cm lata, 1.2–1.3 cm longa, bicornia, cornua 2 mm longa; pedunculus inermis, tomentosus, 6 cm longus (Fig. 1).

Trunk almost subterranean, ovoid to subcylindric, up to 24 cm long, 10 cm maximum diameter, protected by the persistent leaf bases, light brown in color. Leaves 2–4, pinnate, up to 70 cm long, unarmed;

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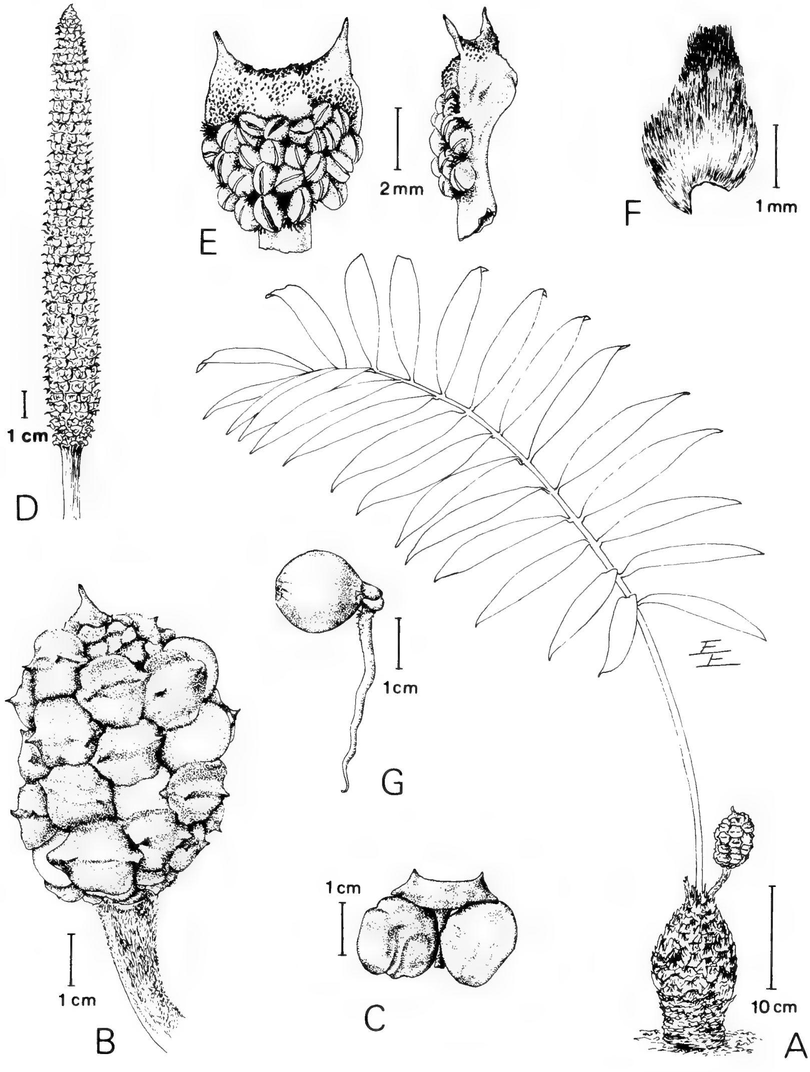

FIG. 1. *Ceratozamia microstrobila* Vovides & Rees. A. Habit of female plant. B. Female cone. C. Megasporophyll with attached seeds. D. Male cone. E. Microsporophyll. F. Cataphyll. G. Seed with emerged radicle and taproot.

petiole tomentose at base. Cataphylls triangular, tomentose, 3–5 mm long. Leaflets lanceolate 15–18 cm long, 2.8–3.2 cm wide, alternate, subopposite or opposite, acute at apex, coriaceous, entire, subrevolute, lustrous green on adaxial surface, lighter green on abaxial surface;

nerves more or less visible. Male cone 17 cm long, 2.3 cm diameter, brown; peduncle 5 cm long, unarmed, tomentose; microsporophylls (from median part of cone) 5 mm wide, 7 mm long, horns 2 mm long, 4.5 mm apart, length of infertile portion between the horns 2 mm. Female cone greenish brown, 4.4 cm in diameter, 6 cm long; peduncle 6 cm long, unarmed, tomentose; cataphyll triangular, 4 mm long, heavily tomentose; megasporophylls peltate, 1.7–2.1 cm wide, 1.2–1.3 cm long, pubescent at edges, horns 2 mm long, spaced 1.4 cm apart; seeds slighty elongate, 1.4 cm in diameter, 1.8–1.9 cm long. $2n = 16$.

TYPE: México, San Luis Potosí, Municipio of Ciudad del Maiz, at Ejido las Abritas, 850 m, ♂, 7 Nov 1974, *J. Rees 1613* (Holotype: XAL).

PARATYPE: Mexico, San Luis Potosí, Municipio of Ciudad del Maiz, at Ejido las Abritas, 24 Sep 1977, *J. Rees 1681* (MEXU).

The new taxon is known only from Ejido las Abritas at 850 m. It grows in shallow reddish clay soil, rich in humus, on limestone outcrops. The site is located in the transition zone between low deciduous forest (selva baja caducifolia) and mixed oak woodland. Genera present at the site include: *Quercus* spp., *Ostrya* sp., *Ulmus* sp., *Dendropanax* sp., *Cupania* sp., *Sabal* sp., *Bursera* [aff. *simaruba* (L.) Sarg.], and *Hamelia* sp. Also present are two other cycads: *Dioon edule* Lindley and *Zamia fischeri* Miq.

Vegetative key

Leaflets fasciculate.
  Leaflets 1 to 3 cm wide, arranged in clusters of 2 to 4 along rachis, up to 11 pairs of clusters .... 1. *C. hildae*
Leaflets not fasciculate.
  Leaves irregularly twisted; leaflets linear lanceolate, not exceeding 1 cm in width, up to 19 pairs .... 2. *C. zaragozae*
  Leaves not irregularly twisted; rachis unarmed; leaflets lanceolate, 15 to 18 cm long, 2.8 to 3.2 cm wide, up to 16 pairs .... 3. *C. microstrobila*

These three small *Ceratozamia* species from eastern Mexico form separate populations and are morphologically distinct from each other. *Ceratozamia microstrobila* is distinguished from *C. hildae* Landry & Wilson by having lanceolate, not fasciculate, leaflets, and from *C. zaragozae* Medellin-Leal by not having irregularly twisted leaflets. The chromosome numbers and karyotypes of the three small species are similar to those of *C. mexicana,* as published by Marchant (1968); however, each of the species differs in the number of satellites present (Vovides, unpubl. data).

Additional field collections are needed of the small *Ceratozamia* species from eastern Mexico. They have been collected at only a few sites, where they are being removed rapidly by commercial collectors.

Their ranges, variation, and cytology have not been adequately studied. The morphology and cytology of these plants and their relationships to the larger *Ceratozamia* species are now undergoing study by authors.

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COMPETITION FOR LIGHT AND A DYNAMIC BOUNDARY BETWEEN CHAPARRAL AND COASTAL SAGE SCRUB

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Abstract

A sharp boundary between mature stands of *Ceanothus* chaparral and coastal sage scrub was found in the Santa Monica Mountains in coastal southern California. The presence of numerous dead coastal sage scrub species in the understory of the chaparral suggests that the chaparral has been progressively invading the coastal sage scrub during the last several fire cycles.

McPherson and Muller (1967) demonstrated that light competition occurred between the chaparral shrub, *Ceanothus cuneatus,* and the drought-deciduous shrub, *Salvia leucophylla,* at an inland site in southern California. Seedlings of both species apparently established together following a fire; however, after 26 years, the evergreen shrubs had overtopped and suppressed the drought-deciduous shrubs. Using both field and lab experiments, McPherson and Muller (1967) eliminated the role of phytotoxins, soil moisture, and soil nutrients in creating the observed pattern. They showed that the taller *Ceanothus* shrubs interfered sufficiently with light reaching shorter *Salvia* shrubs to eliminate them after 26 years.

In this paper, I report a similar case of apparent light competition between the chaparral shrub, *Ceanothus megacarpus,* and several drought-deciduous shrub species at a coastal site in southern California. I also hypothesize about the long-term dynamics of the chaparral/coastal sage scrub ecotone at this site.

At mid-elevations (100–300 m) along the immediate coast of the Santa Monica Mountains 50 km northwest of Los Angeles, mature stands of chaparral and coastal sage scrub occur together and often form a mosaic across the landscape. The chaparral is dominated by *Adenostoma fasciculatum* or *Ceanothus megacarpus* (Bauer 1936), whereas the coastal sage scrub is comprised of the common drought-deciduous shrubs *Artemisia californica, Salvia leucophylla,* and *S. mellifera* (Kirkpatrick and Hutchinson 1977, Gray and Schlesinger 1981, Westman 1981). Where the two vegetation types meet, there often is a sharp boundary between them, even in the absence of obvious edaphic or geologic discontinuities. This pattern suggests that biotic interactions, historic factors (fire, grazing, human activity), or both, may be important.

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FIG. 1. Adjacent, even-aged stands of *Ceanothus* chaparral (dark region, left foreground) and coastal sage scrub (light regions) in the Santa Monica Mountains of southern California. Mixed *Adenostoma* chaparral is in the upper left. There is a road cut in the foreground.

METHODS

Adjacent, mature stands of chaparral and coastal sage scrub, located in the Santa Monica Mountains (150 m elevation and 3 km from the ocean), were the site of a three-year comparative study of productivity and nutrient cycling (Gray 1982, 1983) and are shown in Fig. 1. Wildfire burned through the canyon and study site in 1956 according to local residents and California Department of Park and Recreation officials.

To determine canopy cover and density of individual species in the chaparral and coastal sage scrub, 50-m sample transects were conducted through the center of each community. One-hundred paired, 1 × 1-m quadrats were sampled along each transect line. The presence of all live and dead individuals of all shrub species in each quadrat was recorded. Canopy cover was estimated by measuring the canopy projection of each species along a 50-m tape (line intercept method). Relative cover was calculated for each species as the total distance covered by the canopy of a species divided by the total distance covered by the canopies of all species.

Dead shrubs of all species were remarkably intact, particularly in the chaparral: all were rooted, relatively unweathered, and undisturbed by animal activity. Each dead shrub was identified to species by using species characteristics of branching geometry (*Salvia leucophylla, Eriogonum parvifolium*), stem morphology (*Ceanothus megacarpus*), and bark texture (*Artemisia californica, Adenostoma fasciculatum, Eriophyllum confertiflorum*).

Eighteen whole shrubs of *Ceanothus megacarpus* were harvested in June 1979 using a stratified-random selection (Gray 1982). The age of each shrub was determined by ring counts at the base of the stems.

RESULTS AND DISCUSSION

The chaparral stand was completely dominated by *Ceanothus megacarpus* in terms of cover and density (Table 1). Living *Ceanothus megacarpus* shrubs were 4–6 m in height and the foliage was concentrated in the upper 75 cm. The canopy was completely closed. Numerous, attached dead branches were present in the lower portions of the shrubs, a characteristic of other *Ceanothus* species in the chaparral (Keeley 1975).

The age of the living *Ceanothus* shrubs ranged from 20–22 years in the sample shrubs. *Ceanothus megacarpus* does not crown sprout and reproduces only by seed after a fire. It typically forms rapidly growing stands of even-aged individuals (Schlesinger and Gill 1980).

Several other species were present in the chaparral, but were few in number (Table 1) and 1–1.5 m shorter than *Ceanothus megacarpus*. Several of these species, including *Eriogonum, Cercocarpus,* and *Adenostoma* exhibited broad, etiolated leaves typical of shade plants (Boardman 1977), appeared to be growing slowly, and did not flower during the three years of the study.

Numerous standing dead individuals of both evergreen and drought-deciduous species were also in the understory of the chaparral (Table 1). The dead *Ceanothus megacarpus* shrubs were 10–12 years old and small in stature. These plants appeared to be aggregated, as suggested by the high standard deviation associated with their density values (Table 1). These dead individuals of *Ceanothus* were apparently eliminated by intra-specific competition for water during early stand development as shown by Schlesinger and Gill (1980).

The drought-deciduous species in the understory of the chaparral were the same species that comprised the adjacent coastal sage scrub (Tables 1, 2). All individuals of coastal sage scrub species in the chaparral were dead with the exception of *Eriogonum* and *Yucca*. In contrast, mortality in the coastal sage scrub community was only a small percentage of the total number of shrubs and was restricted to *Artemisia* and *Salvia* (Table 2). The density of dead *Artemisia* and *Salvia* shrubs in the chaparral was significantly less than for live shrubs in the coastal sage scrub. Only 10% of the dead *Artemisia* and *Salvia* shrubs in the chaparral appeared to have arisen from crown sprouts, compared to 33% of the live shrubs in the coastal sage scrub.

TABLE 1. PERCENT RELATIVE COVER AND ABSOLUTE DENSITY OF INDIVIDUALS IN THE *Ceanothus* CHAPARRAL. Standard deviations (S.D.) are given for the density values, n = 100.

Species	Evergreen (E) or drought-deciduous (DD) leaves	Relative cover (%)	Density (individuals per square meter)	S.D.
Live plants				
Ceanothus megacarpus	E	99	2.67	2.68
Adenostoma fasciculatum	E	1	0.13	0.43
Eriogonum parvifolium	DD	1	0.09	0.24
Yucca whipplei	E	1	0.07	0.24
Ceanothus spinosus	E	1	0.03	0.23
Cercocarpus betuloides	E	1	0.02	0.08
Rhus laurina	E	1	0.01	0.07
Dead plants				
Ceanothus megacarpus	E	—	1.73	3.27
Adenostoma fasciculatum	E	—	0.30	0.38
Eriophyllum confertiflorum	DD	—	0.30	0.47
Eriogonum parvifolium	DD	—	0.25	0.43
Artemisia californica	DD	—	0.18	0.42
Salvia leucophylla	DD	—	0.10	0.20
Yucca whipplei	E	—	0.01	0.07
Ceanothus spinosus	E	—	0.01	0.07

The presence of dead coastal sage scrub species in the understory of the chaparral suggests a case of light competition similar to that described by McPherson and Muller (1967). After a previous fire, both evergreen and drought-deciduous species established side by side as seedlings, or in the case of *Artemisia* and *Salvia,* as both seedlings and crown sprouts (Westman et al. 1981). By 7 to 10 years, *Ceanothus* shrubs were tall enough to overtop the coastal sage scrub species. Eventually, the greater biomass and height of the *Ceanothus* shrubs interfered sufficiently with light reaching the smaller drought-deciduous shrubs to suppress and eliminate them. The great attenuation of light by the canopy in mature stands of *Ceanothus megacarpus* has been documented by Schlesinger and Gill (1980), who found light levels well below that needed for net photosynthesis by the related chaparral shrub, *C. greggii.* Indeed, the decrease of available light beneath the canopy during stand development in *Ceanothus megacarpus* is manifest in the death of lower branches (Gray 1982).

Several results of McPherson and Muller (1967) are different from the situation described here. They reported that two cohorts of *Ceanothus cuneatus,* aged 16 and 26 years, were present in their chaparral stand. *Ceanothus* shrubs in this study were even-aged. *Ceanothus megacarpus* seeds require heat alteration for germination (Hadley 1961),

TABLE 2. PERCENT RELATIVE COVER AND ABSOLUTE DENSITY OF INDIVIDUAL SHRUBS IN THE COASTAL SAGE SCRUB. Standard deviations (S.D.) are provided for density values, n = 100. [1] Grasses: *Stipa lepida, Elymus condensatus, Bromus* sp.; herbs: *Castilleja affinis, Eriophyllum confertiflorum* seedlings, *Galium* sp., *Haplopappus squarrosus, Paeonia californica, Pityrogramma triangularis.*

Species	Evergreen (E) or drought-deciduous (DD) leaves	Relative cover (%)	Density (individuals per square meter)	S.D.
Live plants				
Salvia leucophylla	DD	49	0.98	1.24
Artemisia californica	DD	29	0.81	1.64
Yucca whipplei	E	7	0.07	0.32
Eriogonum parvifolium	DD	4	0.20	0.40
Eriophyllum confertiflorum	DD	2	0.55	0.32
Herbs and grasses[1]	—	9	—	—
Dead plants				
Artemisia californica	DD	—	0.13	0.43
Salvia leucophylla	DD	—	0.01	0.07

and successful germination is unlikely to occur between fires; hence, only a single cohort of *C. megacarpus* establishes after a fire. McPherson and Muller (1967) also found that most, if not all, of the *Salvia* shrubs in the chaparral understory were still alive and flowering after 26 years. The absence of any living *Salvia* shrubs in the *C. megacarpus* stand suggests that suppression at this site was more rapid. Annual production in *C. megacarpus* chaparral exceeds all reported values for California chaparral and other mediterranean-type ecosystems of the world (Gray 1982) and may facilitate a rapid overtopping of drought-deciduous shrubs.

HYPOTHESIS OF STAND DYNAMICS

Two mutually exclusive hypotheses can be proposed to explain the observed pattern in the chaparral: (1) The present stand of *Ceanothus* has persisted through many fires with a similar structure and biomass, and the dead, drought-deciduous species in the understory are only the remnants of early successional species that temporarily occupied the site. This successional relationship between coastal sage scrub and chaparral has been described in other chaparral communities (Cooper 1922, Wells 1962, Hanes 1971, 1977). (2) The present chaparral stand was occupied by a mature coastal sage scrub community immediately prior to the last fire. The latter community was completely eliminated by a single invasion of *Ceanothus* as a result of a large influx of seed before or immediately after the fire.

The data and field observations are not consistent with either hypothesis. The existence of *Artemisia* and *Salvia* shrubs that arose from crown sprouts in the chaparral understory indicates that these individuals had been present for at least two fire cycles. Hence, these species do not appear to be temporary, early successional occupants of the chaparral stand. It is also unlikely that the present chaparral stand developed en masse after the last fire, because there is no adjacent, upslope chaparral stand of *Ceanothus* to provide a large seed source (Fig. 1). Indeed, the only upslope chaparral stand is dominated by *Adenostoma* and it is separated from the *Ceanothus* stand by an 80-m strip of coastal sage scrub (Fig. 1).

A third hypothesis to explain the sharp boundary and dead coastal sage scrub species in the chaparral is the slow, progressive, invasion of the coastal sage scrub stand by *Ceanothus* after several fire cycles. In this scenario, a few isolated *Ceanothus* initially became established in the coastal sage scrub stand after a previous fire. These shrubs probably arose from seed that was dispersed by downslope movement or animal activity. Such isolated *Ceanothus* shrubs are now present around the edges of the coastal sage scrub stand (Fig. 1). These scattered shrubs then produced a large seed crop, which in turn gave rise to many more shrubs after the next fire. *Ceanothus* species in the chaparral have been observed to produce up to 835 seeds/m^2 in a single year (Keeley 1977). Given this potential for high seed production, only a few fire cycles may be necessary to permit the development of a relatively pure stand, which in turn would suppress and eliminate drought-deciduous shrubs.

The speed and extent of an invasion by *Ceanothus* would be affected by a variety of factors including variation in seed production, viability of stored seed in the soil, and the degree of seed predation. *Ceanothus* species in the chaparral vary greatly in annual seed output and appear to have very little seed storage potential in the soil (Keeley 1977). Hence, a fortuitous combination of an abundant seed crop followed by a fire and low seedling mortality would be necessary for this encroachment by *Ceanothus* to occur.

The data suggest that *Ceanothus* shrubs are capable of invading coastal sage sites in the Santa Monica Mountains of southern California, resulting in the extension of *Ceanothus* chaparral into lower elevations more typical of coastal sage scrub (Harrison et al. 1971). Thus, in contrast to a recent documentation of a coastal sage scrub/chamise chaparral boundary in interior San Diego County that has been stable for more than 60 years (Bradbury 1978), I suggest that the boundary between *Ceanothus* chaparral and coastal sage scrub is a dynamic one, arising from competitive interactions after fires.

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EVIDENCE OF SALINITY-INDUCED ECOPHENIC VARIATION IN CORDGRASS (SPARTINA FOLIOSA TRIN.)

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Abstract

Results of culturing two height forms of *Spartina foliosa* in NaCl-treated nutrient solutions indicate that they are ecophenes. Growth was best in moderately saline solution and inhibited in fresh water and in a 1.2 osmolal (35 ppt) solution. Comparison of these results with soil salinity from areas supporting populations of each form suggest that the height of *S. foliosa* is influenced by local soil salinity conditions.

Spartina foliosa Trin. is a dominant plant species of the lower and mid-littoral zones of California salt marshes (Macdonald and Barbour 1974). The lower limit of its distribution is thought to be controlled by tidal inundation (Hinde 1954, Rowntree 1973). Its upper limit of distribution, which generally coincides with the mean high water (MHW) level, is governed by high soil salinity (Mahall and Park 1976b). Height and biomass of plants growing in this area of the marsh are generally less than in plants growing at lower intertidal elevations (Purer 1942, Atwater and Hedel 1976, Mahall and Park 1976a).

A population of *S. foliosa* in which adults grow only to 20–30 cm in height occurs along the eastern shoreline of San Francisco Bay. This marsh, located at the mouth of the Alameda River, is situated relatively high in the intertidal zone and is probably a remnant of a more extensive, pre-existing marsh (Mason 1976).

The difference in height between plants growing at high and low intertidal areas has led to the recognition of two forms of *S. foliosa* (Anonymous, 1976). The "robust" form is stout culmed, 0.3–1.2 m tall, and inhabits the lower littoral zone. The "dwarf" form is 0.2–0.3 m tall and typically occurs in the mid-littoral zone. The height distinction between the forms was adopted from criteria established for height forms of *Spartina alterniflora* (Adams 1963, Cooper 1974), a closely related species (Mobberley 1956) that occurs as the dominant vascular plant species of the lower and mid-littoral zones of East and Gulf Coast salt marshes.

The existence of height forms of *Spartina* sp., each occupying rather

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distinct elevational zones within the marsh, has generated studies to determine if the forms are ecotypes, and thus genetically distinct, or ecophenes, and thus genetically homogeneous. Parnell (1976) determined that $2n = 60$ for both the robust and dwarf forms of *S. foliosa.* Based upon chromosome number, then, there is no evidence that these two forms are different polyploid races. However, the same chromosome number for both forms does not negate the existence of ecotypes (Clausen et al. 1941). Based upon results of a field transplant experiment from which data were collected for more than a year, Harvey (1976) concluded that the forms were ecophenes and the variation in height was a physiological response to environmental gradients associated with tidal elevation.

With the exception of elevation, no environmental factors were measured in the study by Harvey (1976), and it is therefore not possible to correlate morphological variation with any specific environmental gradient(s) that may exist as a function of tidal elevation.

It is well documented that soil salinity is a major factor influencing growth and plant distribution within salt marshes (Chapman 1938, 1939; Mall 1969, Mahall and Park 1976b, Penfound and Hathaway 1938, Purer 1942). Furthermore, Mooring et al. (1971) and Nestler (1977) have shown that height of *S. alterniflora* is inversely related to salinity, suggesting that the height forms of this species are ecophenes.

In this study, the genecologic relationship of dwarf and robust *S. foliosa* was further investigated by examining the relative effect of salinity on these height forms under controlled laboratory conditions. It was hypothesized that the height forms are ecophenes and that the morphological dissimilarity observed in the field would vanish when both forms were exposed to a uniform, controlled environment. In order to relate morphological responses to actual field conditions, an assessment was made of the level of soil salinity each form was exposed to during a growing season.

METHODS

Soil samples and plants were collected from two marshes. Palo Alto marsh is located on the western shore of San Francisco Bay at approximately 37°27′N, 122°06′W. *Spartina foliosa* and *Salicornia virginica* L. are co-dominant. Robust *S. foliosa* (1–1.5 m tall) is found in monospecific stands at the low intertidal elevations and along creek channels. There appears to be a clinal variation in height associated with intertidal elevation because at the *Spartina–Salicornia* ecotone (roughly MHW), *S. foliosa* is typically 20–50 cm tall.

Alameda Creek marsh (37°36′N, 122°07′W) is located on the eastern shore of San Francisco Bay at the mouth of Alameda Creek. The marsh is dominated by *Salicornia virginica* and dwarf *Spartina foliosa* (adult plants are 20–30 cm tall). *Spartina* occurs most extensively as a monospecific stand along the shoreward 10 m of the marsh. It is also found hugging the edges of shallow tidal creeks that traverse the marsh.

Soil samples were taken in 1977 at the beginning (May) and end (October) of the growing season from three 3 × 6 m plots staked out in each marsh. The plots were placed so that discrete samples could be taken along the portion of the intertidal zone inhabited by *S. foliosa.* At Palo Alto, plot 1 (PA 1) was located within a stand of robust plants at the lower limit of intertidal distribution of *S. foliosa.* Plot 2 (PA 2) was located adjacent to a tidal creek within a stand of robust *S. foliosa.* This area was higher in the intertidal zone than plot 1. Plot 3 (PA 3), the highest intertidal area sampled, was located at the *Spartina–Salicornia* ecotone. At Alameda Creek, the sample plots were located along a transect that ran the width of the marsh. Plot 1 (AC 1) was located within the strip of *S. foliosa* that occupied the shoreward 10 m of the marsh. Plot 2 (AC 2) was at the *Spartina–Salicornia* ecotone, roughly 4 m from plot 1. Plot 3 (AC 3) was located within a small stand of *S. foliosa* that was restricted to the edges of a salt pan and an adjoining tidal creek. This pan was in the high marsh, an area dominated by *Salicornia.*

Soil samples were collected with a stainless steel soil corer with a 2 cm inner diameter. The cores were immediately sectioned horizontally into 0–5 cm, 5–15 cm, and 15–25 cm soil layers and the sections were sealed separately in plastic bags. The salinity of the root zone was calculated as the mean salinity of the 5–15 cm and the 15–25 cm soil layers. The determination of soil salinity was modified from Mahall and Park (1976b): water-soluble salts were extracted from a soil sample that had been dried at 100°C, and the osmolality of the extract was measured on a Wescor-model 5100 vapor pressure osmometer. Salinity of the original soil solution was calculated as osmole kg^{-1} H_2O.

Dwarf plants were collected from Alameda Creek on 17 March 1978, and robust plants were collected from Palo Alto on 22 March 1978. At Alameda Creek, all the plants were collected along the shoreward edge of the marsh where plot 1 was located. Plants from Palo Alto were collected from the areas where plots 1 and 2 were located. Alameda Creek was selected as the sole source of dwarf plant material. If the forms are ecotypes, then the robust form appears to be completely selected against at Alameda Creek. Thus, this population may represent a relatively homogeneous genetic stock of dwarf individuals. If both the dwarf, i.e., plants at the *Spartina–Salicornia* ecotone, and the robust form were collected from Palo Alto marsh, the expression of genetic differences between them may be diminished due to the greater potential for gene flow between sympatric forms. In order to collect young dwarf and robust plants of roughly the same age, plants approximately the same height with two expanded leaves were preferentially selected from both marshes.

All the plants collected for this study appeared to be new shoots sprouting from underground rhizomes, the species' primary means of reproduction. Asexual reproduction assures that the collected plants were representative of the respective forms observed at each marsh. The parents could not be determined, thus the samples were randomized with respect to the intrinsic genotypic variation within each population.

The plants were carefully uprooted so as to leave soil around the roots. Soil was later rinsed from the roots with tapwater in the laboratory. The plants were immediately rooted in vermiculite, and kept in a greenhouse until May, by which time they had fully recovered from transplanting (a well-developed root system was established, and the shoots had begun to grow).

On 12 May 1980, plants of each form were distributed evenly among four tubs, each containing 20 l of full strength nutrient solution (Machlis and Torrey 1956). Because *Spartina* sp. may require high levels of iron for successful growth (Adams 1963), the concentration of iron (as FeEDTA) was increased from 5 ppm to 10 ppm. Each solution was mixed and aerated by bubbling air through two plastic air diffusers. The air was supplied at a uniform rate by a filtered manifold system. Concentrations of 0.4 osmole kg^{-1} H_2O (11.7 ppt), 0.8 osmole kg^{-1} H_2O (23.4 ppt), and 1.2 osmole kg^{-1} H_2O (35.1 ppt) were established in three tubs by adding reagent grade NaCl at a rate of 0.2 osmole kg^{-1} H_2O every five days (Mahall and Park 1976b). Results of the field soil sampling were used to set the upper limit of the salinity range. The remaining solution consisted of nutrient solution only and served as a control against which salinity effects could be compared. The measured osmolality of this solution was 0.054 osmolal. The salinity of the solutions was monitored, and distilled water and/or NaCl were added as needed to maintain the proper concentrations. Nutrients were added at half strength every four weeks to supplement losses. The mean pH values for the control and the 0.4, 0.8, and 1.2 osmolal treatments were 6.3, 6.8, 7.0, and 6.7, respectively. Ambient air temperatures were maintained at 26°C, and relative humidity at 50%.

At the beginning of the experiment, 19 dwarf and 20 robust plants were measured for height, dry weight, leaf area, and leaf weight ratio (g leaves/g whole plant). Height was measured from the first visible node on the culm directly above the roots to the tip of the longest leaf. Leaf area was determined by treating each leaf as an isosceles triangle (Nestler 1977). Leaf weight ratio was calculated from the dry weight. The material was dried at 80°C for at least 24 hours in a forced draft oven. Plants in the culture solutions were harvested after 12 weeks.

One-way and two-way analysis of variance was used for statistical analysis of the data. Data for leaf area and leaf weight ratio were normalized by square root and arcsine transformation, respectively (Sokal and Rohlf 1969). In cases where the variances of the samples

TABLE 1. HEIGHT, DRY WEIGHT, LEAF AREA, AND LEAF WEIGHT RATIO OF DWARF AND ROBUST FORMS OF *Spartina foliosa* PRIOR TO TREATMENT IN CULTURE SOLUTION.

	Dwarf (n = 19)	Robust (n = 20)
Height, cm ($\bar{x} \pm$ S.E.)	24.7 ± 2.4	23.6 ± 1.1
Dry wt., g ($\bar{x} \pm$ S.E.)	0.307 ± 0.068	0.369 ± 0.039
cm^2 $leaf^{-1}$ ($\bar{x}$; 95% C.L.)	2.99; 2.53–3.50	3.99; 2.89–3.96
Leaf wt. ratio ($\bar{x}$; 95% C.L.)	0.239; 0.198–0.283	0.152; 0.132–0.172

being compared were not homogeneous, the Mann-Whitney test was used (Sokal and Rohlf 1969). Differences were considered significant when $\alpha < 0.05$.

RESULTS

Height, dry weight, and individual leaf area were not significantly different ($p > 0.05$) between the robust and the dwarf form when the culture experiment was started (Table 1). The leaf weight ratio of the dwarf form was significantly higher ($p < 0.001$) than that of the robust form. This difference was partially attributed to the heavier culm characteristic of the robust form. Additionally, the robust plants had a more extensive root and rhizome system, decreasing the dry weight of the leaves relative to the whole plant.

Survival of the two forms was similar after 12 weeks exposure to the same salinity (Table 2). Although the concentration of Fe was increased to 10 ppm, symptoms of Fe deficiency began to appear after about 45 days. Chlorosis was exhibited by all plants, but it was most pronounced in the plants in freshwater and the 0.4 osmolal treatment. Iron deficiency symptoms have also been described for cultured adult and seedling *S. alterniflora* (Adams 1963, Mooring et al. 1971). At present, it is not known if these observations are the result of a physico-chemical interaction between Fe and NaCl (Adams 1963), whereby

TABLE 2. SURVIVAL OF DWARF AND ROBUST FORMS OF *Spartina foliosa* GROWN IN SALINE CULTURE SOLUTION.

	Number of surviving plants	
Treatment	Dwarf	Robust
Control	10	7
0.4 osmolal	8	9
0.8 osmolal	17	16
1.2 osmolal	12	12

Fe availability to the plant is enhanced at high ionic strengths, or if there is a physiological requirement for one or both NaCl ions (Mooring et al. 1971). Mooring et al. (1971) reported that chlorosis was relieved by foliar application of ferrous sulfate; however, in our study, foliar spraying of FeEDTA did not alleviate leaf yellowing.

Height and dry weight (Figs. 1, 2) were greatest at 0.4 osmolal for the robust form and 0.8 osmolal for the dwarf form, suggesting that they may possess different salinity optima. However, the differences in height and dry weight between the forms at any given concentration were not significant. Height and dry weight did vary significantly with salinity. There were no significant interaction effects of salinity and form on height, the only character we were able to analyze by two-way ANOVA.

The maximum leaf area for the robust and dwarf forms (Table 3) occurred in the 0.4 osmolal and the 0.8 osmolal solutions, respectively, coincident with the maximum values for height and dry weight. The forms were significantly different at 0.4 osmolal ($0.01 < p < 0.05$), but not in freshwater, or in the 0.8 and 1.2 osmolal solutions. For each form, there were significant differences with salinity. Leaf area of the dwarf form was significantly greater at 0.4 and 0.8 osmolal than in freshwater or at 1.2 osmolal. Leaf area of the robust form was significantly greater at 0.4 osmolal than at 1.2 osmolal.

Differences in the leaf weight ratios between the forms was not significant (Fig. 3). This character was inversely related to salinity. Leaf weight ratio was significantly less in the 1.2 osmolal solution than in the less saline solutions.

The salinity of the root zone (5–25 cm) for Palo Alto and Alameda Creek marshes is given in Table 4. Generally, soil salinity was higher within the Alameda Creek marsh. In May, the salinity of PA 1 and 2 was significantly less than any of the three locations sampled within Alameda Creek marsh. However, the salinity of PA 3, the highest intertidal area sampled, was equal to the salinity of AC 1. Soil salinities were relatively stable throughout the Alameda Creek marsh between May and October, whereas at Palo Alto the concentration of salts of plots 2 and 3, the two higher intertidal areas, increased to levels approximately equal to those of AC 1 and 3. This type of seasonal variation is well-documented for temperate zone coastal salt marshes (Chapman 1939, 1940; Mahall and Park 1976b, Purer 1942).

DISCUSSION

The classic approach to studying ecotypic variation within plant species is to collect specimens from populations that are phenotypically distinct under natural conditions and then grow them together under uniform conditions (Clausen et al. 1941, Goodman 1973, McMillan 1959). Any differentiation in the measured characteristics among pop-

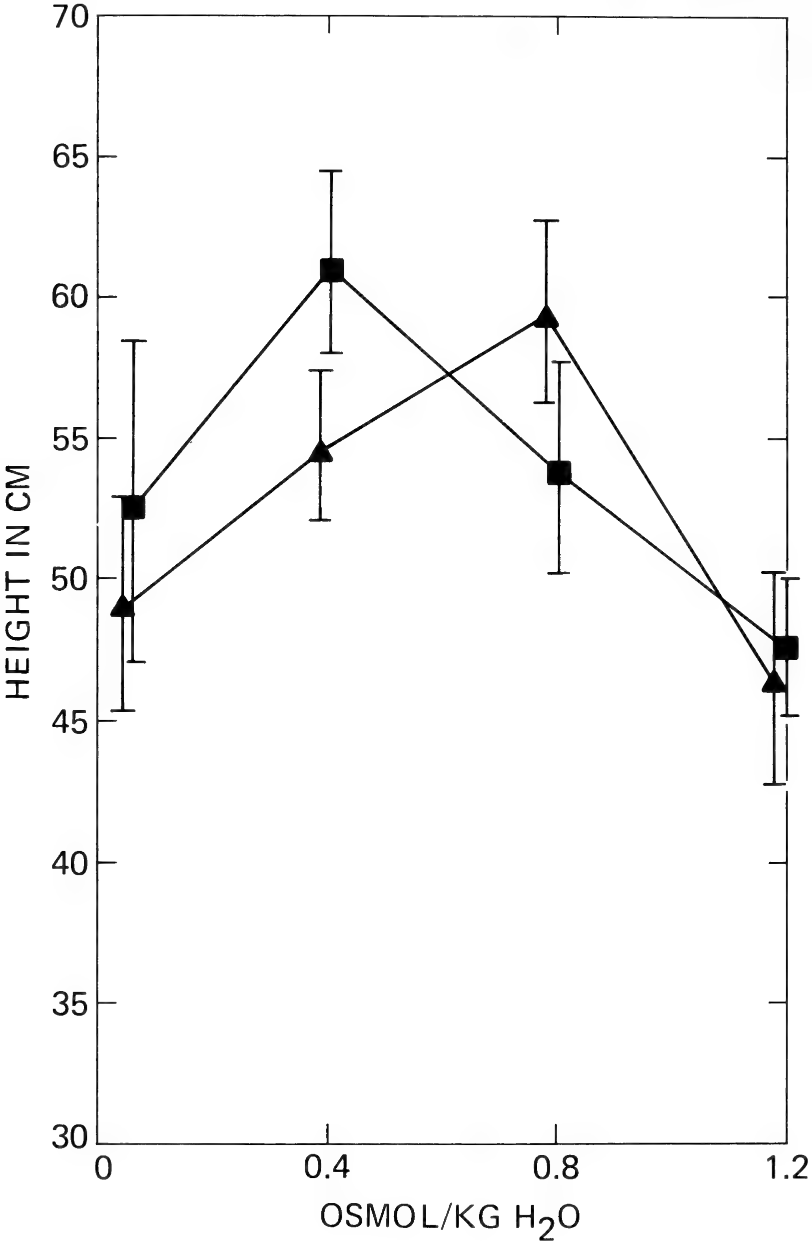

FIG. 1. Height ($\bar{Y}$ ± S.E.) of dwarf (△) and robust (□) forms of *Spartina foliosa* grown in NaCl-treated nutrient solution.

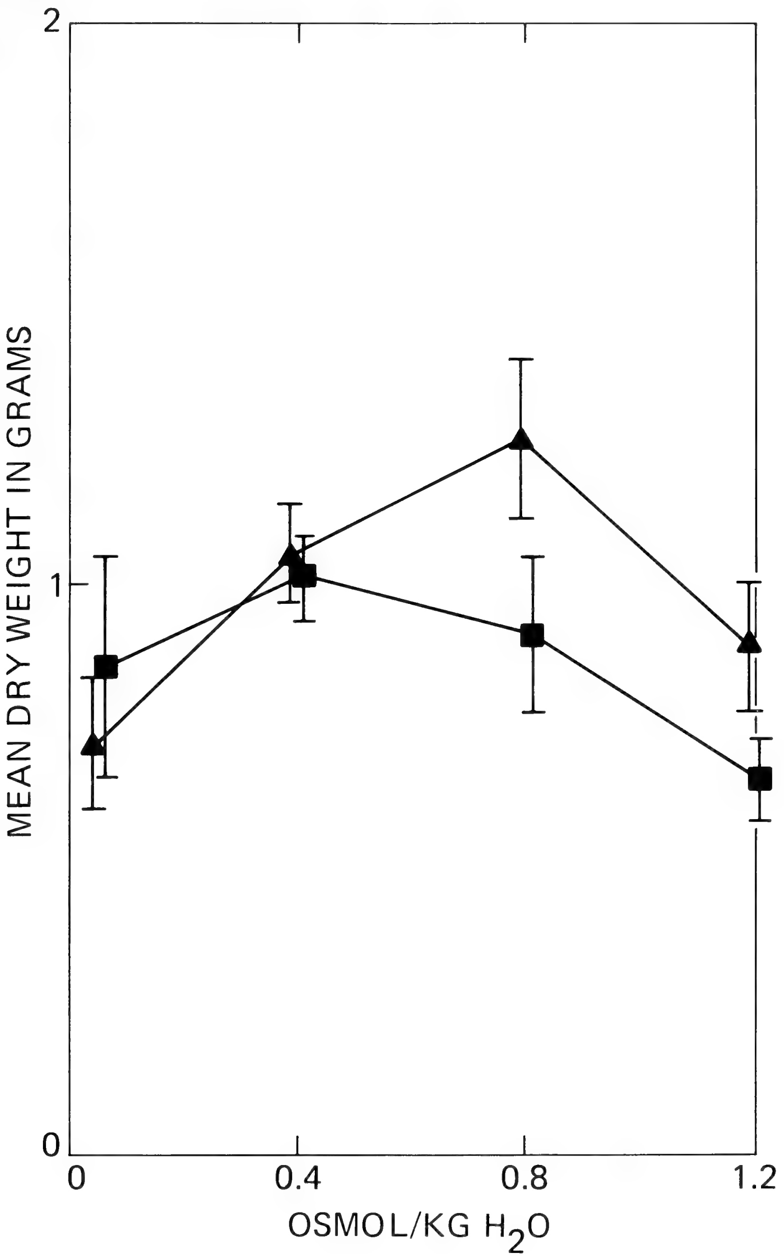

FIG. 2. Dry weight ($\bar{Y}$ ± S.E.) of dwarf (△) and robust (□) forms of *Spartina foliosa* grown in NaCl-treated nutrient solution.

TABLE 3. MEAN LEAF AREA (CM^2 LEAF^{-1}) WITH 95% CONFIDENCE LIMITS OF THE DWARF AND ROBUST FORMS OF *Spartina foliosa* GROWN IN SALINE CULTURE SOLUTION.

	Dwarf	Robust
Treatment	x̄; 95% C.L.	x̄; 95% C.L.
0.0	7.08; 6.00–8.29	8.64; 7.13–10.2
0.4 osmolal	7.51; 6.20–8.94	10.1; 8.35–12.0
0.8 osmolal	9.49; 8.47–10.5	8.53; 7.29–9.86
1.2 osmolal	7.29; 6.00–8.76	6.76; 5.48–8.24

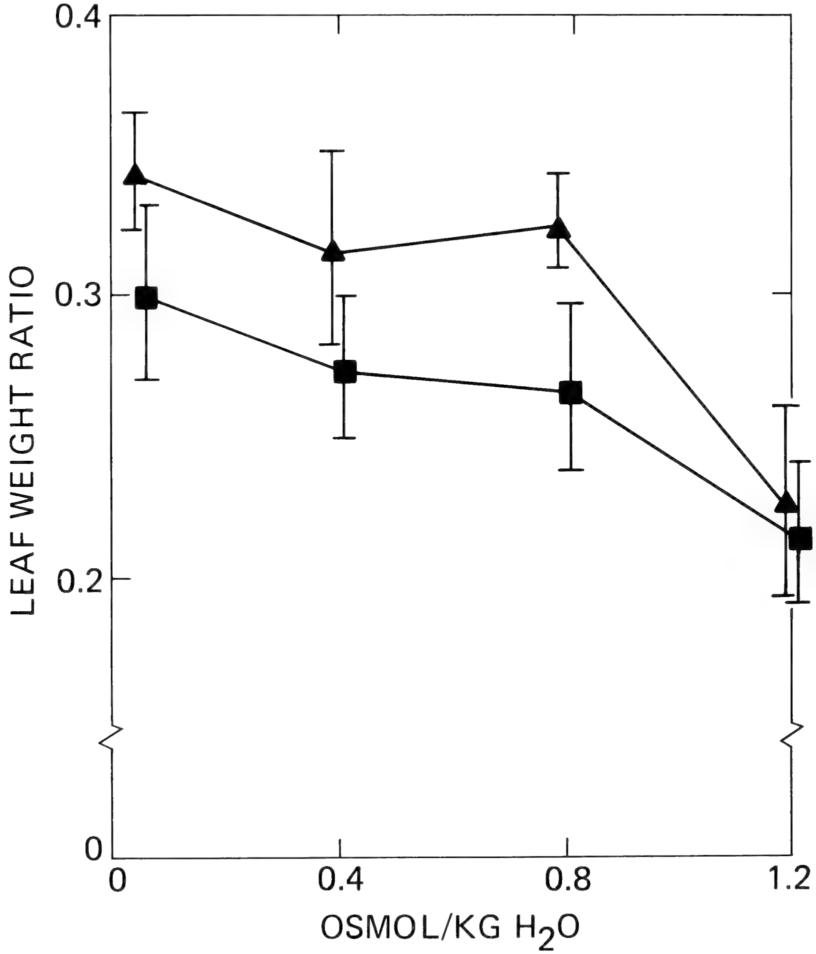

FIG. 3. Leaf weight ratio (Ȳ ± S.E.) of dwarf (△) and robust (□) forms of *Spartina foliosa* grown in NaCl-treated nutrient solution.

Table 4. Soil Salinity ($\bar{x}$ ± S.E.) as Osmole kg^{-1} H_2O of Root Zone of Palo Alto (PA) and Alameda Creek (AC) Marshes During the 1977 Growing Season. a: n = 3; n = 4 for all others.

	May			October		
	Plot			Plot		
Station	1	2	3	1	2	3
PA	0.89 ± 0.01	0.99 ± 0.01	1.05 ± 0.03	0.89 ± 0.02[a]	1.09 ± 0.04	1.18 ± 0.02
AC	1.18 ± 0.07	1.37 ± 0.02	1.30 ± 0.03	1.07 ± 0.02	1.41 ± 0.06	1.23 ± 0.02

ulations is assumed to be genetic. The results of the culturing experiment in this study indicate that the dwarf and robust forms of *S. foliosa* are not salinity ecotypes. When the experiment was started, dwarf and robust plants displayed different leaf weight ratios. However, by the end of the experiment, this distinction no longer existed. With the exception of the difference in leaf area between the forms grown at a salinity of 0.4 osmolal, dwarf and robust were not distinguishable by any of the characters measured. Furthermore, the height of dwarf *S. foliosa* grown in the laboratory exceeded the height of dwarf plants in nature, suggesting that the growth of plants at Alameda Creek is inhibited by unfavorable environmental conditions.

Significant differences in the responses of plants were associated with salinity. Survival, height, biomass and leaf area were greatest when the plants were grown under moderately saline conditions. However, in freshwater and the 0.4 osmolal solution, iron was apparently less available for plant uptake, making the direct assessment of the effect of NaCl on the growth of *S. foliosa* in those solutions difficult. Iron chlorosis was not severe in the two highest NaCl concentrations, indicating that iron was more available and not limiting plant growth. Inhibition of plant growth occurred over a narrow range of salinity between 0.8 and 1.2 osmolal. This inhibition was probably due to energy expended maintaining the internal salt balance, a process regulated by actively secreting salts through salt glands. Mahall and Park (1976b) found that shoot growth of cultured *S. foliosa* was significantly reduced at concentrations greater than 0.6 osmole kg^{-1} H_2O. The reduction in leaf weight ratio with increasing salinity may be an aspect of a common strategy in the adjustment of a plant to salinity by which the transpirational surface area is decreased relative to the water absorbing surface area (Bernstein and Hayward 1958).

Because soil salinities were recorded at the beginning and end of the growing season, we have no detailed information on how long plants from the two marshes and from different intertidal areas of the same marsh were exposed to particular salinities. These data would be valuable if growth rate is an integrated response to salt concentration over time. Assuming that it is, and using the available data, soil salinity at Alameda Creek appeared to remain relatively high throughout the growing season, suggesting that plant growth may be inhibited by prolonged salinity stress. At Palo Alto, soil salinity increased with increasing distance from the shoreward edge of the marsh, and, unlike Alameda Creek, displayed a seasonal increase that was increasingly more pronounced at higher intertidal areas. Salinity of the lowest intertidal area, PA 1, was seasonally constant, but at PA 2 salinity increased in October to concentrations equal to those recorded at Alameda Creek. However, the duration of exposure to the October concentrations may have been relatively brief. Plants at PA 3 (where height and biomass were reduced relative to plants at PA 1 and PA 2) were continuously exposed to concentrations as high as those recorded at Alameda Creek. Thus soil salinity conditions, at least in terms of concentration and duration of exposure, were similar between PA 3 and Alameda Creek, the two areas where dwarf plants occur.

In this study, only one environmental factor, salinity, was examined. It is rather unlikely that single cause and effect relationships affecting variation are prevalent in nature (Gould and Johnston 1972). Also, the occurrence of polygenic inheritance systems (Nobs and Hiesey 1957) indicates that the physiological and morphological response of an individual may depend upon the interaction of several environmental components within the genotype. Therefore, it cannot be discounted that the dwarf and robust forms would not segregate under a different set of factors. Nonetheless, the salinity effects observed for cultured plants complement the findings of the field survey: dwarf plants were associated with soils that displayed relatively high soil salinity throughout the growing season, whereas robust plants occurred in less saline soils. The results of this study, consistent with those of Harvey (1976) for *S. foliosa* and Mooring et al. (1971) and Nestler (1977) for *S. alterniflora,* indicate that the height forms of *S. foliosa* are ecophenes, and that the phenotypic expression of the species is partially a function of soil salinity.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

PEDICULARIS DUDLEYI Elmer (SCROPHULARIACEAE).—San Luis Obispo Co., mesa s. of Arroyo de la Cruz, 1.6 km e. CA 1, 18.5 km n. San Simeon, 16 Mar 1980, *Riggins 1195* (OBI, JEPS); 11 Apr 1981, *Riggins 1208* (OBI, JEPS). (Determined by L. R. Heckard)

Significance. A range extension of 80 km s. from Little Sur River, Monterey Co. The species is considered rare and endangered (CNPS Inventory, 1980). The chromosome number has been determined by D. J. Keil as $n = 8$.—RHONDA RIGGINS, Biological Sciences Dept., California Polytechnic State Univ., San Luis Obispo 93407.

IDAHO

ASTRAGALUS GILVIFLORUS Sheld. (FABACEAE).—Clark Co., s. end of Beaverhead Mts. near Reno Point (T8N R31E S15), 1646 m, 25 May 1981, *S. Goodrich 15431* (BRY, ID, NY, OGDF). (Verified by R. Barneby, NY)

Significance. First record for ID and extension sw. of ca. 190 km from Madison and Park co's., MT.

HACKELIA DAVISII Cronq. (BORAGINACEAE).—Lemhi Co., Salmon River Mts., canyon bottom along Camas Cr. between Forge Cr. and Dry Gulch (T18N R16E S21–22), 1434 m, 28 May 1981, *S. Goodrich & E. W. Tisdale 15496* (BRY, ID, NY, OGDF) (Verified by A. Cronquist, NY); granite talus along trail, Camas Cr., between Forge Cr. and Little Dry Cr. with *Pseudotsuga menziesii* (T18N R16E S15 sw.¼), 1464 m, 7 Jul 1981, *D. Henderson & A. Cholewa 5989* (ID).

Significance. This narrow endemic, currently listed in Cat. 1, *Federal Register,* 15 Dec. 1980, was known only from the general area near the confluence of the main Salmon Riv. and the Middle Fk. on moist, limestone cliffs associated with *Pinus ponderosa* (Steele, R. 1981, *Vasc. Plt. Spp. of Concern in Idaho.* Univ. Idaho College of For., Wildl., & Range Sci., FWR Expt. Sta. Bull. 34. p. 20) and along Panther Cr., vic. Cobalt (R. Carr, pers. comm.). These new collections establish its presence on a granitic substrate and association with *Pseudotsuga menziesii* ca. 45 km s. of the type locality, and suggest the likelihood of additional populations occurring elsewhere within the Salmon River drainage.—SHEREL GOODRICH, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT 84401 (stationed in Provo, UT, at Shrub Sciences Laboratory); and DOUGLASS HENDERSON and ANITA CHOLEWA, Dept. Biological Sciences, Univ. Idaho, Moscow 83843.

LESQUERELLA KINGII S. Wats. var. COBRENSIS Roll. & Shaw (BRASSICACEAE).—Butte Co., Idaho National Engineering Laboratory, 6.4 km se. of CFA (T2N R30E S22 se.¼ of ne.¼), 1494 m, 1 Jun 1981, *A. Cholewa 632* (ID); vic. Middle Butte (T2N R32E S21 sw.¼ of nw.¼), 1615 m, 18 Jun 1981, *A. Cholewa 787* (GH, ID); ca. 5 km n. of Middle Butte (T2N R32E S7 sw.¼ of sw.¼), 1615 m, 18 Jun 1981, *A. Cholewa 789* (GH, ID). (Collections indicated GH identified by R. Rollins, GH, 1981)

Significance. First records for ID and extension ne. of ca. 310 km from Elko Co., NV.

ASTRAGALUS KENTROPHYTA Gray var. JESSIAE (Peck) Barneby (FABACEAE).—Butte Co., Idaho National Engineering Laboratory, se. end of Lemhi Range (T6N R30E S23 n.½), 1606 m, 17 Jun 1981, *A. Cholewa & D. Henderson 777* (ID, NY). (Det. by R. Barneby, NY, 1981)

Significance. Previously known in Idaho only from Owyhee Co., and an extension ne. of ca. 252 km.

GILIA POLYCLADON Torrey (POLEMONIACEAE).—Butte Co., Idaho National Engineering Laboratory, se. end of Lemhi Range (T6N R30E S35 sw.¼ of sw.¼), 1508 m, 16 Jun 1981, *A. Cholewa 759* (CS, ID). (Det. by D. Wilken, CS, 1981)

Significance. Reported from sagebrush zones of sw. ID (Davis, R. J. 1952, *Flora of Idaho*), but without locations.—ANITA F. CHOLEWA and DOUGLASS HENDERSON, Dept. Biological Sciences, Univ. Idaho, Moscow 83843.

ASTRAGALUS LEPTALEUS Gray (FABACEAE).—Custer Co., Boulder Mts., N. Fk. Big Lost River (T7N R19E S23 ne.¼), 2191 m, 31 Jul 1981, *S. L. Caicco & J. Civille 287* (ID, NY). (Det. by R. Barneby, NY)

Significance. Represents only the second known site in ID and the first collection in the past 30 years.

PENSTEMON PROCERUS Dougl. var. FORMOSUS (A. Nels.) Cronq. (SCROPHULARIACEAE).—Custer Co., Pioneer Mts., head of Bellas Gulch (T5N R21E S6 se.¼), 3226 m, 15 Jul 1981, *S. L. Caicco & J. Civille 210* (ID, NY) (Verified by N. Holmgren, NY); Lake Creek drainage, ½ km ese. of southernmost lake in upper basin (T4N R22E S4 se.¼), 3104 m, 21 Jul 1981, *S. L. Caicco & J. Civille 256* (ID); Surprise Valley, near outlet of upper lake, ca. 1.3 km n. of Standhope Pk. (T6N R21E S31 sw.¼), 3089 m, 27 Jul 1981, *D. Henderson & C. Wellner 6024* (ID); ridge, e. side Betty Lake, 1.4 km e. of Standhope Pk. (T5N R21E S6 se.¼), 3165 m, 3 Aug 1981, *S. L. Caicco & J. Civille 302* (ID).

Significance. First records of this taxon from ID and extensions ese. of ca. 300 km from Baker Co., OR.—STEVEN CAICCO, JANIE CIVILLE, and DOUGLASS HENDERSON, Dept. Biological Sciences, Univ. Idaho, Moscow 83843.

PARNASSIA KOTZEBUEI Cham. (SAXIFRAGACEAE).—Custer Co., Lost River Range, lakeshore near head of w. br. E. Fk. Pahsimeroi River (T9N R23E S26 nw.¼ of nw.¼), 2967 m, 10 Aug 1979, *S. & P. Brunsfeld 1359* (ID, UC) (Verified by R. B. Phillips, UC); Pioneer Mts., cliffs s. of Kane Lake (T5N R19E S1 s.¼), 2891 m, 30 Jul 1981, *S. L. Caicco & J. Civille 280* (ID); upper Wildhorse Cr. drainage, ca. 1 km w. of Arrowhead Lake (T5N R20E S21 s.½), 2860 m, 14 Aug 1981, *S. L. Caicco & J. Civille 340* (ID).

Significance. First records for ID.—STEVEN BRUNSFELD, College of Forestry, Wildlife and Range Sciences, Univ. Idaho, Moscow 83843; and STEVEN CAICCO and DOUGLASS HENDERSON, Dept. Biological Sciences, Univ. Idaho, Moscow 83843.

MONTANA–IDAHO

ERIGERON RADICATUS Hook. (ASTERACEAE).—MT, Deer Lodge Co., Anaconda-Pintlar Wilderness, Little Rainbow Mt., 1.6 km w. of Storm Lake (T4N R13W S31 n.½), 3018 m, 8 Jul 1972, *Lackschewitz 3770* (MONTU, NY, WTU); Madison Co., Gravelly Range, crest of Red Hill (T10S R2E S17), 2830 m, 5 Jul 1979, *Lackschewitz 8989* (MONTU); Flathead Co., Bob Marshall Wilderness, Flathead Mts., North Chinese Wall, s. of Sock Lake (T24N R11W S31 w.½), 2500 m, 26 Jul 1979, *Lackschewitz 9102* (MONTU, NY, WTU). ID, Butte Co., e. slope Lemhi Range, Meadow Canyon area, Summit Pk. 10858 (T10N R28E S4), 3309 m, 14 Jul 1975, *D. Henderson 2636* (ID); Lemhi Co., s. Beaverhead Mts., wsw. ridge of Italian Pk. (T12N R10W S18), 3030 m, 10 Jul 1977, *S. & P. Brunsfeld 464* (ID, NY); Custer Co., e. slope Lost River Range, upper Merriam Lake basin (T9N R23E S17), 2909 m, 21 Jul 1978, *D. Henderson, S. & P. Brunsfeld 4692* (ID). (Collections deposited at NY det. by A. Cronquist)

Significance. The Lackschewitz collections represent the first record for MT and contiguous US; the ID collections are first records for that state.—KLAUS LACKSCHEW-

ITZ, Dept. Botany, Univ. Montana, Missoula 59812; DOUGLASS HENDERSON, Dept. Biological Sciences, Univ. Idaho, Moscow 83843; and STEVEN BRUNSFELD, College of Forestry, Wildlife, and Range Sci., Univ. Idaho, Moscow 83843.

ANNOUNCEMENT

LAWRENCE MEMORIAL AWARD

The Award Committee of the Lawrence Memorial Fund is pleased to announce that Ms. Janet R. Sullivan of the University of Oklahoma was selected to receive the 1982 Lawrence Memorial Award. A student of Dr. James R. Estes, Ms. Sullivan is investigating the taxonomy, ecology, and evolution of the genus *Physalis* (Solanaceae). She will use the proceeds of the Award in travel to the southeastern United States and the Gulf Coast for field studies.

Nominations for the 1983 Award are now being entertained. Major professors are urged to submit letters in behalf of outstanding doctoral students who have achieved official candidacy for their degrees, will be conducting dissertation research in relevant fields, and whose work would benefit significantly from the travel enabled by the Award. The Committee will consider nominations only—no direct applications will be entertained. Letters of nomination and supporting materials should be addressed to Dr. R. W. Kiger, Hunt Institute, Carnegie-Mellon University, Pittsburgh 15213; the deadline for their receipt is 1 May 1983.

ERRATUM

Madrono 29(3):217 has an error. The family given for *Cenchrus incertus* should be Poaceae instead of Cyperaceae. I thank Duncan Porter for bringing this to my attention.—Ed.

REVIEWS

Genera of the Western Plants. By WADE T. BATSON. 207 p. Published by the author, 1120 Blake Dr., Cayce, South Carolina 29033. $8.50. (20% discount to bookstores and libraries.)

This is a useful basic guide to the genera of ferns and seed plants of North America west of the 98th meridian and north of Mexico. Also included are a few of the commoner ornamentals of the region. It is clearly aimed at students and amateurs with some familiarity with arcane taxonomese, but plant geographers can also profit from a quick learning of what genera occur west of the 98th meridian, a boundary perhaps no more arbitrary than the Continental Divide. A great deal of information is packed into this pocket-sized volume.

Despite this, the book has a number of serious drawbacks. I would suggest typing the genus names in italics (the book is produced from camera-ready copy) and omitting the synonyms, or at least using the designation "syn:" to avoid some confusion. I did not use any of the keys but they appear to be typical of this kind of work from a reading of several in families whose members are familiar to me. The key leads are not always parallel, and I suspect some will be hard to use, whereas others will work fine. Each brief genus description is accompanied by a tiny drawing of leaf, flower, or habit. Some of the drawings are too small to be of much value, others will be better than nothing.

Apacheria (Crossosomataceae) and *Dedeckera* (Polygonaceae) are missing, and *Forsellesia* is still included in Celastraceae. *Mollugo, Paeonia, Menyanthes,* and *Simmondsia* are now usually placed in separate families; *Cephalanthera* (*Eburophyton*), *Ceratoides* (*Eurotia*), *Eremalche* (*Malvastrum*), *Geocaulon* (*Comandra*), *Swallenia* (*Ectosperma*), and *Tiquilia* (*Coldenia*) are the widely accepted segregates or names used in preference over the names in parentheses (used in this book). *Zauschneria* has been submerged into *Epilobium* but is retained here. Missing from the families treated is Proteaceae, surely as worthy of appearance as Myoporaceae and Caricaceae. The range of *Vitis* should be CA–CO, rather than UT–CO. These are a selection of the 33 errors I encountered. I was dismayed by the number of typos and feel that because the book is intended for students, more effort should have been made to eliminte them. In the main text I found 51, and in the index alone, 85. *Pieris* (Ericaceae) has crept into the key for Cichorieae and replaced *Picris.* The student must use this guide with caution.—C. DAVIDSON, Idaho Botanical Garden, P.O. Box 2140, Boise 83701.

A Field Guide to Mushrooms and their Relatives. By COURTENAY BOOTH and HAROLD H. BURDSALL, JR. 144 p., black-and-white drawings, over 400 color photographs. Van Nostrand Reinhold Co., New York, Cincinnati, Toronto, London, Melbourne. 1982. ISBN 0-442-23117-2 (cloth). $18.95. ISBN 0-442-23118-0 (paper).

Although this book was intended primarily for the northeastern and central United States, it includes many species that occur in the West. It is the only handbook providing color photographs of some of these species. For this reason, there will be many who will wish to add it to their libraries. The book was not intended as a guide for mycophagists. They should regard it as a supplementary volume because of the absence of many important anatomical details and information about mushroom poisons. In my opinion, the statement in the preface that the book was intended to permit quick identification of species by amateurs is overly optimistic. The abundance of color illustrations and common names will appeal to many casual observers, however.

The book includes a very brief, simplified discussion about the nature of fungi and an explanation of scientific names. Simple words rather than scientific terms are used in a list of macroscopic characters used in identification (unfortunately the caption below the grouped and clumped habits were interchanged). The groups into which the fungi are divided are illustrated by simple line drawings. The photographs, which are arranged in the same order, are not numbered. The position of some photographs makes it difficult to determine the identity of the fungus illustrated. Although the color in some photographs is poor (for example, *Coprinus atramentarius*), an asset is the inclusion of various color variations of *Armillariella mellea*. Although there are many photographs of polypores, the use of currently accepted scientific names and absence of synonyms will confuse some readers. For each species there are brief comments about color, size, various surface features, habitat, and edibility. It would have been better to list both *Pholiota aurivella* and *Agaricus sylvicola* as "not recommended" and to point out that the gills of *Chlorophyllum* may remain white for a long period. The section on boletes is of limited usefulness in the West. A glossary and index are included; the latter contains a number of misspellings.—ISABELLE TAVARES, Department of Botany, University of California, Berkeley 94720.

ANNOUNCEMENTS

THE 1982 JESSE M. GREENMAN AWARD

The 1982 Jesse M. Greenman Award has been won by Walter S. Judd for his publication "A monograph of *Lyonia* (Ericaceae)" (Jour. Arnold Arbor. 62:63–209; 315–436. This monographic study is based on a Ph.D. dissertation from the Department of Biology, Harvard University.

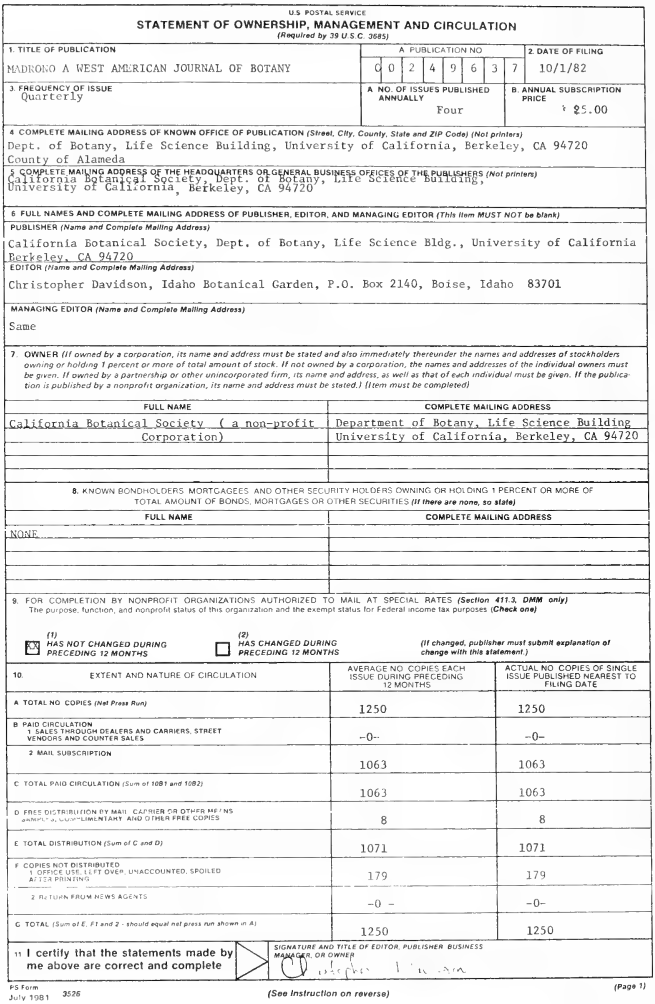
The Greenman Award, a cash prize of $250, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation which was published during the *previous* year. Papers published during *1982* are now being considered for the 16th annual award, which will be presented in the summer of 1983. Reprints of such papers should be sent to: Greenman Award Committee, Department of Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, U.S.A. In order to be considered for the 1983 award, reprints must be received by 1 July 1983.

WILDLAND SHRUB SYMPOSIUM

The second in a series of symposia dealing with the biology of wildland shrubs is announced by Brigham Young University. Entitled "The biology of *Atriplex* and related chenopods," it will be held on 4–6 May 1983, in the Brigham Young University Conference Center, Provo, UT. An application and call for papers form can be obtained from Cooperative Extension Service, % Dr. Kendall L. Johnson, Utah State University, UMC 49, Logan, UT 84322.

PUBLICATION NOTE

Re-publication of *Flora of the Mount Hamilton Range of California* (1982) by Helen K. Sharsmith is most welcome. Originally published in American Midland Naturalist in 1945, this extremely useful local flora, covering a prominent area in the central Inner Coast Ranges, has long been out of print. Addition of an index that contains cross references to names as given in Munz, *A California Flora and Supplement* (1973) enhances the value to users. The Santa Clara Valley Chapter of the California Native Plant Society is to be commended for making this Flora once again available. Copies may be obtained from: California Native Plant Society, SCVC-Book, 20531 Black Road, Los Gatos, CA 95030.



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(Page 1)

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Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren and Keuken, Index Herbariorum, 6th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted eight pages in MADROÑO over a two year period. Joint authors are each assessed the full page number. Beyond that number of pages a required editorial fee of $40.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

CALIFORNIA BOTANICAL SOCIETY

MADROÑO

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NOTES AND NEWS

NOTEWORTHY COLLECTIONS

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A CLIFF BRAKE HYBRID, PELLAEA BRIDGESII × MUCRONATA, AND ITS SYSTEMATIC SIGNIFICANCE

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Berkeley 94720

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ABSTRACT

The taxonomic position of *Pellaea bridgesii* has been questioned because of its distinctive soriation and lack of strongly reflexed segment margin. In these characters, *P. bridgesii* differs from its presumed congeners only in degree. Furthermore, its peculiar glands appear no different from those of other pellaeas. The discovery of hybrids between this species and *P. mucronata* var. *mucronata,* a "typical" member of the genus, suggests an unexpectedly close relationship between *P. bridgesii* and other species of *Pellaea* sect. *Pellaea,* particularly the *P. mucronata* group in western North America. This hybrid, here named **P. ×glaciogena,** shows morphological intermediacy in nearly all characters between the putative parents, 58 univalents at meiosis, and mostly malformed spores or abortive sporangia. It is known from several localities at middle elevations in the central Sierra Nevada of California.

Studies of interspecific hybrids may yield clues to the relationships of their parents. In ferns if hybrids form at all this gives significant evidence of affinity between species. There are indications that interactions of strongly different parental characters may take various forms (Wagner 1960), and we may be able to obtain from hybrids valuable insights into morphogenetic processes. The plants to be described in this paper provide an excellent example of hybridization that involves plants of seemingly very different morphology. The presumed parents have been suspected by some on morphological grounds of belonging to different sections or even genera.

SYSTEMATICS

The problem of *Pellaea bridgesii*

Pellaea bridgesii Hooker has given rise to speculation concerning its taxonomic position. The problem of the relationships of this plant

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will be noted briefly, and then its cross with a more "normal" member of the genus will be described in detail.

This distinctive fern grows in exposed rocky places in the Sierra Nevada of California (Howell and Long 1970); disjunct populations occur in Oregon and Idaho (Hitchcock et al. 1969, Taylor 1970). Botanists generally have been uncertain about its precise generic relationships. Hooker (1858, p. 238), for example, wrote: "This is a very remarkable Fern, with much in the habit and in the nature of fructification of *Pellaea* (Platyloma, *J.Sm.*) *paradoxa, falcata,* and *rotundifolia* . . . and quite destitute of involucre. In short, as far as the sori are concerned, one can hardly see why it should not range with *Gymnogramme.*" In her monograph of *Pellaea* sect. *Pellaea,* A. Tryon (1957) stated that "the position of *Pellaea bridgesii* . . . remains a problem. I have excluded it on the basis of the conduplicate segments lacking reflexed margins, the short stalked sporangia which are borne on an elongated receptacle one quarter to one half the distance to the costa and which persist in a cup-like form after dehiscence. It resembles some species of *Notholaena* in the length of the receptacle and in the abundant waxy indument produced among the sporangia." Cronquist (in Hitchcock et al. 1969) commented further that *"Pellaea bridgesii* is transitional between *Pellaea* and *Notholaena,* and is anomalous in either genus, without being sufficiently distinctive to warrant its erection as a monotype."

Thus, *P. bridgesii* has remained more or less an enigma among North American adiantoid ferns. In particular the absence of the reflexed margin so characteristic of *Pellaea,* the gymnogrammoid pattern of sori, and resemblances to members of the genus *Notholaena* have left authors undecided about its taxonomic affinities. In the course of our investigations on the hybrid cliff brake to be described below we have been able to arrive at a clearer conception of the homologies of *P. bridgesii* vis-à-vis *Pellaea* and to adduce strong evidence for its actual relationships.

The hybrid between *P. bridgesii* and *P. mucronata*

It is interesting to find morphological intermediates between *P. bridgesii* and an unquestioned member of *Pellaea* sect. *Pellaea.* For reasons to be given, we believe these intermediates are with little doubt of hybrid origin between *P. bridgesii* and *P. mucronata.* Because of the unusually wide morphological differences between the putative parents and also the apparent repeated formation of the hybrid, we choose to designate the intermediates by a hybrid binomial:

Pellaea ×glaciogena Wagner, Pray & Smith, hybr. nov.

Planta inter *P. bridgesii* Hook. et *P. mucronata* (D. C. Eaton) D. C. Eaton quasi intermedia et verisimiliter ex hybridatione harum specierum orta, ab ambobus rhachidi parum sulcata differt, pinnis 1-pinnatis 2–8 paribus pinnularum, apicibus pinnularum angularibus vel parum mucronatis, venis tantum fortuito anastomosantibus, margine segmentorum fertilium revoluto undulato vel dentato, et sporis abortivis.

Intermediate between *P. bridgesii* and *P. mucronata,* differing from both in the slightly grooved rachis (terete in *P. bridgesii,* strongly grooved in *P. mucronata*); pinnae 1-pinnate with 3–4 (2–8) pairs of pinnules per pinna (1-pinnate in *P. bridgesii,* 3-pinnate in most *P. mucronata*); pinnule tips angular to slightly mucronate (obtuse in *P. bridgesii,* strongly mucronate in *P. mucronata*); veins casually anastomosing with 0–1 union per segment (4–5 anastomoses in *P. bridgesii,* veins free in *P. mucronata*); fertile leaf margins revolute but with the lower epidermis well exposed (faintly or not at all revolute in *P. bridgesii,* strongly revolute in *P. mucronata*); segment margins undulate to toothed (entire in *P. bridgesii,* strongly toothed in *P. mucronata*); spores malformed (well-formed and globose in putative parents).

TYPE: CA: Tuolumne Co.: south rim of Tuolumne Canyon, ca. 1 mi (1.6 km) n. of Mather, 5200 ft (1580 m), 5 Jun 1961, *Pray 1860* (UC; isotype MICH).

PARATYPES: CA: Mariposa Co., Little Yosemite, Jun 1878, *Bradley s.n.* (UC—2 sheets); Yosemite National Park, along Hwy 41 midway between turnoff to Glacier Pt. and Wawona Tunnel, ca. 5500 ft (1670 m), 30 May 1981, *Smith 814a, 814b* (UC). Tulare Co.: Palisade Cr. near junction with King's River, 22 Jul 1920, *Perkins s.n.* (USC); Sequoia Natl. Park, Tokapah Falls, dry stony slope, below bluff ca. ¼ mi (0.4 km) n. of base of falls, 7500 ft (2300 m), 28 Jul 1963, *Kiefer 617a* (MICH); near Dorset Cr., Sequoia Natl. Park, 26 Jun 1958, *Rodin 6222* (UC); Kings Canyon Natl. Park, Mist Falls, South Fork of Kings River, ca. 6000 ft (1830 m), 20 Jun 1962, *Pray 1903* (USC); along General's Hwy, near summit ca. 5.5 mi (8.8 km) n. of Sequoia Park boundary, 7500 ft (2300 m), 21 Jun 1962, *Pray 1904* (USC); Upper Tokapah Valley, near Tokapah Falls, n. slope of valley about ¼ mi (0.4 km) w. of base of falls, 7500 ft (2300 m), 23 Jun 1965, *Pray 3204–3206, 3208, 3209* (USC). Tuolumne Co.: Yosemite Natl. Park, ca. 1 mi (1.6 km) n. of Mather Ranger Station, on south rim of Tuolumne River Canyon, 5200 ft (1580 m), 1955–1959, 1961, *Pray 1014, 1020, 1048, 1049, 1070, 1515–1518, 1520, 1521, 1852–1858, 1861–1864* (all USC).

Hybrids from the type locality were fairly common and were growing with abundant *P. mucronata* var. *mucronata* (tripinnate form) in the most exposed areas; *Pellaea bridgesii* was common on more sheltered, north-facing slopes.

Additional stations for *P.* ×*glaciogena* are also consistent with a hypothesis of hybridization. Both parents were found growing with

Smith 814a and *814b*: *P. mucronata* var. *mucronata* was abundant on exposed west-facing rocky slopes, *P. bridgesii* was common at the bases of overhanging boulders on north- and northwest-facing slopes, and two plants (5 m apart) of *P.* × *glaciogena* grew at the crest of a small knoll within 5 m of both parents. *Kiefer 617a* was from a single large clump growing amid an extensive population of *P. mucronata*. *Pellaea bridgesii* was growing nearby, about 6 m away. Fronds of all three entities from this locality are illustrated in Fig. 1. Later collections by Pray (*3204* to *3206, 3208, 3209*) from this same locality indicate that the hybrids were associated with *P. mucronata* var. *mucronata* and that *P. bridgesii* was growing nearby. At this locality, Pray observed *P. mucronata* growing only on the warmer south-facing slope, whereas *P. bridgesii* was on the cooler north-facing side of the valley. *Pray 1903* was found growing with *P. mucronata* var. *mucronata,* whereas *Pray 1904* was associated with *P. bridgesii.*

All localities are granitic ones and were formerly glaciated; the exposed rocky areas thus allow the two parents to occur very near one another, rather than being elevationally separate, as is usually the case. The known localities for the hybrid form a north–south line a little over 170 km in extent at mid-elevations on the west side of the central Sierra Nevada. At these sites, topographic and climatic conditions are such that the truly montane *P. bridgesii* does come in close contact with the hot-lowland *P. mucronata.* In the Sierra, *P. bridgesii* occurs mostly between 1800 and 3000 m from Plumas to Tulare County, except in the vicinity of Yosemite National Park, where it is recorded as low as 1215 m (Howell and Long 1970). Throughout most of its range, *P. mucronata* var. *mucronata* is found below 1200 m, except in the central and southern Sierra Nevada where it extends in elevation up to 2300 m (Howell and Long 1970). Thus, the putative parent are sympatric only from Tuolumne to Tulare County at elevations between 1200 and 2300 m.

The only other species of *Pellaea* known from the Sierra Nevada are *P. brachyptera* (Moore) Baker, which occurs only as far south as Placer County (Howell and Long 1970); *P. breweri* D. C. Eaton, which is found generally above 2700 m in the central Sierra Nevada; and the more distantly related *P. andromedifolia* (Kaulf.) Fée, usually at elevations below 1200 m. Reports of *P. brachyptera* and *P. wrightiana* Hook. in the Yosemite region (Hall and Hall 1912) are probably based in part on *P.* ×*glaciogena.* Both species are bipinnate and in that respect are superficially similar to the hybrid. The closest stations for *P. wrightiana,* as it is now understood, are in Utah and Arizona (Wagner 1965, Pray 1967). Rodin's (1960) illustration of *P. mucronata* var. *californica* (Lemmon) Munz & Johnston is based on *Rodin 6222,* which we identify as *P.* ×*glaciogena.*

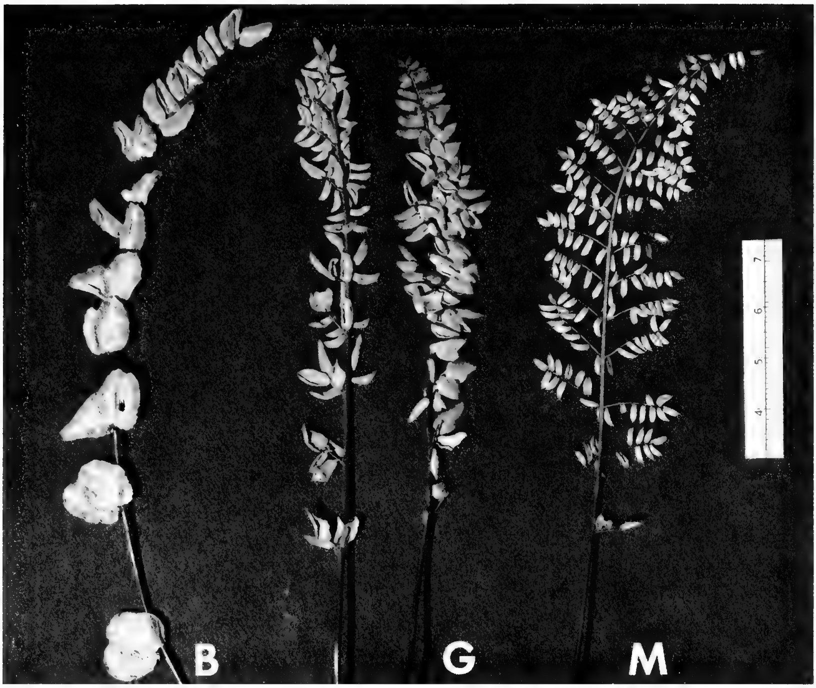

FIG. 1. Specimens of *Pellaea,* all from Califonia, Tulare Co., Tokapah Falls. B. *Pellaea bridgesii, Kiefer 625* (MICH). G. *Pellaea ×glaciogena, Kiefer 617a* (MICH). M. *Pellaea mucronata* var. *mucronata, Kiefer 617b* (MICH).

Variation within *P. mucronata* is complex and still not completely understood, but the species comprises two more or less discrete varieties (A. Tryon 1957). At the type locality of *P. ×glaciogena* only fully tripinnate forms of var. *mucronata* occur. At other localities (excluding *Pray 1904*), tripinnate and sometimes bipinnate forms of var. *mucronata* are found. These latter are distinct from var. *californica,* which is a more compact plant of generally higher elevations, in that the pinnules are well separated in a manner similar to the pinnules of the tripinnate forms of var. *mucronata.* Variety *californica* is not known from any of the localities where *P. ×glaciogena* has been collected. In spite of minor variation within var. *mucronata* at the various localities, the nature of the hybrid is much the same in all.

At the one place where we have found var. *californica* near *P. bridgesii,* an entirely distinct intermediate was collected. This plant (*Pray 1053,* USC, Little Yosemite Valley, ca. 2150 m) is morphologically much closer to *P. bridgesii* and has fewer, much larger segments than in *P. ×glaciogena.* The distinctiveness of this putative hybrid

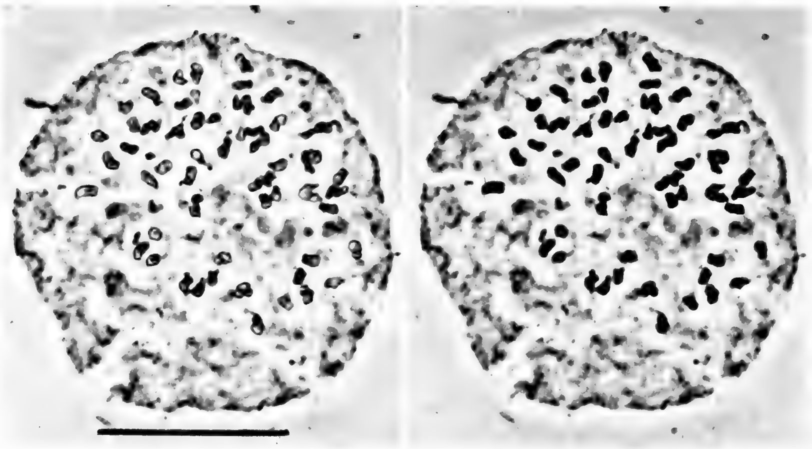

FIG. 2. Chromosomes of *Pellaea* ×*glaciogena, Smith 814a* (UC). Bar scale represents 30 μm.

suggests that sufficient genetic differences distinguish the varieties of *P. mucronata* that when the respective hybrids are formed with *P. bridgesii* they are morphologically distinct.

Chromosome counts for *P.* ×*glaciogena* showing 58 univalents at meiotic metaphase were obtained from *Smith 814a* (Fig. 2). Numerous cells were examined and none showed evidence of chromosome pairing. *Pellaea bridgesii* was counted from this same locality and showed 29 bivalents at meiotic metaphase (*Smith 816,* UC); counts of this species from several additional localities, to be reported fully later (Smith, ms.), also showed 29 bivalents at meiosis. These represent the first counts for *P. bridgesii* and agree with the base number ($x = 29$) known for *Pellaea. Pellaea mucronata* has heretofore not been examined cytologically (reports by Löve et al. 1977, are errors for *P. truncata*), but counts showing 29 bivalents at meiosis have now been made on several populations (Smith, ms.).

Phenology of *P.* ×*glaciogena* and parents at one locality (Mariposa County, *Smith 814a*) is noteworthy. In late May 1981, in a drier than average year, nearly all plants of *P. bridgesii* had fully expanded fronds on which most sporangia already had passed through meiosis and some had mature spores. This same year's fronds of *P. mucronata* var. *mucronata* were just beginning to emerge and uncoil, were still less than one-half of their mature height, and were probably premeiotic by 1–2 months. The two plants of *P.* ×*glaciogena* showed intermediate development, perhaps closer to that of *P. bridgesii,* but with most fronds just beginning to undergo meiosis. The earlier development of *P. bridgesii* may reflect its adaptation to a shorter growing season at its usually higher montane elevations.

TABLE 1. COMPARISON OF *Pellaea bridgesii, P. mucronata* VAR. *mucronata,* AND *P.* ×*glaciogena.* An asterisk indicates the most obvious macroscopic diagnostic characters.

	P. bridgesii	*P.* ×*glaciogena*	*P. mucronata*
Rhizome scales	cells 22 (16–32) μm wide, thin-walled	cells 25.5 (16–37) μm wide, thicker-walled	cells 31 (21–40) μm wide, thick-walled
Scale tip margins	smooth or undulate	± toothed	toothed
*Rachis cross-section	cylindrical	narrowly grooved adaxially	widely grooved adaxially
*Pinna cutting	undivided	1-divided	commonly 2-divided
Undivided distal pinna pairs	all	2–8	1–3
Pinna margin	broad layer 1-cell thick	unmodified	unmodified
*Pinnule pairs per pinna	0	3–4 (2–8)	6–7 (4–15)
Epidermis (lower)	middle lamella not obscured, no secondary thickenings	irregular thickenings	middle lamella obscured by secondary thickenings
*Segment tips	obtuse-rounded	angular to mucronate	strongly mucronate
Vein anastomoses per pinna	4–5 (1–8)	2–3 (0–5)	0
Individual segments with anastomoses	all	one-third	none
*Young pinnae with mature spores	conduplicate	flattened ventrally to conduplicate	flattened ventrally
*Mature fertile pinnae (last year's leaves)	flat, adaxial surface fully exposed	margins revolute, but with lower epidermis well exposed	margins revolute and entirely covering lower epidermis
*False indusium	slightly to not at all reflexed	reflexed	reflexed
*Indusial margin	smooth to undulate	undulate to toothed	strongly toothed
Spores	normal, 32.0 (30–45) μm diam.	malformed, rarely very large, 65 (52–76) μm diam.	normal, 34.4 (29–42) μm diam.

Comparative information regarding the three plants involved in this study is summarized in Table 1 (most obvious gross features of intermediate and parents denoted by asterisk). These characters and a few others are here discussed in more detail.

Rhizome scales were removed from stem tips and petiole bases and soaked in KOH before mounting in diaphane. All drawings were made

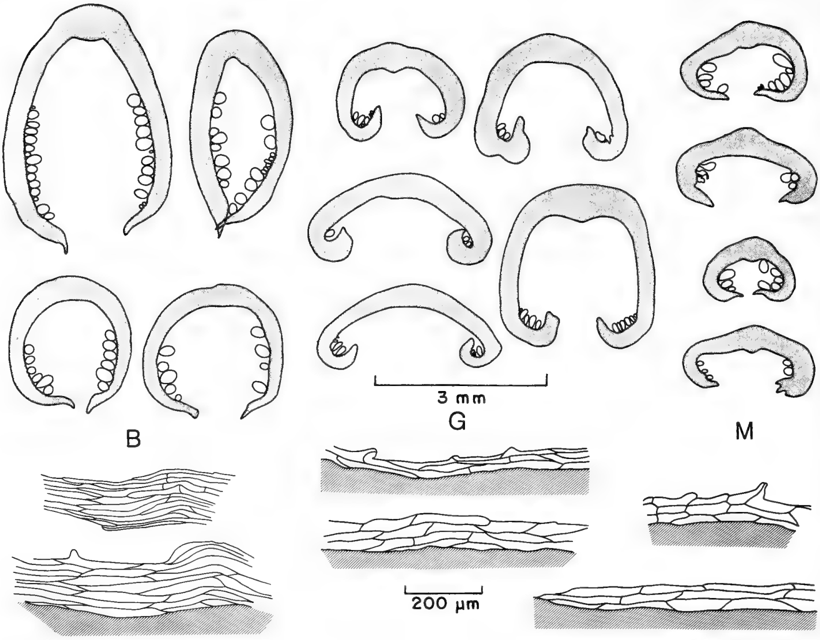

FIG. 3. Fertile segments (cross-sections) and rhizome scales of pellaeas. B. *Pellaea bridgesii*. G. *Pellaea ×glaciogena*. M. *Pellaea mucronata* var. *mucronata*. Specimen data as in Fig. 1, except as indicated. *Upper drawings:* thick sections at spore maturation stage, dried specimens relaxed. *Lower drawings:* cells of scales (M, *Collins 422,* MICH).

using a Bausch and Lomb Microprojector. Scales of *P. bridgesii* differ in two respects from those of *P. mucronata* in having narrower cells (with thinner walls) and mostly smooth margins in the distal half (Fig. 3). Scales of *P. mucronata* have wider cells (with conspicuously thicker walls) and the scale tips are definitely toothed (Fig. 4). The scales of the hybrid are intermediate (Figs. 3, 4).

Rachis shapes of *P. bridgesii* and *P. mucronata* are sharply different in cross-section, especially in their distal halves. Those of the former are cylindrical or nearly so in outline; those of the latter are strongly flattened and have a wide groove on the adaxial surface. The midrib of *P. ×glaciogena* has only a shallow, narrow, less pronounced adaxial groove.

Pellaea bridgesii is well differentiated from *P. mucronata* in the segment tips: smoothly rounded and obtuse in the former and prominently mucronate in the latter (Fig. 5). The mucro in *P. mucronata* is a hardened, sharply pointed structure 0.2–1.0 mm long. In the hybrid, very few tips were observed that lacked mucros and practically all have at least some projection. However, none of the mucros in the

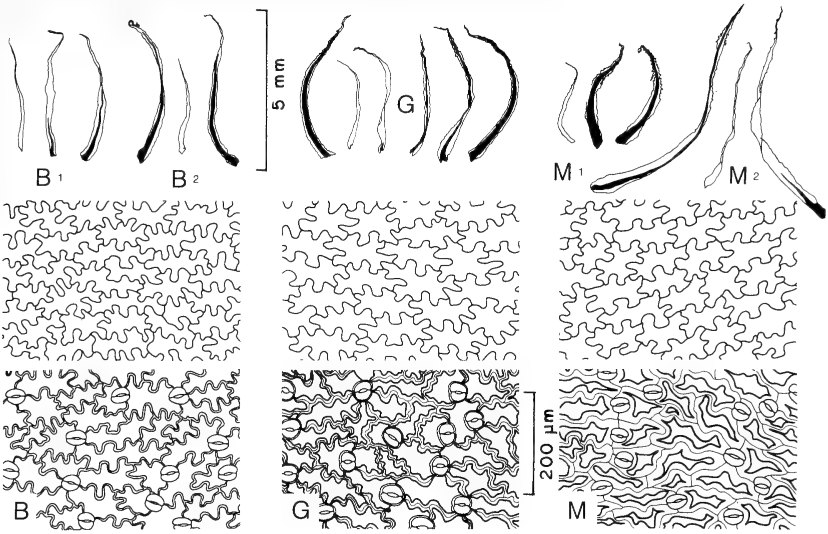

FIG. 4. Rhizome scales and epidermises of pellaeas. B. *Pellaea bridgesii*. G. *Pellaea* ×*glaciogena*. M. *Pellaea mucronata* var. *mucronata*. Specimen data as in Fig. 1, except as indicated. *Upper drawings:* scales from rhizome apex. B_1, *Kiefer 625* (MICH); B_2, *Hunnewell 7610* (MICH). M_1, *Collins 422* (MICH); M_2, *Wiggins 2317* (MICH). *Middle drawings:* upper epidermises. *Lower drawings:* lower epidermises.

intermediate are longer than 0.4 mm. Segment margins of *P. bridgesii* show a definite whitish border 1–4 cells wide and 1 cell thick (indicated by pale dotted line in Fig. 5). This margin is absent in *P. mucronata* and apparently in the intermediate.

Pellaea is generally regarded as a free-veined genus, but in a few species anastomoses are in fact more or less common. Long ago, Eaton (1879) noticed in *P. bridgesii* that "Here and there the veinlets are seen to anastomose angularly, especially near the midvein . . . ." Approximately a dozen segments each of the three taxa involved were cleared and examined in detail: all of those of *P. bridgesii* revealed anastomoses, but none of *P. mucronata* did (Fig. 5). In the intermediate some segments have vein anastomoses and others do not. The average number of vein conjunctions in segments of *P. bridgesii* was 4.4 (1–8), in the presumed hybrid 0.3 (0–1), and in *P. mucronata* none. The venation pattern may be described as free with incipient intrasegmental anastomoses, discal and mainly marginal, and without included veinlets (terms from Wagner 1979). Venation differences clearly distinguish specimens of the hybrid from immature or bipinnate specimens of var. *mucronata* and convincingly show the participation of *P. bridgesii* in the hybridization. The only other dark-stiped *Pellaea* with foliar vein anastomoses is *P. ternifolia,* which occurs in Texas

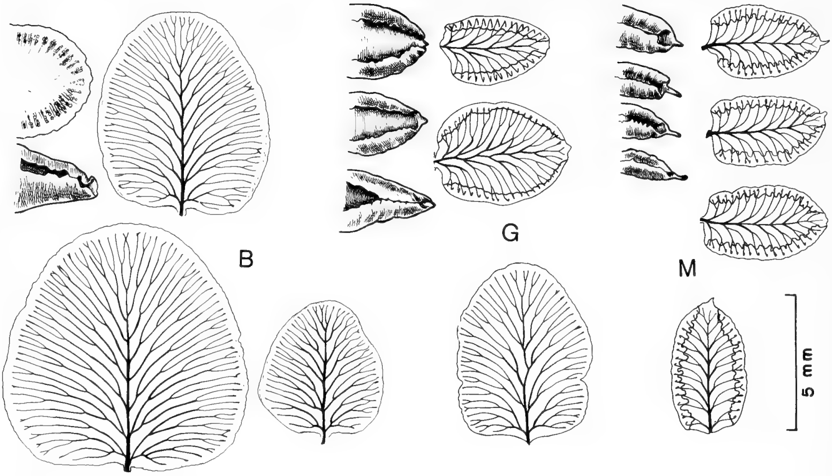

FIG. 5. Segment tips and venation of pellaeas. B. *Pellaea bridgesii*. G. *Pellaea* ×*glaciogena*. M. *Pellaea mucronata* var. *mucronata*. Specimen data as in Fig. 1. *Shaded drawings:* segment tips shown in dried state, the lowest one in each group at spore maturation stage, the upper ones from previous year's fronds. *Unshaded drawings:* cleared segments showing venation patterns.

and perhaps Arizona southward. Figures for the hybrid in Table 1 express the total average number of anastomoses in whole pinnae, so as to be comparable to figures for *P. bridgesii*. Segments illustrating venation (Fig. 5) were artificially flattened; in life they are often conduplicate, at least those of fertile segments.

Cross-sections of the segments show few anatomical differences among the putative parents and hybrid. Upper and lower epidermises are well marked from the mesophyll, and the outer paradermal walls of each are only slightly thicker than the inner walls. Palisade cells are tightly packed, roughly oval-oblong, and they occur in 4–6 layers to make up about two-thirds (one-half to three-fourths) of the mesophyll thickness. Spongy parenchyma is thus developed only in a rather narrow stratum on the abaxial side. The veins, which pass through the spongy cells, are thus quite close to the abaxial epidermis. The only striking difference involves the anticlinal walls of the epidermal cells. In *P. mucronata,* the entire pattern of the middle lamella (lower epidermis) is obscured by presumed secondary layers of extraordinary thickness (Fig. 4). In *P. bridgesii,* the situation is approximately average for ferns in general. In the hybrid, the anticlinal epidermal walls are clearly intermediate, strongly but irregularly thickened but with layers not so massive as in *P. mucronata*.

Fertile pinnae of pellaeas tend to undergo changes in orientation from the time of spore formation to spore discharge (or senescing fronds). Young fertile segments of *P. bridgesii* vary from more or less conduplicate and laterally flattened to rolled and tubelike; those of *P. mucronata* (relaxed from the dried condition with hot KOH) are not so deformed, except for the false indusia that are rolled inward (Fig. 3). In *P.* ×*glaciogena* we find both conditions (Fig. 3): some of the segments are not strongly deformed, others are nearly conduplicate. The previous year's fronds (1962) that still remained on these same specimens show the final orientation of the mature segments, as seen in the dried condition (Fig. 5, uppermost shaded drawings). Dried specimens of *P. bridgesii* are fully open, and all parts are completely exposed. Those of *P.* ×*glaciogena* show much exposed lamina, but the false indusium is revolute. Those of *P. mucronata* become completely involute, almost like bean pods. The false indusia from the two sides of the segments meet each other in an interlocking line; thus, none of the abaxial lamina is exposed except at the base and tip.

The false indusia of the hybrid are apparently more or less intermediate between the putative parents in their orientation, at least in the living condition. Sori of *P. mucronata* are completely covered by the reflexed margin, whereas in *P. bridgesii* the soral band is completely exposed at maturity. In *P.* ×*glaciogena,* the indusium does not cover the sori completely. Furthermore, the contour of the margin is intermediate in the hybrid. In *P. bridgesii* the indusial outline is straight or nearly so; in the hybrid it is undulate to shallowly toothed (Fig. 5); and in *P. mucronata* it is prominently toothed, with the teeth from opposing margins tending to fit together in a tightly interlocking system (not shown in Fig. 5).

Diaphane mounts of spores cleared in KOH show that the spores of *P. bridgesii* and *P. mucronata* are of the usual, nearly spherical, trilete type found in the genus. There are 64 spores or nearly that number per sporangium in each species. In the hybrid, the spores are usually malformed, reflecting the inability to complete normal meiosis. Formation of normal-appearing spores is, however, occasionally possible under optimum conditions (Pray 1971). Observations by Pray at the Tuolumne River site from 1955 to 1961 usually showed only aborted sporangia and malformed spores. Collections made in 1961, apparently an unusually good year, showed some very large spores 52–76 μm in diameter; these were capable of germination, gametophyte development, and sporophyte formation (Pray 1971, unpubl.) and perhaps represent unreduced "mitospores" of the kind described by Morzenti (1962).

DISCUSSION

The ferns treated (for example, by Christensen 1938) as "Gymnogrammeoideae" tend to fall into two categories based on soriation—

those that are strictly gymnogrammoid with sporangia borne abaxially along the veins (e.g., *Pterozonium, Jamesonia, Eriosorus, Syngramma, Coniogramme, Anogramma, Pityrogramma, Gymnopteris, Bommeria, Hemionitis*); and those that are cheilanthoid, the sporangia borne along the tips of veins and forming "marginal" sori (e.g., *Cheilanthes, Notholaena, Pellaea, Doryopteris*). Most of the latter cheilanthoid types bear "false indusia," which are more or less altered margins that fold over the sporangia, at least until time of spore maturity. Although this large assemblage falls readily into two categories, it is not at all certain that soriation per se defines a wholly natural division. Also, when examined in detail, these ferns prove to have various intermediate types of soriation. *Coniogramme,* for example, tends to have all the veins covered by sporangia, so that the entire abaxial surface of the pinna is "fertile." In *Pterozonium* the sporangiferous area is only a band, and this is situated roughly between the middle and the margin of the segment. In three species of *Bommeria,* sporangia occur along the veins over much of the abaxial surface, while in a fourth species, *B. ehrenbergiana,* sporangia are more restricted to the margins and cover only a quarter to a third of the distance from the lamina margin to the costa of each ultimate segment (Haufler 1979). In the Old World, soriation patterns have caused great confusion in delimitation of the closely related genera *Syngramma* (gymnogrammoid sori) and *Taenitis* (sori gymnogrammoid, or in marginal or inframarginal bands) (Holttum 1968, 1975).

There are also examples of obviously closely related species in this general circle of affinity in which the sori are more or less radically different. *Pteris lidgatii* differs from its obvious relatives (*P. quadriaurita* group) in having discrete marginal sori rather than a continuous coenosorus (Wagner 1949). In California, *Cheilanthes* (or *Aspidotis*) *californica* and *C. siliquosa* show a striking contrast: sori of the former are solitary, separate units with 1–5 sporangia; and of the latter are continuous, band-like clusters (with hundreds of sporangia) that run nearly the length of the segment. The systematic relationship between this pair of ferns is very close, as judged by the totality of resemblances. Also, they are connected by an intermediate, *C. carlotta-halliae,* of allopolyploid origin (Wagner and Gilbert 1957, Smith 1975). In general, it is becoming increasingly apparent that soriation by itself may be an unreliable character if used solely to the exclusion of other taxonomic information.

The sorus of *Pellaea bridgesii* seems actually to be different only in degree from more typical species of its genus. In all pellaeas, including *P. bridgesii,* there is a marginal "flap" or false *indusium* that extends beyond the veinlet terminations. Stomata occur on the abaxial surface of this flap. Also, in all species, including *P. bridgesii,* the sorus is not a line but actually a band, many sporangia wide. From a strictly homological standpoint, Hooker (1858) was incorrect in saying that an "involucre" (=indusium) is absent in *P. bridgesii* as contrasted to other pellaeas. Although *P. bridgesii* may be the only species in which the indusium is not reflexed, there are intermediate forms (as mentioned by Hooker himself). For example, *P. atropurpurea* has the margins reflexed over the sporangia in young sori, but the margins become completely open at maturity, fully exposing a broad band of sporangia. The most extreme opposite condition in the genus is illustrated by such species as *P. mucronata* (D. C. Eaton) D. C. Eaton in which the false indusium remains reflexed and covers the sorus at all times. The hybrid is of special interest for combining characters of species at opposite ends of the morphological spectrum in *Pellaea* as regards soriation.

One of the characters used by A. Tryon (1957) to exclude *P. bridgesii* from *Pellaea* sect. *Pellaea* was the possession of short-stalked sporangia; the stalk cells are approximately as long as wide, unlike many members of this section that have long stalks with stalk cells many times longer than wide. However, as she noted, *P. mucronata* is one of the species of this section that does possess short stalks. Thus the length of the sporangial stalk does not constitute a barrier for including *P. bridgesii* in sect. *Pellaea.*

The problem of the taxonomic placement of *Pellaea bridgesii* was exacerbated by the presence of glands among the sporangia. Secretory trichomes are widespread among gymnogrammoid and cheilanthoid ferns and are found in such well known farinose genera as *Pityrogramma* and *Notholaena.* Most authors have failed to notice that such glands also occur in sori of certain species of *Pellaea.* Eaton (1879, p. 329) wrote that "A thing which has escaped notice hitherto is the presence on the back of the frond [of *P. bridgesii*], especially between the lines of sporangia, of a little of the same ceraceous powder which is characteristic of the section *Cincinalis* of *Notholaena,* and of certain species of *Cheilanthes* and *Gymnogramme.* Indeed the very scantily reflexed involucre would seem to indicate that the plant would be quite as well placed in *Notholaena* as in *Pellaea,* a genus in which, I believe, no other species with farinaceous fronds have been placed." However, Eaton overlooked these trichomes in other species of unquestioned *Pellaea,* i.e., *P. mucronata, P. brachyptera, P. truncata, P. wrightiana,* and *P. ternifolia* (A. Tryon 1957). Very likely, the glands usually have not been observed because they are buried as paraphyses in a narrower sorus covered by a reflexed margin (unlike the situation in *P. bridgesii* in which the broader sorus is completely exposed). Glands of *P. bridgesii* and other pellaeas apparently do not extend beyond the fertile area to the sterile surfaces of the lamina, and thus such glands are paraphyses in the narrow sense of the word.

The ability of *P. bridgesii* and *P. mucronata* to hybridize repeatedly in nature suggests a close relationship between them. Fern species, in general, are not prone to hybridize across generic (or even subgeneric) lines, and those few intergeneric hybrids that are known are between very closely related genera about which there is disagreement over circumscription. Failure of synapsis and consequent sterility is the usual condition in interspecific fern hybrids, at least those that have not become stabilized by chromosome doubling (allopolyploidy) or apogamy. Thus, lack of pairing in *P.* ×*glaciogena* is expected.

In summary, doubts by Eaton (1879), A. Tryon (1957), Hitchcock et al. (1969), and others regarding placement of *P. bridgesii* can now, we believe, be dismissed. "Distinctions" between *P. bridgesii* and *Pellaea* species proper involve only the aforementioned broadening of the soral band and lack or near lack of reflexing of the segment margin over the sorus. In all other characters, and in its geographical distribution, *P. bridgesii* is patently a member of the group that includes typical pellaeas (sect. *Eupellaea* Prantl, in Diels, 1902; sect. *Pellaea* of A. Tryon 1957), and should be so treated. More specifically, it is most closely related to the *P. mucronata* group, centered in California and Arizona and comprising the dark-stiped species with bicolored rhizome scales treated by A. Tryon (1957). It is best interpreted as the simplest member of a reduction series in frond complexity with *P. mucronata* var. *mucronata* as the alternate and most dissected extreme (Pray 1968).

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ANNOUNCEMENT

MEETING NOTICE

The Society for Economic Botany will hold its 24th annual meeting at Miami University, Oxford, Ohio, June 13–15, 1983. This year's symposium will deal with ETHNOBOTANY IN THE NEOTROPICS. Information on the meeting can be obtained from Dr. Charles Heimsch, Botany, Miami University, Oxford, OH 45056 or Dr. Hardy Eshbaugh, Systematic Biology Program, National Science Foundation, Washington, DC 20550. Those wishing to contribute papers should contact Dr. Gregory Anderson, Biological Sciences Group, University of Connecticut, Storrs, CT 06268.

A REVISION OF ABUTILON SECT. OLIGOCARPAE (MALVACEAE), INCLUDING A NEW SPECIES FROM MEXICO

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Abstract

Abutilon subsect. **Oligocarpae** is raised to sectional status. It was originally established when *Abutilon* was a section of the genus *Sida*. Within this section, the identities of *Abutilon pringlei* and *A. incanum* have long been confused. *Abutilon pringlei* proves to be a synonym of *A. incanum,* which grows in the Sonoran Desert and Hawaii. The species in Texas commonly known as *A. incanum* is properly named *A. fruticosum,* and does not extend into the Sonoran Desert. A key to the species of section *Oligocarpae* is given, along with full species descriptions. **Abutilon mucronatum** is described as new from western Mexico. It is distinctive because of its mucronate-tipped petals, glandular indumentum, and pungent odor.

Miller established the genus *Abutilon* in 1754. Later, Candolle, in the *Prodromus* treatment (1824), created the subsections *Oligocarpae* (with 5–8 carpels) and *Polycarpae* (with more than 8 carpels) under *Sida* section *Abutilon.* Sweet (1826) included *Oligocarpae* and *Polycarpae* under *Abutilon,* which he, like all subsequent authors, treated as a genus. His treatment, however, left unclear the rank of these subgeneric categories. Only two species included in the *Prodromus* treatment (*A. incanum* and *A. trisulcatum*) now remain in section *Oligocarpae.* The other seventeen members of his subsection have been transferred to other genera or clearly have other affinities within *Abutilon,* e.g., *A. umbellatum* (L.) Sweet and *A. giganteum* (Jacq.) Presl. *Abutilon incanum, A. trisulcatum, A. percaudatum, A. parvulum, A. malacum,* and *A. fruticosum* form a distinct and cohesive group comparable to other natural groupings within the genus, and merit recognition as a section.

Abutilon Section **Oligocarpae** (A.DC.) J. Fryxell, comb. et stat. nov.—*Sida* sect. *Abutilon* subsect. *Oligocarpae* Candolle, Prodromus 1:467. 1824.—Type (here designated): *Abutilon trisulcatum* (Jacq.) Urban.

Plants suffrutescent to herbaceous. Leaves cordate at base, acute to acuminate at apex, with regularly or irregularly serrated margins, canescent to tomentose throughout with fine stellate trichomes or mixed stellate and gladular trichomes. Fruits cylindro-truncate schizocarpic

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capsules with loculicidal dehiscence and 3 reniform seeds per carpel; carpels 5 (6–9 in *A. fruticosum*). Chromosome base number: $x = 7$.

The identities and ranks of two members of this section, *Abutilon pringlei* and *A. incanum,* have been confused for many years. The epithet *incanum* previously has been applied to a taxon with yellow to orange, spreading petals, occurring from Texas to Arizona, northern Mexico and Hawaii. The epithet *pringlei* has traditionally been applied to the taxon, with yellow or pink reflexed petals each with a maroon basal spot, whose range was considered to be from Arizona to Sinaloa and west into Baja California (Kearney and Peebles 1942, Correll and Johnston 1970). Kearney (1955) treated the two taxa as separate species in his key to *Abutilon,* but noted that "*Abutilon pringlei* apparently intergrades with *A. incanum* and is probably only subspecifically distinct." Felger and Lowe (1970) merged the two taxa, recognizing two subspecies, *A. incanum* subsp. *incanum* and *A. incanum* subsp. *pringlei,* stating that "the differences for the most part involve . . . minor distinctions of color." My studies have shown that there are several other characters, e.g., petal attitude, carpel number, and leaf shape, that differ and that distinguish these two taxa consistently (Fig. 1). Their separation at the specific level is warranted. In addition, field and herbarium observations revealed that their ranges do not, in fact, overlap. As noted above, the taxon known as *Abutilon pringlei* ranges from Arizona to Sinaloa west into Baja California, whereas the taxon that has been called *A. incanum* is confined, in North America, to Texas and northeastern Mexico, with isolated populations in Oklahoma and Arkansas. In addition, this taxon is found in tropical and northern Africa, Arabia, southern Persia, Pakistan and northwestern India (Riedl 1976).

Link (1822) originally described *Sida incana* from the Sandwich (Hawaiian) Islands. Sweet transferred this species to *Abutilon* in 1826. Link did not include floral characters in his description, and the type specimen, housed in Berlin, has been destroyed. However, because there is only one taxon from this section occurring in the Hawaiian Islands, it is not difficult to determine what floral characters should be associated with the name. The taxon from western Mexico, previously known as *A. pringlei,* has, for example, the reflexed petals with a basal spot and the trichome pattern identical to that of the Hawaiian taxon (*A. incanum*) and must be considered conspecific with it. Hochreutiner described *A. pringlei* from the Sierra Tucson in Arizona in 1902. Because Link's epithet antedates Hochreutiner's, the correct name for the Sonoran Desert and Hawaiian species is *A. incanum.* The more eastern (Texas) species, to which the epithet *incanum* has been incorrectly applied, must therefore have another name. Torrey and Gray (1838) described two species, *A. texense* and *A. nuttallii,* in the same article. Both of these names were quickly recognized as synonymous (e.g., Standley 1923). My field and herbarium

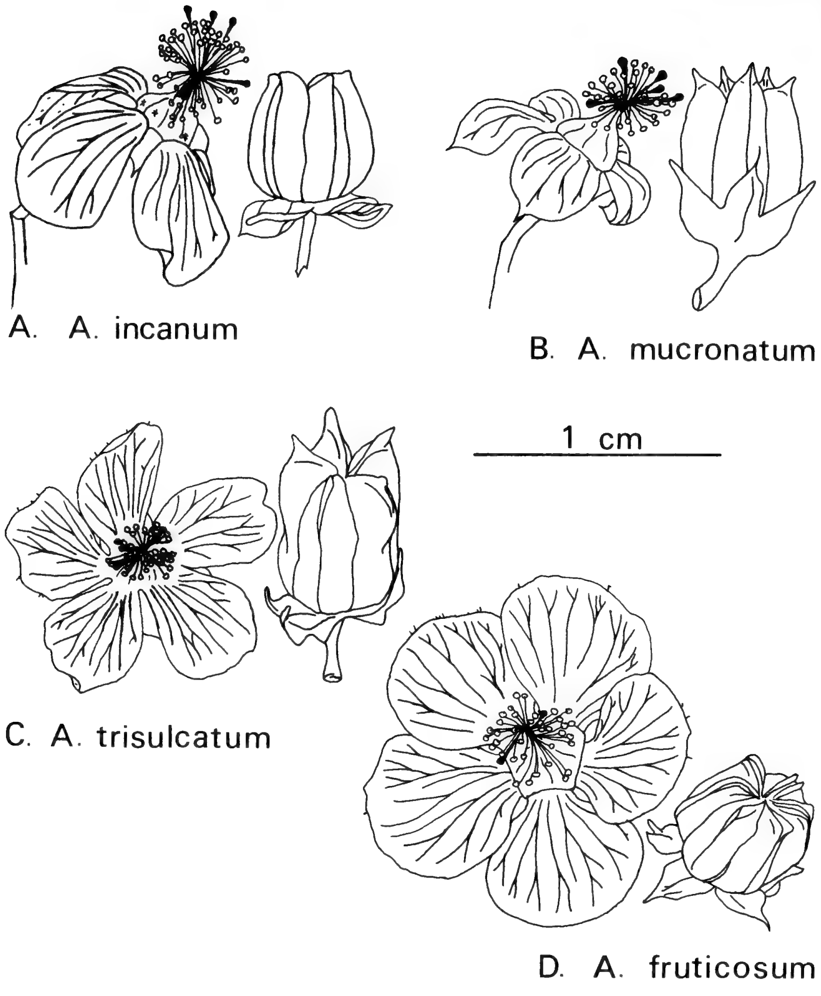

FIG. 1. Comparisons of flower and fruit characteristics for four species of *Abutilon:* —A. *Abutilon incanum.*—B. *Abutilon mucronatum.*—C. *Abutilon trisulcatum.*—D. *Abutilon fruticosum.*

studies showed that this eastern taxon conforms in all respects to Torrey and Gray's description. However, checking a bit further in the herbarium, I found that the African and Asian species, *Abutilon fruticosum* Guill. & Perr. (Guillemin et al. 1832) is identical to that described by Torrey and Gray (1838). A complete list of synonyms is included with the treatment of the species.

Abutilon incanum, unlike the other species mentioned in this paper, occurs down to sea level on the Pacific coast of Mexico. This must have facilitated its dispersal to Hawaii, where it apparently arrived by natural means. Prior to 1822, ships from Mexico to the Hawaiian Islands left from Acapulco (Merrill 1954), which is quite out of the range of *A. incanum.* The fruits and seeds are buoyant, the seeds have a thick, hard coat, and the currents, as indicated by Richards (1958), favor such dispersal. Also, only the pink-petaled plants are found in Hawaii, whereas in Mexico both the pink- and yellow-petaled phases are present, possibly indicating a restricted source for the Hawaiian populations.

Field study in support of the preceding interpretations revealed that an undescribed species exists within this section. This is described below.

Key to *Abutilon* section *Oligocarpae*

Carpels 6–9; petals cream to orange, spreading; plants covered with stellate trichomes, lacking obvious glandular trichomes . . . . 1. *A. fruticosum*

Carpels 5; petals yellow, pink, orange or red, spreading or reflexed; plants covered with stellate and/or simple and/or glandular trichomes.

  Plants with glandular trichomes, at least on stems.

    Petals spreading, with a dark basal spot, obtuse to rounded or emarginate at tip; fresh foliage not strongly scented.

      Young stems terete; flowers 20–25 mm in diameter . . . . 2. *A. percaudatum*

      Young stems three-ribbed; flowers 8–10 mm in diameter . . . . 3. *A. trisulcatum*

    Petals reflexed, lacking a basal spot, lobes mucronate at tip; fresh foliage pungently scented . . . . 4. *A. mucronatum*

  Plants lacking glandular trichomes.

    Petals reflexed, with a well-developed basal spot, lobes obtuse to rounded or emarginate at tip; plant a diffuse shrub to 2 m high . . . . 5. *A. incanum*

    Petals spreading, lacking a basal spot, lobes obtuse to rounded or emarginate at tip; plants either compact herbs to 50 cm high, or sprawling herbs with stems to 30 cm long.

      Petals yellow; leaves densely covered with stellate trichomes; plants erect . . . . 6. *A. malacum*

      Petals pink to brick red; leaves covered with scattered unbranched trichomes and rarely stellate ones; plants procumbent . . . . 7. *A. parvulum*

1. ABUTILON FRUTICOSUM Guillemin & Perrottet *in* Guillemin, Perrottet and Richard, Fl. Seneg. Tent. 1:73. 1832.—TYPE: Senegal, Suffal, *Leprieur s.n.* (Holotype: P).

A. microphyllum A. Richard, Tent. Fl. Abyss. 1:70. 1847.—TYPE:

Abyssinia, Chocho, *Petit s.n.* (Holotype: P).—*A. fruticosum* var. *microphyllum* (A. Richard) Abedin, Malvaceae *in* Fl. W. Pakistan 130:58. 1979.

A. texense Torrey & Gray, Fl. N. Amer. 1:231. 1838.—Type: Texas, *Drummond 43* (Isotypes: BM! OXF!).

A. nuttallii Torrey & Gray, Fl. N. Amer. 1:231.1838.—Type: Texas, on the Red River, *Nuttall s.n.* (Lectotype, here designated: NY!; isolectotype: BM!).

Plants suffrutescent, 2–60 cm tall, branched from a perennial rootstock; stems terete, minutely stellate-tomentose throughout. Leaves ovate, cordate at base, acute at apex, 1–10 cm long, blade pubescent; leaf-margins irregularly serrate. Flowers solitary or in few-flowered, leafy-bracted panicles, calyx 2–4 mm long, lobes ovate, acute to acuminate at tip with bifurcated trichomes along margins; petals spreading, cream to orange-yellow, 5–10 mm long (Fig. 1D). Chromosome number: $n = 7$ (Bates and Blanchard 1970).

Distribution. Dry areas on cliffs, slopes, prairies, open woodlands and chapparal, 0–1000 m; Texas, Oklahoma and Arkansas to Coahuila, Nuevo Leon and Tamaulipas in North America. Also tropical and northern Africa, Arabia, southern Persia, Pakistan and northwestern India.

2. Abutilon percaudatum Hochreutiner, Annuaire Conserv. Jard. Bot. Genève 21:438. 1920.—Type: San Luis Potosí: Rioverde, *Palmer 19* (Holotype: NY!; isotypes: GH! K! MO!).

Suffrutescent shrubs 5–20 dm tall; stems terete; plant glandular-pubescent throughout. Leaves ovate, cordate at base, long-acuminate at apex, 8–13 cm long; blade pubescent and glandular; margins irregularly serrate. Flowers solitary or in subpaniculate inflorescences; calyx 7–8 mm long, lobes ovate, acuminate at tip, bifurcated trichomes covering inside surface, petals spreading, cream-colored to yellow with carmine basal spot; 8–10 mm long. Chromosome number: $n = 14$ (Bates 1976, Fernandez 1974).

Distribution. San Luis Potosí and Hidalgo to Chiapas.

3. Abutilon trisulcatum (Jacq.) Urban, Repert. Spec. Nov. Fedde 16:32. 1919.—*Sida trisulcata* N. J. Jacq., Enum. Pl. Carib. 26. 1760. —Type: insula Domingo (no specimen cited or traced; see comment following description).—*Sida triquetra* L., Sp. Pl. ed. ii. 9621. 1763 (based on *S. trisulcata* Jacq.).—*Abutilon triquetrum* (L.) Sweet, Hort. Brit. ed. i. 1826.—*Bastardia triquetra* (L.) Morales *in* Maza, Anal. Soc. Esp. Hist. Nat. 19:218. 1890.

A. ramosissimum Presl, Rel. Haenk. 2:116. 1835.—Type: Mexico, Acapulco, *Haenke s.n.* (Holotype: PR?).—*Sida ramosissima* (Presl) D. Dietrich, Syn. Pl. 853. 1847.

A. nealleyi Coulter, Contr. U.S. Natl. Herb. 1:32. 1890.—TYPE: Texas: Hidalgo County, near Hidalgo, *Neally 50* (Holotype: US!).

Suffrutescent shrubs, 1–20 dm tall; stems strongly 3-angled to terete in stems 2 or more years of age, glabrous to densely tomentose or glandular. Leaves ovate, cordate at base, abruptly acuminate at apex, 2–12 cm long; blade finely velvety; leaf-margins serrate to crenate. Flowers solitary or in subpaniculate inflorescences; calyx 3–4 mm long, lobes ovate, acuminate at tip, with bifurcated trichomes covering inside surface; petals spreading, yellow with red spot at base, 4–5 mm long (Fig. 1C). Chromosome number: $n = 7$ (Bates and Blanchard 1970).

Distribution. Disturbed areas in south Texas, through Central America to Nicaragua and the West Indies at lower elevations.

No lectotype is designated here for Jacquin's description, because I have not yet traced a reasonable specimen. There is a good possibility that one exists, however, so I will not designate a neotype. See D'Arcy (1970) and Stafleu (1966) for information on typification of Jacquin names.

4. **Abutilon mucronatum** J. Fryxell, sp. nov.

Frutex debilis ad 2 m altus aromaticissimus dense tomentosus partibus viridibus totis dense tomentosis trichomatibus glandularibus stellatis, annotinis interdum leviter porcatis, hornotinis teretibus. Folia 30–100 mm longa, 20–60 mm lata, longeacuminata, serrata, ad basin cordata. Inflorescentia paniculata diffusa foliata foliis valde reductis. Lobi calycis adaxialiter pro parte maxima glabri ad marginem trichomatibus bifurcatis ad apicem trichomatibus bifurcatis adpressis. Petala 5, recurvata, 3–5 mm longa 2–3 mm lata eburnea ad marginem roseola et interdum venis roseolis, ad apicem mucronata, abaxialiter trichomatibus sparsis simplicibus ca. 0.1 mm longis; columna staminum viridis vel leviter roseola; segmenta fructuum unumquidque 3-sperma aristata aristis 0.1–1 mm longis longitudine dehiscentia; semina fuliginea 1 mm diametro reniformes irregulariter pubescentes trichomatibus stellatis minutis (Fig. 1B).

Suffrutescent shrubs, 0–2 m tall; stems terete, young stems sometimes slightly ribbed; plant densely tomentose with glandular and stellate trichomes throughout. Leaves ovate, cordate at base, long-acuminate at apex; leaf-margins finely serrate. Flowers in diffuse, leafy-bracted panicles; calyx 3–4 mm long, inside surface glabrous, but lobes sparsely edged with bifurcated trichomes; petals recurved, cream-colored with pink margins, 3–5 mm long, mucronate at tip, abaxial surface covered with scattered unbranched trichomes; staminal column green or faintly pink. Chromosome number: $n = 7$ [*Fryxell and Lane 7* (TEX)], (Fryxell 1980).

TYPE: Mexico, Sonora, on the road from Navojoa to Alamos, about 15 km e. of Hwy 15 (near 27°02′N, 109°30′W), 200 m. 22 Oct 1978, *Fryxell and Whitacre 128*) (Holotype: TEX!; isotypes: ARIZ! NY! US!).

Distribution. Disturbed areas with good drainage, such as roadsides and fallow fields; Sonora, Sinaloa, Nayarit, Jalisco, Colima, Michoacan, Guerrero, Puebla, and Guanajuato, 100–1500 m.

5. ABUTILON INCANUM (Link) Sweet, Hort. Brit. ed. i. 53. 1826.–*Sida incana* Link, Enum. Pl. 2:204. 1822.—TYPE: "in insulis Sandwich" (specimen housed in Berlin, now destroyed; written description here designated as lectotype).

A. pringlei Hochr., Annuaire Conserv. Jard. Bot. Genève 6:14. 1902.—TYPE: Arizona: Sierra Tucson, *Pringle s.n.,* 21 Apr 1884 (Holotype: NY!; isotype: US!).—*A. incanum* subsp. *pringlei* (Hochr.) Felger & Lowe, J. Ariz. Acad. Sci. 6:83. 1970.

A. mochisense Hochr., Annuaire Conserv. Jard. Bot. Genève 21:447. 1920.–TYPE: Sinaloa: near Los Mochis, *Rose 13329* (Holotype: NY!; isotype: US!).

A. pringlei var. *sinaloensis* Hochr., Annuaire Conserv. Jard. Bot. Genève 21:437. 1920.—TYPE: Sinaloa, in vicin. Topolobampo, *Rose 12372* (Holotype: NY!).

Suffrutescent shrubs 1–20 dm tall; stems terete, densely covered with minute stellate trichomes. Leaves ovate, cordate at base, long-acuminate at apex, 1–10 cm long; blade densely stellate-canescent; leaf-margins irregularly serrate to crenate. Flowers solitary or in open, leafy-bracted panicles; calyx 2–4 mm long, lobes ovate, acute to acuminate at tip, with bifurcated trichomes along inner margins; petals reflexed, yellow or pink with maroon basal spot, 4–6 mm long. Chromosome number: $n = 7$ (Bates 1976, Bates and Blanchard 1970, Carr 1970) (Fig. 1A).

Distribution. Dry hills and arroyos from Arizona and Baja California to Sinaloa, and (pink phase only) in Hawaii.

6. ABUTILON MALACUM S. Wats., Proc. Amer. Acad. Arts 21:446. 1886.—TYPE: Texas, El Paso, 10 Sep 1883 (on label), 1884 (in text), *Jones 4193* (here designated as Lectotype: POM!; isolectotypes: BM, BR, NY! POM!).

Compact herbs 1–10 dm tall; stems terete; plant stellate-pubescent throughout, trichomes yellowish. Leaves suborbicular, cordate at base, obtuse to acute at tip, 3–10 cm long; blade densely stellate-canescent;

leaf-margins acuminate denticulate. Flowers in compact panicles; calyx 6–8 mm long, lobes lanceolate, acute to acuminate at tip, inside surface covered with bifurcated trichomes; petals spreading, orange to yellow, 6–8 mm long. No chromosome data available.

Distribution. Dry hills, slopes and flats in the southern half of Texas and New Mexico, and Sonora, Chihuahua, Coahuila, Durango, and San Luis Potosí.

Watson cites 6 collections: *Palmer 2139, Havard 8, 130; Jones 4193; Pringle 164* (GOET! K! US!), *363* (GOET! K! US!). Standley (1923) says "type from Texas." To be consistent with Standley's designation, I have assigned lectotypic status to the Jones collection because it is from Texas.

7. ABUTILON PARVULUM Gray, Pl. Wright. 1:21. 1852.—TYPE: Texas: calcareous hills of the San Felipe and San Pedro Rivers, *Wright (56)* (Holotype: GH!; isotypes: BM, NY! OXF! US).

Stems spreading or trailing from a woody rootstock, stems 1–30 cm long, terete; plants sparsely covered with minute stellate and unbranched trichomes. Leaves broadly ovate, 1–5 cm long, cordate at base, obtuse to acute at apex; leaf-margins coarsely dentate. Flowers solitary, axillary; calyx 3–4 mm long, lobes ovate, acuminate at tip with bifurcated trichomes present along inner margins; petals spreading, pink or red, 4–6 mm long. Chromosome number: $n = 7$ (Bates and Blanchard 1970).

Distribution. Hills, dry ledges and similar areas from Texas to Colorado, California and Baja California, Sonora, Chihuahua, and Coahuila.

All five specimens of Wright's are numbered 56, but this may be a distribution number added by Gray, and not Wright's collection number.

LIST OF EXSICCATA

A list of specimens examined is on file at the University of Texas, and in Fryxell 1980. Additional copies are available on request from the author.

ACKNOWLEDGMENTS

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NEW TAXA OF WESTERN AMERICAN ERYNGIUM (UMBELLIFERAE)

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Abstract

Three local, polyploid taxa of *Eryngium,* **E. constancei, E. mathiasiae,** and **E. aristulatum** var. **hooveri**, are described from California.

In a detailed eco-systematic study of *Eryngium* in western North America north of Mexico (Sheikh 1978), I treated the component taxa as section *Armata* of that nearly cosmopolitan genus. The section comprises 12 species and three varieties, of which the following two species and one variety are believed to be new. The two new species are already on the list of rare and endangered plants of California (Smith et al. 1980) and are currently under federal review; the new variety is of comparable rarity.

Eryngium constancei Sheikh, sp. nov.

Plantae perennes graciles debiles effusaeque ramosissimae dense puberulentes; folia basalia adulta lineari-lanceolata vel lanceolati-acuminata margine spinoso-serrata lobataque vel remote spinulosa; petioli quam laminae multo longiores; inflorescentia cymosa ramosa; capitula globosa laxa alba dilute purpureaque, floribus paucibus; bracteae involucrales et bracteae florales distinctae, bracteis involucralibus lineari-lanceolatis lateraliter paucispinosis quam capitula longioribus, bracteis floralibus margine paucispinosis ad basim scarioso-alatis; sepala lanceolata quam styli multo breviores; fructus ovoidei teres dense squamati, squamellis acuminatis obscure colliculosis dense puberulentis; chromosomatum numerus $n = 16$. (Fig. 1.)

Plants slender, weak, spreading, decumbent or ascending, densely puberulent, 20–30 cm tall from a rootstock bearing fascicled fibrous roots, the first node of principal flowering scape 1–2 cm above rootstock, the scape diffusely branched with 4–6 slender, spreading branches from first or occasionally second node. Basal leaves septate, the earliest bladeless, 15– 20 cm long, the later leaves 10–15 cm long with slender, elongate, laterally spinulose petioles 8–12 cm long, usually much longer than blade; blades linear-lanceolate to lanceolate-acuminate, 3–4 cm long, 3–4 mm broad, spinose-serrate to lobed or remotely spinulose, the lobes usually decreasing toward base and grading into petiole, acute; cauline leaves of first or second node like basal

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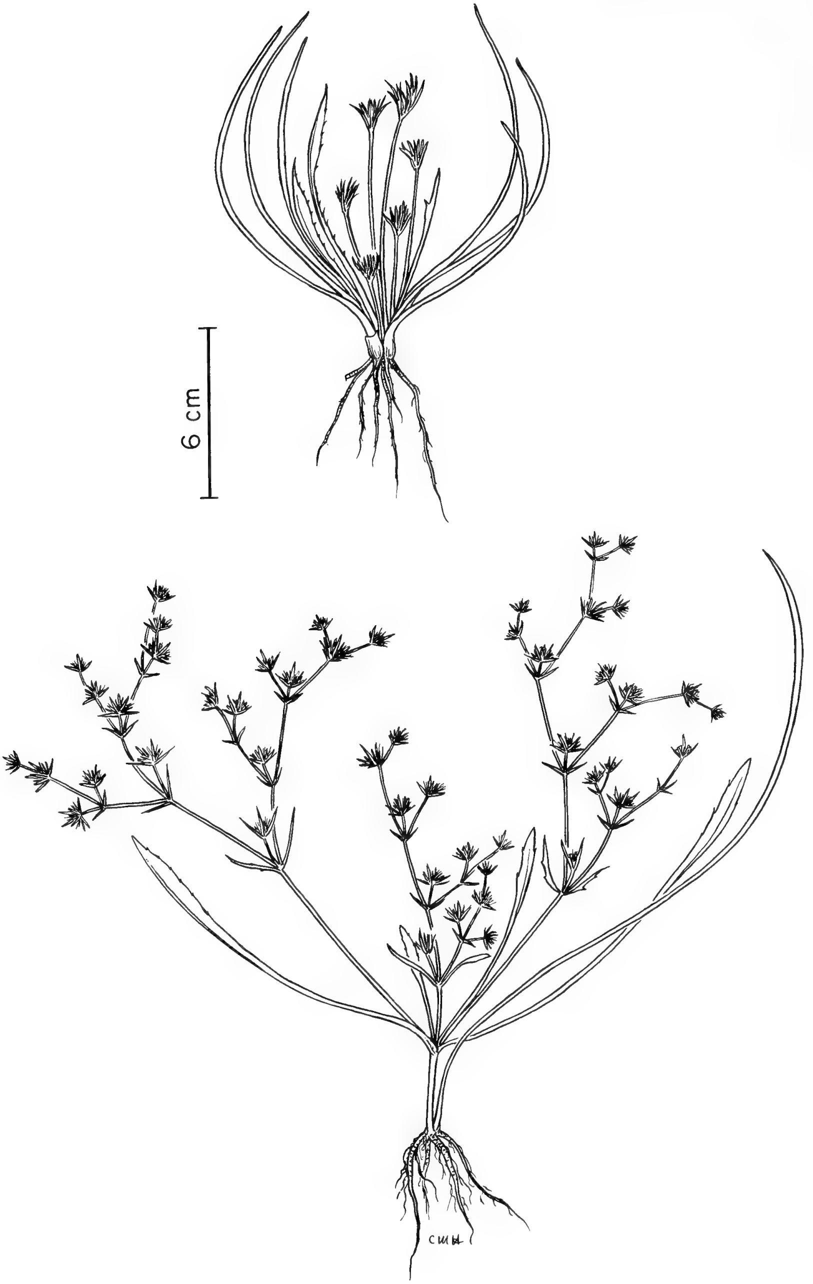

FIG. 1. *Eryngium constancei.* From the type collection.

but smaller, abruptly reduced above to bract-like structures. Inflorescence of cymosely arranged heads, white or often faintly purplish, the peduncles slender, 5–8 cm long, the heads globose, 3–5 mm long, 4–6 mm broad, rather loosely 5–7-flowered. Involucral bracts 4 or 5, distinct from bractlets, linear-lanceolate, ascending, 6–7 mm long and ca. 1 mm broad in flower, becoming 7–9 mm long and 1.5–2 mm broad in fruit, exceeding head, marginally spinose with 2 or 3 pairs of spines to 1.5 mm long, subulate, scarious-winged at base with broad, short, distally spinose wings, densely puberulent dorsally. Bractlets 1–3, 5–6 mm long and 0.6–0.8 mm broad in flower, exceeding flowers, becoming 6–6.5 mm long and 0.7–1 mm broad in fruit, with 2 pairs of marginal spines to 1 mm long and with short, broad, scarious basal wings enfolding fruit, densely puberulent dorsally. Sepals lanceolate, ca. 2 mm long and 0.5–0.6 mm broad in flower, becoming 2.2–2.5 mm long and ca. 0.7 mm broad in fruit, scarious-margined, entire, cuspidate; petals white (rarely purplish distally), oblanceolate, ca. 1 mm long and ca. 0.5 mm broad, puberulent on margin, 3-fid; styles 2–2.5 mm long, equalling to longer than sepals in flower, becoming 3–3.5 mm long and much longer than fruiting sepals. Fruit ovoid, 1.6–2.2 mm long, 1.2–1.5 mm broad, shorter than styles but almost equalling sepals, densely squamate, the scales acuminate with an obscure calycine row, 0.5–0.7 mm long and ca. 0.2 mm broad, appressed, the calycine and lateral scales longer and ascending, becoming abruptly smaller toward base, white or brown, obscurely colliculate, densely puberulent. Cotyledons linear, 1.5–1.8 cm long, ca. 0.5 mm broad. $n = 16$.

TYPE: USA, CA, Lake Co., drying vernal pool along roadside in meadow with *Pinus ponderosa* and *Quercus kelloggii,* Loch Lomond, 12 May 1973, *Sheikh and Constance 545* (Holotype: UC; isotypes: BM, F, GH, K, LE, MAK, MEXU, MO, NY, ORE, OSU, P, PH, RM, RSA, S, US, WS, WTU).

PARATYPES: USA, CA, Lake Co., Loch Lomond, 8 Jun 1941, *Hoover 5342* (UC, US); 19 Aug 1958, *Crampton 5108* (UC). Known only from the type locality.

Eryngium constancei closely resembles *E. aristulatum* var. *aristulatum* but can be distinguished readily by the dense puberulence and the sparse flowers, which usually number five (but never more than seven) per head.

This species is named for Dr. Lincoln Constance, Professor Emeritus of Botany, University of California, Berkeley, who is a long-time student of the family Umbelliferae, with a particular interest in New World *Eryngium.*

Eryngium mathiasiae Sheikh, sp. nov.

Plantae perennes aliquantum crassae adscendentes vel erectae ramosae glabrae; folia basalia adulta lanceolata vel anguste obovata margine spinoso-serrata spinoso-lobataque; petioli quam laminae longiores; inflorescentia cymosa ramosa; capitula subglobosa condensata pedunculata alba, floribus numerosis; bracteae involucrales et bracteae florales haud distinctae lineares dorsaliter lateraliterque spinosae, bracteis floralibus ad basim scarioso-alatis; sepala lanceolata styli subaequantes; fructus oblongi teres dense squamati, squamellis acuminatis aristatis subtiliter colliculosis; chromosomatum numerus $n = 32$. (Fig. 2.)

Plants rather stout, ascending to erect, glabrous, 30–40 cm tall from a rootstock bearing fascicled fibrous roots, the first node of principal flowering scape 1.5–2 cm above rootstock, the scape 3–4-branched from first (or second) node. Basal leaves obscurely septate, subrosulate, the earliest bladeless, or with a few linear segments, or bearing an elliptic blade 10–28 cm long, the later leaves 10–17 cm long with a petiole 6–10 cm long, dilated, laterally spinulose to spinose-lobed, longer than blade; blades lanceolate to narrowly obovate, 3–5.5 cm long, 1.5–2.5 cm broad, finely to coarsely spinose-serrate to spinose-lobed, tapering at base and merging into petiole, acute to obtuse; cauline leaves like basal, the upper sessile, opposite, and reduced. Inflorescence of cymosely arranged heads, the peduncles slender to moderately stout, 0.8–1.8 cm long, the heads subglobose, 8–11 mm long, 8–12 mm broad, compactly 30–37-flowered. Involucral bracts 6 or 7, scarcely distinct from bractlets, linear, somewhat rigid, spreading to ascending, 12–15 mm long and 1–1.3 mm broad in flower, becoming 13–23 mm long and 1.2–1.8 mm broad in fruit, 1.5 to twice as long as head, sparsely to densely spiny both dorsally and laterally (occasionally naked dorsally), the lateral spines up to 5 mm long, acuminate-pungent, slightly dilated at base. Bractlets flexuous, spinose-margined but not callous-margined, like bracts, 7–10 mm long and 0.6 mm broad in flower, slightly to greatly exceeding flowers, becoming 9–15 mm long and 1–1.3 mm broad in fruit, usually densely spiny both dorsally and laterally, the spines 2–3 mm long, the dorsal spines inserted ca. 2–2.5 mm above base of bractlet, the base with scarious, distally spinose wings enfolding fruit. Sepals lanceolate, ca. 2.7 mm long and ca. 0.7 mm broad in flower, becoming 3–3.5 mm long and 1 mm broad in fruit, the margins scarious, entire or scarious-toothed, cuspidate to pungent; petals white, oblong, 1.7 mm long, 0.5–0.6 mm broad, 4-fid; styles 2.5–3 mm long, equalling to slightly exceeding fruiting sepals. Fruit oblong, 2.5–3 mm long, 1.3–1.5 mm broad, shorter than styles but equalling to longer than sepals, densely squamate, the scales lanceolate, acuminate to aristate, the calycine 0.8–1.2 mm long, 0.2–0.5 mm broad, laterally appressed, subequal, the calycine and lateral ones longer, becoming smaller toward base, the surface colliculate, glabrous to finely puberulent. Cotyledons linear, ca. 2 cm long, ca. 1 mm broad. $n = 32$.

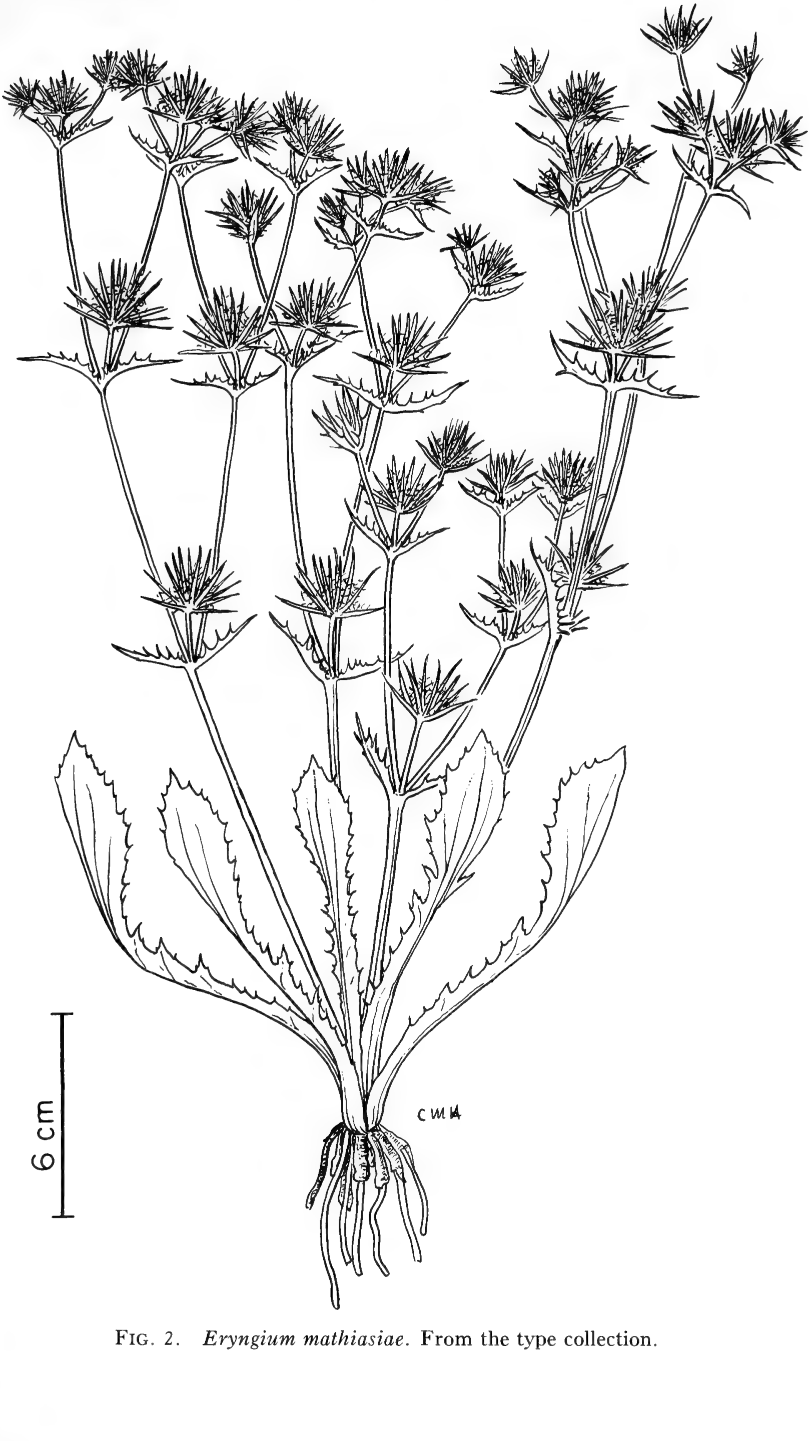

FIG. 2. *Eryngium mathiasiae*. From the type collection.

TYPE: USA, CA, Modoc Co., drying roadside swale, opening in *Pinus-Juniperus* woodland 15.8 km nww. of Canby on State Hwy 139, 27 Jun 1973, *Sheikh and Constance 551* (Holotype: UC; isotypes: F, MAK, S).

PARATYPES: USA, CA, Modoc Co.: 1.6 km s. of Doublehead, 2 Jul 1934, *Howell 12347* (CAS, DS, GH, POM, US); 12.9 km nw. of Canby, 14 Jun 1940, *Eastwood and Howell 8212* (CAS, GH); nw. of Lookout, 27 Jun 1973, *Sheikh and Constance 552* (UC), 18 Jun 1958, *Raven and Solbrig 13322* (UC); Lassen Co.: 5.4 km n. of Bieber, 27 Jun 1973, *Sheikh & Constance 553* (UC); 8 km se. of Bieber, 3 Jul 1934, *Howell 12382* (CAS, DS, GH, POM, US); Shasta Co.: 4.3 km ne. of McArthur, 27 Jun 1973, *Sheikh and Constance 554* (UC).

This northeastern Californian taxon appears to blend the distinctive characters of two species: leaf size and shape are like that of *E. alismaefolium,* whereas the dorsally spinose bracts and bractlets recall those of *E. castrense.* The taxon is, nevertheless, quite distinct because the basal leaves are much shorter than the branches and the petioles are longer than the spinose-serrate to spinose-lobed blade.

The species is named for Dr. Mildred E. Mathias, Professor Emeritus of Biology, University of California, Los Angeles, who has contributed greatly to knowledge of the family Umbelliferae, especially in the New World.

Eryngium aristulatum Jepson var. **hooveri** Sheikh, var. nov.

Plantae infirme adscendentes vel erectae; folia basalia adulta subintegra vel grosse incisa; capitula 10–32-flora; bracteae involucrales et bracteae florales spinosi dorsales destituti, bracteis floralibus lateraliter paucispinosis; sepala ovati-lanceolata quam styli plerumque leviter longiores; chromosomatum numerus $n = 16$. (Fig. 3.)

Plants weakly ascending to rarely erect, glabrous, 10–54 cm tall, the first node of principal flowering scape 0.4 cm above rootstock, the scape with 4 or 5 branches radiating from first, second, third, or fourth node. Later basal leaves 9–26 cm long with petioles 5–13 cm long; blades 3–6 cm long, 0.7–2 cm broad, spinose-serrate or coarsely incised (rarely entire). Heads 5–23 mm in diameter, 10–32-flowered; involucral bracts usually 5, 5–15 mm long and 1–2.5 mm broad in flower, becoming 20–22 mm long and 1.5–3 mm broad in fruit, marginally entire or with 3 or 4 pairs of subopposite spines 1–2 mm long, glabrous dorsally; bractlets exceeding flowers, with 1 or 2 pairs of lateral spines, naked dorsally; sepals ovate-lanceolate, 1–1.5 mm long and 0.4–0.7 mm broad in flower, becoming 1.3–2 mm long and 0.8 mm broad in fruit; petals ca. 1 mm long, 3-fid (rarely 4-fid); styles 0.6–1.5 mm long, shorter than sepals in flower, becoming 0.9–2.4 mm long, shorter than to slightly exceeding fruiting sepals. Fruit 1.7–2 mm long, 1–1.6 mm

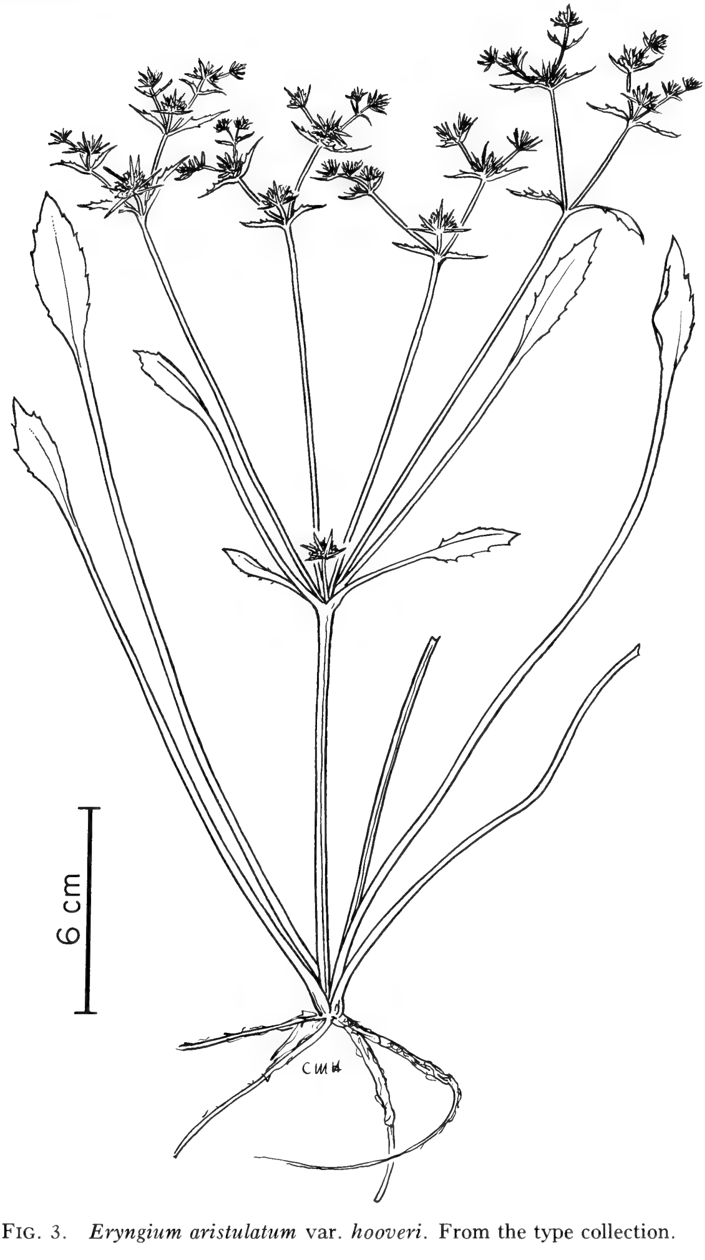

FIG. 3. *Eryngium aristulatum* var. *hooveri*. From the type collection.

broad, equalling to longer than styles and sepals, the scales ovate-lanceolate, acuminate, 0.5–1 mm long, 0.2–0.5 mm broad. Cotyledons not seen. $n = 16$.

TYPE: USA, CA, San Benito Co., slightly alkaline depressions in lacustrine plain at n. end of San Felipe (Soap) Lake, on State Hwy 152, 4.7 km w. of intersection with San Felipe Rd, 31 Jul 1978, *Sheikh and Constance 632* (Holotype: UC; isotypes: BM, F, GH, K, LE, MAK, MEXU, MO, NY, ORE, OSU, P, PH, S, US, WS).

PARATYPES: USA, CA, San Benito Co.: 11.3 km n. of Hollister, 16 Aug 1933, *Rose 33318* (CAS, DS, LE, RM, S, WTU); Gilroy–Hollister, 14 Aug 1917, *Abrams 6673* (DS); San Luis Obispo Co.: 20 Jul 1908, *Jepson 3070* (JEPS, WTU); Laguna, 3 Aug 1940, *Hoover 6265* (CAS, UC), 24 Aug 1946, *Hoover 6328* (CAS), 25 Aug 1969, *Hoover 11555* (CAS, UC), 31 Oct 1908, *Condit s.n.* (UC); Cambria, 26 Jun–17 Jul 1876, *Palmer 155* (F, GH, MO, NY, US); Santa Clara Co.: Alviso, 20 Oct 1902, *C. F. Baker 1827* (GH, K, MO, NY, POM); Agnew, 19 Oct 1902, *Abrams 3089* (DS, JEPS, POM): Gilroy–Morgan Hill, 1 Jun 1916, *Abrams 5667* (DS, NY); 1.6 km e. of Palo Alto, 18 Oct 1899, *Ward 121* (GH, NY, US); Palo Alto, Oct 1901, *Abrams 2232* (DS, MO, NY, POM); Stanford University, 1899, *Elmer 1806* (DS, POM).

This taxon, which appears to be intermediate between *E. armatum* and *E. aristulatum* var. *aristulatum,* occurs in coastal California from San Francisco Bay to San Luis Obispo County. The aspect of the plant, especially size and shape of leaves, is like that of *E. aristulatum,* whereas shape of bracts and bractlets and the short styles (shorter than calyx) resemble those of *E. armatum.*

This variety is named for the late R. F. Hoover, who had a lifelong devotion to the California flora and who did much of the research for the taxonomic treatment of *Eryngium* in Jepson's "Flora of California" (1936). In his "Vascular Plants of San Luis Obispo County" (1970, p. 214), Hoover referred to it as "*E. aristulatum* Jepson. Locally found only around the Laguna near San Luis Obispo (6265, 6328)."

ACKNOWLEDGMENTS

The writer wishes to thank Professor Robert Ornduff for provision of a Research Associateship and facilities; the staffs of the Botanical Garden and the herbarium at the University of California, Berkeley, for various assistances; and Professor Lincoln Constance, for general thesis supervision. The illustrations in this paper were prepared by C. M. Hannan from sketches made by the author.

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ANNOUNCEMENT

Additions to the flora of the White Mts., California and Nevada. Dean Wm. Taylor and Mary DeDecker have published a list of over 40 range extensions for the White Mts. (CNPS Bristlecone Newsletter Vol. 1, No. 4:3–5. A reprint of the list is available upon request (send 20¢ stamp) to: PO Box 194, Lee Vining, CA 93541.

EURASIAN WEED INFESTATION IN WESTERN MONTANA IN RELATION TO VEGETATION AND DISTURBANCE

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Abstract

Along a vegetational gradient from cool-moist subalpine forests to warm-dry steppe, Eurasian weed infestation was restricted to the low-montane (*Pinus ponderosa*) to dry steppe (*Bouteloua/Stipa*) portion of the gradient for relatively undisturbed vegetation. With intensive disturbance the infestation segment of the gradient was extended through the mid-montane (*Pseudotsuga menziesii*) zone. The subalpine (*Abies lasiocarpa*) zone was essentially weed-free with or without disturbance. In the absence of deep shade, weed infestation was correlated with mean July temperature.

During a survey of exotic weeds in Montana in August 1980, we observed that roadside weeds can invade adjacent native vegetation in significant numbers, but only within a restricted segment of a vegetation gradient (i.e., temperature-precipitation). Moreover, if the native vegetation is disturbed, the range of infestation along the gradient is extended. In this report we document these observations along a transect from cool-moist subalpine forests to warm-dry grasslands in western Montana. Additionally, we explore a few of many possible reasons for such differential weed infestation.

Methods

Along US Highway 12 from Lolo Pass (1700 m; 46°38′N, 114°36′W) to the Waterworks Hills just northeast of Missoula, Montana (1040 m; 46°53′N, 113°59′W) 14 paired roadside/native vegetation plots were surveyed. Plots were 5 m by 50 m (narrower if roadside communities were less than 5 m wide) with the long axis positioned parallel to the roadside. Native vegetation plots were always 5 m distant from the roadside/native vegetation boundary. This distance assured the possibility of weed diaspore dispersal into our plots, but was far enough from the road edge to preclude previous and/or continuous physical disturbance. A vascular plant species list, as complete as possible, was recorded in each plot along with species-specific cover-abundance data (sensu Braun-Blanquet 1964). The habitat type (~plant association) of each native vegetation plot was identified through the dichotomous

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vegetation keys provided by Pfister et al. (1977) for forests, and Mueggler and Stewart (1980) for grasslands.

Eighteen forest vegetation plots that had been clearcut 1–7 years prior to sampling were surveyed as described above. These plots spanned the mid- to high-montane vegetation zones of the region. Habitat types of clearcut plots were identified by inspection of neighboring undisturbed forests of similar slope and aspect when possible, otherwise from the presence or absence of indicator species in the plots themselves. (In no cases were Eurasian weeds found in neighboring undisturbed forests.) Clearcut plots were located in Flathead, Granite, Lincoln, Mineral, and Missoula Counties, Montana.

Indices of similarity (Bray and Curtis 1957) between roadside plots and native vegetation were calculated using (1) species presence, and (2) species coverage. Percent coverage (Daubenmire 1959) was calculated by converting Braun-Blanquet cover-abundance scale data to the appropriate average percent, i.e., *5* = 88%, *4* = 63, *3* = 38, *2* = 15, *1* = 3, ± = 0.5, and *r* = 0.1.

Weed species were divided into two categories for the purpose of this report. (*A*) the first category was introduced Eurasian taxa that are generally considered to be troublesome to human endeavors (Reed 1971, and see lengthy discussions of "weed" in Baker and Stebbins 1965). This category included taxa such as *Bromus japonicus, B. tectorum, Centaurea maculosa, Cirsium arvense, C. vulgare, Filago arvensis, Lactuca serriola, Melilotus alba, M. officinalis, Thlaspi arvense, Verbascum thapsus,* etc. (Forcella and Harvey 1981). Eurasian taxa introduced for forage, etc., widely planted, and not considered weedy in most environments were not included in our weed categories (e.g., *Dactylis glomerata, Phleum pratense, Poa pratensis, Medicago sativa, Trifolium pratense, T. repens.* (*B*) The second weed category included native weed taxa that exhibit weedy behavior following disturbance, but are not prominent components of undisturbed vegetation (e.g., *Chrysopsis villosa, Deschampsia elongata, Epilobium angustifolium, E. paniculatum, Grindelia squarrosa,* and *Rubus parviflorus*).

Species nomenclature follows Hitchcock and Cronquist (1973), vegetation nomenclature is that of Pfister et al. (1977) and Mueggler and Stewart (1980).

In this report we use "infest" to indicate colonization in large numbers, a standard English dictionary definition, and restrict the term colonize to indicate few in number. Infestation was considered to be indicated when European weed coverage was actually 15% or was 10% of total plant cover.

RESULTS AND DISCUSSION

In the subalpine and mid-montane zones (i.e., *Abies lasiocarpa* and *Pseudotsuga menziesii* series of Pfister et al. 1977) alien weeds were

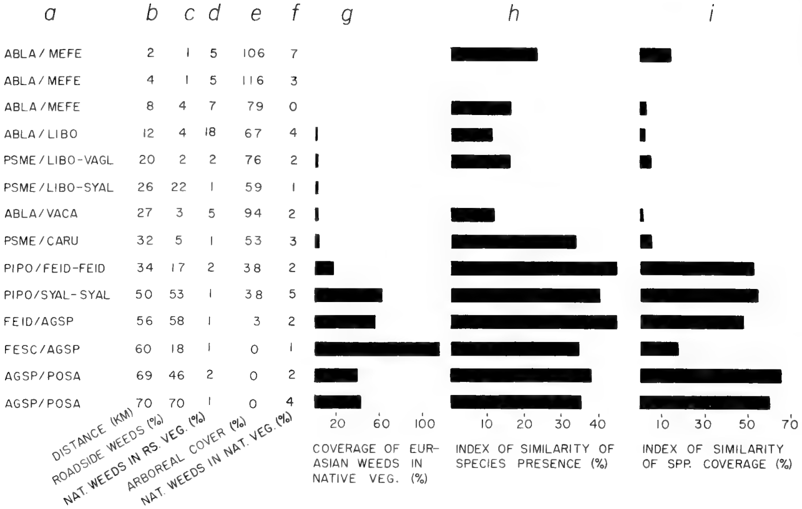

FIG. 1. Relationships of 14 paired roadside/native vegetation plots along a transect from Lolo Pass to Missoula, Montana. Data columns represent: (a) abbreviated habitat type designations (see below), (b) plot distance from Lolo Pass, (c) coverage of alien weeds in roadside plots, (d) coverage of native weeds in roadside plots, (e) coverage of trees in native vegetation plots, (f) coverage of native weeds in native vegetation plots, (g) coverage of alien weeds in native vegetation plots, (h) index of similarity by species-presence between roadside and native vegetation plots, and (i) index of similarity by species-coverage between roadside and native vegetation plots. ABLA, *Abies lasiocarpa*; AGSP, *Agropyron spicatum*; ARUV, *Arctostaphylos uva-ursi*; CAGE, *Carex geyeri*; CARU, *Calamagrostis rubescens*; CLUN, *Clintonia uniflora*; FEID, *Festuca idahoensis*; FESC, *F. scabrella*; LIBO, *Linnaea borealis*; MEFE, *Menziesia ferruginea*; PIEN, *Picea engelmannii*; POSA, *Poa sandbergii*; PSME, *Pseudotsuga menziesii*; PHMA, *Physocarpus malvaceus*; THPL, *Thuja plicata*; TSHE, *Tsuga heterophylla*; VACA, *Vaccinium caespitosum*; VAGL, *V. globulare*; VASC, *V. scoparium*; XETE, *Xerophyllum tenax*: SYAL, *Symphoricarpos alba*.

almost entirely restricted to roadsides; they occasionally colonized, but never infested relatively undisturbed native vegetation (Fig. 1). The exchange of species that did occur between roadside and native vegetation was that of forest plants colonizing roadsides (e.g., *Alnus sinuata, Abies lasiocarpa, Picea engelmannii, Pinus contorta, Senecio triangularis, Symphoricarpos alba,* etc.).

In the low-montane zone (*Pinus ponderosa* series) and extending into the grasslands (*Festuca idahoensis, F. scabrella,* and *Agropyron spicatum* series of Mueggler and Stewart 1980), however, colonization and infestation of native vegetation by roadside Eurasian weeds increased markedly (Fig. 1f, g, h). Indices of similarity between roadsides and adjacent communities often exceeded 50% on a coverage basis (Fig. 1h). Coverage of alien weeds in low-montane and grassland vegetation ranged from about 20 to over 100% (Fig. 1f). Such coverage values suggest that introduced plants can greatly reduce the abundance of plants supplying economically important forage and forest products in low-montane and grassland areas of western Montana. It should be noted, however, that nearly all northern Rocky Mountain vegetation types that are not under intensive cultivation are grazed by livestock to some extent, with grassland and low-montane vegetation receiving more use than mid-montane and subalpine environments (Mueggler and Stewart 1980, Pfister et al. 1977). The results portrayed in Fig. 1 must partially, but not fully, reflect this pattern of land utilization.

In mid-montane forests, intensive disturbance (clearcut logging) enabled introduced weeds to colonize and infest, with absolute coverage up to 60% (Table 1c). Wildlife and livestock movements, forage production and tree regeneration might all be adversely affected by the abundance of alien weeds in these sites (cf. Anderson 1977, Chap. 1). The very lowest habitat types of the *Abies lasiocarpa* series was the upper limit of introduced weed colonization (Table 1). Species such as *Cirsium arvense* and *C. vulgare* were able to infest *A. lasiocarpa*/*Linnaea borealis* habitats, but not cooler and wetter environments even though they were present along proximal logging roads. Native weedy species such as *Anaphalis margaritacea, Epilobium* spp. and *Rubus parviflorus* were prominent in these high elevation sites as well as in warmer and dryer forest sites at lower elevations (Table 1c, d). Perhaps native taxa competitively displace aliens in cool, moist environments.

Two factors that appear likely to control the ability of alien weeds to infest relatively undisturbed vegetation in our study are: (a) quantity of radiation incident upon the herbaceous vegetation layer, and (b) climate. Percent light reaching herbaceous layers of plant communities increases as arboreal canopy cover is reduced (Daubenmire 1968); light intensity is also an important factor in weed plant growth (Harper 1977). The natural reduction in tree coverage along a cool-moist to warm-dry vegetation gradient (Fig. 1, cf. Pfister et al. 1977) may be the prime factor allowing alien weed infestation of native vegetation (Frenkel 1970). Similarly, reduction in canopy cover by clearcutting facilitates weed colonization and infestation in formerly weed-free communities (Table 1, Fig. 1).

Climate may also limit weed infestations (Lindsay 1953, Salisbury 1961). To explore this possibility we pooled, by vegetation zone, all of our weed coverage data for 53 native and 71 roadside communities (from unpublished surveys), and then compared native and roadside coverage means to Weaver's (1979, 1980) climatic summarizations for each vegetation type (Table 2). (No statistical comparisons of weed and climatic data were made because of the inherent variability of

TABLE 1. CHARACTERISTICS OF CLEARCUT FORESTS BY HABITAT TYPES. (a) Number of Eurasian weed species, (b) coverage of Eurasian weeds as percent of total plant coverage, (c) actual percent coverage of Eurasian weeds, (d) total weed coverage, (e) total plant coverage, (f) tree-species coverage. Habitat types arranged along a presumed temperature-precipitation gradient.

Habitat type	a	b	c	d	e	f	Stand age	Stand-county
Abla/Vasc-Vasc	0	0.0	0.0	32.1	67.6	4.1	6	1-Lincoln
Abla/Mefe	0	0.0	0.0	57.5	97.5	1.0	6	4-Lincoln
Abla/Mefe	0	0.0	0.0	6.5	59.1	6.1	6	1-Missoula
Abla/Xete-Vagl	3	0.5	0.3	38.1	64.1	0.0	1	3-Lincoln
Abla/Libo-Vasc	2	0.3	0.2	22.3	58.8	16.5	6	2-Lincoln
Abla/Libo-Libo	8	29.3	19.8	39.9	67.6	0.6	2	1-Flathead
Pien/Libo	7	8.7	5.2	38.9	60.1	0.0	1	2-Flathead
Tshe/Clun	4	17.9	16.1	70.7	90.0	1.5	4	9-Lincoln
Thpl/Clun-Clun	3	23.4	30.5	67.0	130.1	0.5	4	10-Lincoln
Thpl/Clun-Clun	4	6.3	2.0	7.2	32.0	3.8	3	8-Lincoln
Psme/Libo-Syal	7	30.8	27.5	32.6	88.7	3.2	3	1-Granite
Psme/Cage	3	62.3	63.6	64.1	102.1	3.6	7	1-Mineral
Psme/Caru-Caru	7	10.6	7.7	16.8	72.9	1.0	6	6-Lincoln
Psme/Caru-Caru	5	21.5	16.2	32.8	75.2	1.5	4	7-Lincoln
Psme/Caru-Aruv	3	1.8	1.5	9.8	83.1	1.7	6	5-Lincoln
Psme/Caru-Aruv	5	15.8	7.5	11.2	47.4	1.1	5	5-Missoula
Psme/Phma-Phma	5	39.5	42.5	44.0	107.7	6.1	5	6-Missoula
Psme/Fesc	4	26.3	16.5	17.1	62.7	0.6	4	4-Mineral

both data sets.) The marked increase in alien weed coverage in native vegetation of *P. ponderosa* and grassland series is most closely linked to the number of months with one or fewer frosts; subalpine and mid-montane forests have no months without frosts, whereas warmer and dryer environments have three months with one or no frosts. Length of drought is also associated with alien weed abundance in native vegetation (Table 2). Along roadsides and in clearcut forests, where introduced weed coverage is relatively high through all but the coolest and wettest vegetation types, mean July temperature (and perhaps duration of drought) is most closely associated with weed abundance (Table 2). Lindsay (1953) has previously shown that July temperature may play an important role in limiting Eurasian weed distributions and abundance in north-central North America.

There are a number of possible explanations for the lack of alien weeds in western Montana's subalpine zone, and their relative abundance on mid-montane slopes and lower environments. Seven explanations are listed below; they are not mutually exclusive, nor are any supported by conclusive evidence.

(1) Native weeds are better adapted to local subalpine environments than are alien weeds. Physiological limitations as well as competitive constraints may exclude aliens from high-montane sites.

(2) The majority of alien weeds in North America are of temperate

Table 2. Comparison of Climatic Measurements in Six Vegetation Zones in Western Montana (from Weaver 1979, 1980) and the Absolute Coverage of Introduced Weeds in Roadside and Native Vegetation in Those Zones. Vegetation zones are ordered along a precipitation gradient from wet (left) to dry (right). Abla, *Abies lasiocarpa*; Psme, *Pseudotsuga menziesii*; Pipo, *Pinus ponderosa*; Fesc, *Festuca scabrella*; Agsp, *Agropyron spicatum*; and Bogr, *Bouteloua gracilis/Stipa comata*.

	Vegetation zone					
Measurement	Abla	Psme	Pipo	Fesc	Agsp	Bogr
Mean July Temp. (°C)	14	17	20	17	20	21
Mean Jan. Temp. (°C)	−8	−8	−3	−6	−7	−8
Mean annual precipitation (cm)	82	58	55	43	38	35
Number of months with 1 or fewer frosts	0	0	3	3	3	3
Drought period (months)	0	0.3	1.7	2.0	1.8	2.0
Percent coverage of introduced weeds in roadside vegetation.	5.4	20.3	43.9	46.8	30.8	28.0
Mean ± standard deviation	±8.2	±16.0	±19.3	±24.4	±19.7	±23.2
(sample size)	(8)	(20)	(13)	(5)	(9)	(16)
Percent coverage of introduced weeds in native vegetation.	0.3	0.5	24.8	62.8	21.9	3.3
Mean ± standard deviation	±0.5	±0.9	±25.5	±36.2	±19.2	±5.6
(sample size)	(7)	(14)	(4)	(4)	(6)	(18)

or subtropical Eurasian origin. The relatively mild environments (i.e., long frost-free periods, high July temperatures; Table 2) to which they are restricted in western Montana may reflect the habitats whence they originated (Moore and Perry 1970, Mulligan 1965, Salisbury 1961). Unfortunately, weed plants originating in one climate are often much better adapted to quite different climates in foreign regions (Moore and Perry 1970, p. 73). Moreover, it is often difficult just to determine which country or region a specific weed is native to, let alone its exact native habitat (Mulligan 1965).

(3) Alien weeds that have the potential to infest subalpine zones are selected against and/or genetically changed during transcontinental migrations to the northern Rocky Mountains from their point(s) of introduction. Lindsay (1953) claimed *Hieracium aurantiacum* to be of a European alpine origin. Thus it might be expected to possess the ability to invade disturbed alpine and subalpine sites. However, this plant has migrated to the northern Rocky Mountain region (where it is currently spreading; Forcella and Harvey 1981), and neither here nor in the northeastern USA, where it is common, does the species infest subalpine environments. Rather, *H. aurantiacum* thrives in low-elevation roadsides and pastures where it is often considered noxious.

(4) Species richness is normally lower in subalpine environments than at lower elevations (Whittaker 1965). Therefore the pool of taxa

that could behave as weeds is smaller in subalpine vegetation than elsewhere. The low number of potential weeds physiologically capable of infesting subalpine environments will reduce the probability of such weeds successfully migrating to foreign subalpine sites.

(5) Subalpine environments are analogous to small islands resting upon a vast sea of low elevation landscapes. The probability that alien weeds tolerant of subalpine conditions will reach such limited sites is low (cf. MacArthur and Wilson 1967).

(6) Many weeds may have evolved in response to land use by humans (Anderson 1952, Stebbins 1965). Throughout the world land use in the subalpine has been relatively minor in comparison to lower elevations (Espenshade and Morrison 1974). Thus not only is the landscape available for rapid weed colonization extremely limited in the subalpine zone but the selection pressure for weed behavior is reduced as well.

(7) Eurasian weeds may well occur in subalpine environments of the northern Rocky Mountains, but they are not recorded as alien taxa. The most conspicuous upper montane weed of the northern Rocky Mountains is *Epilobium angustifolium,* a circumboreal species. Despite differing polyploid levels, European and American material of *E. angustifolium* is extremely similar morphologically (Salisbury 1961). Possibly, Eurasian *Epilobium* was introduced into North America and subsequently proliferated without being recognized as Eurasian.

CONCLUSIONS

As a group, Eurasian weeds seem unable to tolerate the cool, moist conditions of subalpine environments, whether the site is shaded or light-saturated. In the mid-montane zone, temperature and moisture conditions seem adequate for introduced weed infestations, but the shade of arboreal canopies apparently preclude effective colonization by these species in undisturbed sites. The increase in light intensity within *Pinus ponderosa* vegetation allows significant Eurasian weed infestation, and this continues into light-saturated grassland communities. Decrease in alien weed coverage in very warm, dry grassland (*Bouteloua/Stipa* series; Table 2) is likely related to the general lack of plant coverage and harshness of this zone.

Because land management is becoming increasingly intense and sophisticated, the importance of predicting differential weed infestation of native and disturbed vegetation from existing and future roads (as well as other developments) will increase accordingly. This report suggests that in western Montana primary interest in regard to introduced-weed control be aimed at the *Pinus ponderosa* and grassland vegetation series for relatively undisturbed vegetation. For highly disturbed vegetation, weed control interests need to be concerned with all vegetation types except the *Abies lasiocarpa* series.

Acknowledgments

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CHEMOSYSTEMATIC AFFINITIES OF A CALIFORNIA POPULATION OF ABIES LASIOCARPA

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ABSTRACT

A California population of *Abies lasiocarpa* has volatile leaf oil composition similar to an Oregon Cascade population. Both are distinct from a Colorado population that contains greater percentages of santene, *alpha*-pinene and camphene and smaller relative proportions of *beta*-phellandrene and limonene.

Subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., is a western cordilleran species of major importance in high elevation forests (Fowells 1965). In the Rocky Mountains it is abundant along with *Picea engelmannii* Parry ex Engelm. and *Pinus contorta* Dougl. ex Loud. In the Cascade Range its associates are *Abies amabilis* (Dougl.) Forb. and *Tsuga mertensiana* (Bong.) Carr. (Franklin and Dyrness 1973, Liu 1971). The range of the species in the Cascades is more or less continuous southward to 44°N except for the Columbia River gap. Three disjunct populations occur at lower latitudes in Oregon and California (Sawyer et al. 1970, Sawyer and Cope 1982). These populations grow in the Klamath Mountains, a region that is geologically (Oakeshott 1971) and floristically (Whittaker 1961) distinct from the volcanic Cascades of Oregon and northern California. The southernmost California population is separated from the Cascade trees by some 180 km.

Subalpine fir shows considerable geographic variation morphologically and chemically, especially in volatile oil composition (Hunt and von Rudloff 1974, 1979; Zavarin et al. 1970). Analysis of terpenes of leaves and cortex (Hunt and von Rudloff 1974, 1979; von Rudloff 1975, Zavarin and Snajberk 1972, Zavarin et al. 1971) also showed that *Abies lasiocarpa* introgresses with *Abies balsamea* (L.) Miller in Canada. The taxonomic conclusions vary. Boivin (1959) proposed varietal status for *A. lasiocarpa,* and Hunt and von Rudloff (1979) suggested the recognition of three species, *A. balsamea, A. bifolia* Murr., and *A. lasiocarpa.* Comparison of Klamath Mountains populations with those of the Oregon Cascades and Rocky Mountains adds information by describing subalpine fir at its southwestern range limit.

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TABLE 1. PERCENT OF TOTAL LEAF TERPENE COMPOSITION OF THE MEANS AND RANGES OF FOUR *Abies lasiocarpa* POPULATIONS. Terpenes listed in order of elution on SE-30 column. Albertan population values listed from Hunt and von Rudloff (1974). Values listed across from suspected major component of each group where terpenes did not sufficiently separate. Albertan means grouped where necessary. + = terpene present in amounts less than 0.1%. – = terpene not detectable.] = grouped. * = may not be present in Colorado, Oregon, and California samples.

Peak number	Terpene or terpene group	Colorado		Alberta			Oregon		California	
		Range	Mean	Range	Mean	Groups	Range	Mean	Range	Mean
1.	Santene	0.8–3.0	2.2	1.8–3.9	3.1		—	—	—	—
2.	Tricyclene			0.6–1.5	1.0	5.8				
3.	*alpha*-Pinene	3.6–7.9	5.7	3.7–6.4	4.8		1.4–3.3	2.5	1.1–3.0	2.1
4.	Camphene	11.3–24.5	17.0	7.3–16.2	12.5		+–+	+	+–0.4	0.2
5.	*beta*-Pinene	7.1–27.7	19.4	8.5–22.8	12.0	13.1	12.2–35.5	19.1	11.6–19.4	15.6
6.	Myrcene*			0.8–1.5	1.1					
7.	*delta*-3-Carene	—	—	+–0.3	+		+–0.2	0.2	0.2–1.3	0.9
8.	Limonene			5.1–20.2	11.2	32.9				
9.	*beta*-Phellandrene	10.2–43.0	26.8	10.0–29.0	20.9		53.1–75.4	63.0	56.9–67.9	64.0
10.	*trans*-Ocimene			0.4–1.8	0.7					
11.	Terpinolene	0.3–2.1	1.1	0.6–1.1	0.9		+–0.4	0.2	+–2.7	0.8
12.	Borneol*			0.1–0.7	0.4	0.7				
13.	Terpinen-4-ol*	0.2–1.2	0.4	+–0.2	0.1		––+	+	+–2.0	0.5
14.	*alpha*-Terpineol*			0.1–0.3	0.2					
15.	Piperitone	—	—	1.2–4.8	3.2		0.3–5.0	2.4	2.5–8.0	4.8
16.	Bornyl acetate	14.2–50.0	27.4	13.0–31.6	22.8	24.9	2.1–15.4	9.6	3.5–16.3	9.9
17.	Methyl thymol*			0.3–3.7	1.2					
18.	Thymol*			0.2–1.9	0.9					
19.	Unidentified	—	—				––+	+	––0.7	0.3
20.	Unidentified (C15)]	+–0.6	0.3				1.8–10.2	5.1	+–3.6	1.7
21.	Unidentified (C15)]									

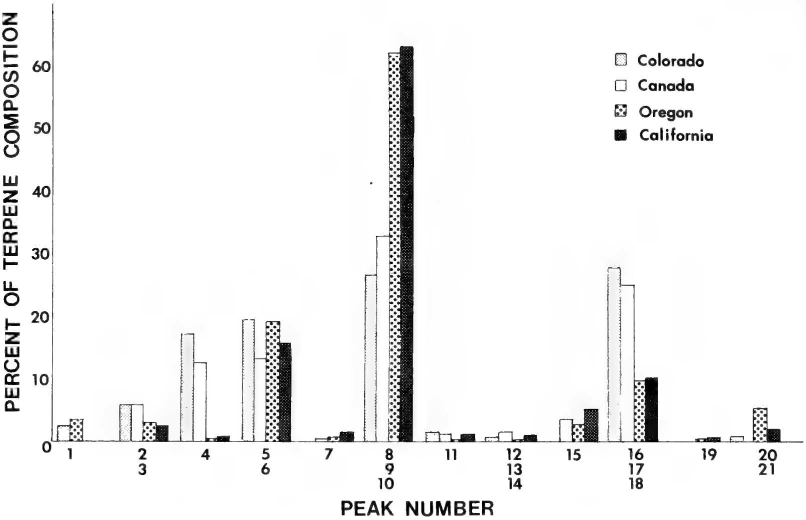

FIG. 1. Percent of total terpene composition in order of elution of each terpene or terpene group from SE-30 column.

METHODS

Samples containing leaves only were taken in September and early October 1977 from: 9 trees at 2050 m elevation from the edges of Little Duck Lake, Siskiyou County, California (123°W, 41°30′N); 5 trees at 2150 m on rocky slopes surrounding O'Dell Butte Lookout station, Klamath County, Oregon (122°W, 43°30′N); and 5 trees at 3400 m in moist meadow edges, Park County, Colorado (106°W, 39°N). Procedures for collection, transportation, storage and preparation for monoterpene analysis of leaf oil using gas-liquid chromatography followed Hunt and von Rudloff (1974).

After steam distillation, quantitative runs were made on two CLC columns (3% SE-30, 60-80 mesh Gaschrom Q, inside diameter 2.5 mm, length of 300 mm; 2% Carbowaxx 20M and 1% OV17, 80-100 mesh Chromasorb G-H.P. with inside diameter 2.5 mm, length of 300 mm).

Relative percentages of the monoterpenes were determined by integration of peak areas. It was necessary in some cases to calculate percentages for groups of terpenes because not all terpenes were separated sufficiently for individual calculation of terpene amount. Error in peak area calculation was estimated to vary from 1% (major peak representing at least 50% of the sample) to 30% (minor peaks representing less than 2% of the sample).

TABLE 2. RANGES OF TWO TERPENES AND TWO TERPENE GROUPS SEPARATING ALBERTA AND COLORADO POPULATIONS OF *Abies lasiocarpa* FROM CALIFORNIA AND OREGON POPULATIONS.

Peak no.	Terpene or terpene group	Oregon and California	Alberta and Colorado
1.	Santene	0	0.8–3.9
2.3.	*alpha*-Pinene	1.1–3.3*	3.6–7.9
4.	Camphene	trace–0.4	7.3–24.5
8.9.10.	*beta*-Phellandrene	53.1–75.4	10.0–51.5

* Hunt and von Rudloff's (1979) values are higher (3.5–4.5) for their coastal sample, thus overlapping with Rocky Mountain *alpha*-Pinene data.

RESULTS AND DISCUSSION

Table 1 lists the range and mean for each terpene in order of its elution. Hunt and von Rudloff's (1974) data from Alberta are included for comparison. Terpenes that did not permit individual calculation of percentages are tricyclene and *alpha*-pinene (Peaks 2 and 3), *beta*-pinene and myrcene (Peaks 5 and 6), limonene, *beta*-phellandrene and *trans*-ocimene (Peaks 8, 9 and 10), bornyl acetate, methyl thymol and thymol (Peaks 16, 17 and 18) and the sesquiterpenes (Peaks 20 and 21). These peaks are designated by their suspected major components, *alpha*-pinene, *beta*-pinene, *beta*-phellandrene and bornyl acetate, respectively. The percentages of these groups are listed (Table 1) and graphed (Fig. 1) by group. Hunt and von Rudloff's (1974) data are grouped where appropriate by adding percentages of the individual terpenes involved.

The relative amounts of monoterpenes of the Klamath Region population of California are similar to those of the Oregon Cascades. The *beta*-phellandrene group, santene, camphene, the *alpha*-pinene group and the bornyl acetate group in the Klamath and Cascade populations are similar in percent of the total terpene composition (Fig. 1). There are substantial monoterpene differences between these populations and the Rocky Mountain populations of both this work and Hunt and von Rudloff's (1974, 1979) studies.

The distinctive character of the volatile oil composition of Rocky Mountain populations in comparison to Klamath/Cascade populations is shown in Table 2. The western populations have no detectable santene, an *alpha*-pinene group of less than 3.5% (contrasting with Hunt and von Rudloff's (1979) *alpha*-pinene range of 3.5–4.5%), a trace of camphene and a *beta*-phellandrene group of greater than 50% of total terpene composition. The Rocky Mountain populations contain evidence of the presence of santene, *alpha*-pinene in amounts greater than 3.5%, camphene greater than 7%, and the *beta*-phellandrene group less than 50% of the total terpene composition. These results argue for Hunt and von Rudloff's (1979) recognition of *Abies bifolia* as specifically distinct from *Abies lasiocarpa*.

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A NEW VARIETY OF PERITYLE STAUROPHYLLA (ASTERACEAE) FROM NEW MEXICO

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Abstract

Perityle staurophylla (Barneby) Shinners var. **homoflora** Todsen is described from the San Andres Mountains of New Mexico.

Barneby (1957) described *Laphamia staurophylla* from La Luz Canyon on the west slope of the Sacramento Mountains in Otero County, New Mexico. Shinners (1959) transferred the species to *Perityle* without specimen citation. Niles (1970) further discussed the proper generic placement of the species and cited another location in Dog Canyon of the Sacramento Mountains. After our search program to define the distribution of the species had begun, Powell (1973) published a revision of *Perityle,* section *Laphamia,* in which he cited four of our new locations. Figure 1 shows the locations of the presently known populations, in the Sacramento Mountains of Otero County from the type locality on the north to Grapevine Canyon on the south; in the San Andres Mountains from Johnson Park Canyon in Socorro County on the north through Sierra County to Quartzite Mountain and Black Mountain in Dona Ana County on the south; in a few canyons at the high southern end of the Sierra Caballo (Sierra County); and in the center of the small Fra Cristobal range (Sierra County). Locations are disjunct because the required stable protected cliff habitat, on limestone or granite underlying limestone, is not continuous.

Perityle staurophylla is variable in leaf morphology [*Spellenberg and Todsen 2641* (NMC) from Goat Mountain in the San Andres Mountains shows strongly contrasting forms within one dm of each other], in the number of awns in the pappus, and in the number of ray flowers in the head. An extreme example of the latter variation occurs at the northern end of the San Andres Mountains. There a fault runs southeast along the west end of Rhodes Canyon and then east along the ridge of Hardscrabble Mountain dividing the species into two phases. Plants east and north of the fault have no ray flowers, whereas those west and south of the fault and those outside of the San Andres have ray flowers. The rayless phase differs sufficiently from the type to be considered a separate variety, identifiable by the following key.

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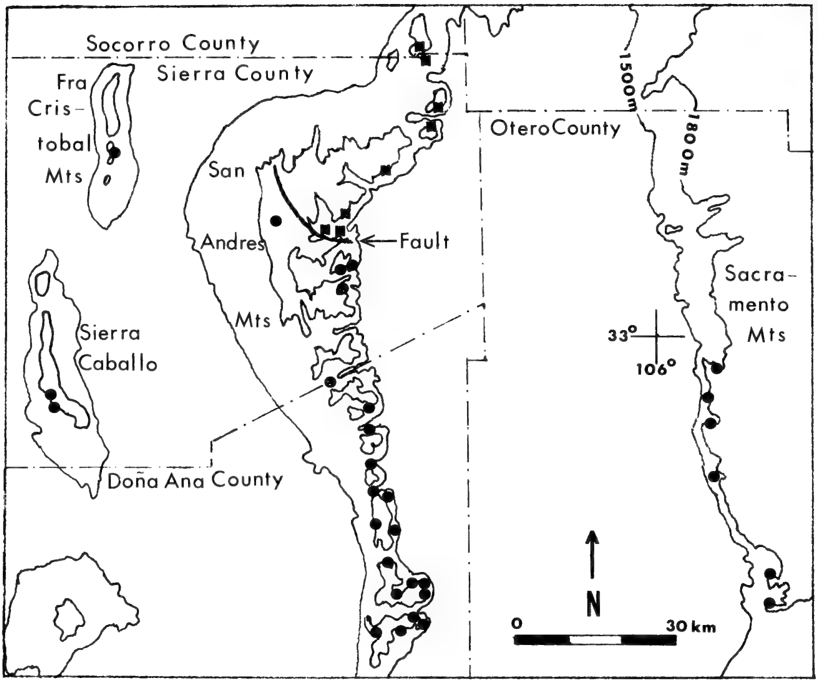

FIG. 1. Distribution of *Peritylе staurophylla* in south-central New Mexico. Closed circles show known locations of var. *staurophylla* and closed squares those of var. *homoflora*.

Ray flowers present; mature achenes dark brown to black; plants elsewhere than the northern San Andres Mountains .... var. *staurophylla*

Ray flowers absent; mature achenes silvery; plants from Rhodes Canyon and northward in the San Andres Mountains .... var. *homoflora*

Perityle staurophylla (Barneby) Shinners var. *staurophylla,* Leafl. W. Bot. 8:168–170. 1957.—TYPE: USA, NM, Otero Co., Sacramento Mts., La Luz Canyon below High Rolls, crevices of dry n.-facing limestone cliff, 6300 ft, 2 Sep 1956, *Barneby 12889* (Holotype: CAS 405624!; isotypes: GH! K! NY! RSA! UNM 2286! US 2235449!).

Perityle staurophylla var. **homoflora** Todsen, var. nov.

Similis varietatis typici sed flores radiales absens vice praesens et achenia argentea vice nigra. $n = 17$.

TYPE: USA, NM, Sierra Co., San Andres Mts., Rhodes Canyon 17 km w. of Rhodes Canyon Range Center in S13 R3E T13S. Locally common on protected limestone bluffs, 1650 m, 7 Aug 1971, *R. Spellenberg and T. K. Todsen 2637* (Holotype NY; isotypes NMC, SRSC).

PARATYPES: USA, NM, Sierra Co., Rhodes Canyon 14 km w. of Rhodes Canyon Range Center in S17 R4E T13S, *Spellenberg and Todsen 2537* (NMC, SRSC); narrow canyon on se. side of Skillet Knob in S4 R4E T12S, *Todsen 2262* (NMC); se. slope of Salinas Pk. in S7 R5E T12S, *Todsen 2289* (NMC); n. side of Sheep Mt. in S18 R6E T11S, *Todsen 2286* (NMC); cliffs of Capitol Pk. in S7 R6E T11S, *Todsen* (recorded only); s. side of Johnson Park Canyon in S5 R5E T10S, *Todsen 2287* (NMC). Socorro Co., side canyon n. from Johnson Park Canyon in S31 R5E T9S, *Todsen 810921* (NMC).

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VEGETATION OF THE ALABAMA HILLS REGION, INYO COUNTY, CALIFORNIA

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ABSTRACT

All woody and succulent vegetation in the arid Alabama Hills region was sampled, using 24 0.07 ha plots regularly placed over an area of 80 km^2. Density and canopy volume were measured and the data treated by polar ordination. Intensity of grazing, geologic substrate, and topographic roughness were environmental features that correlated with local variation in the regional vegetation type. Overall, the vegetation is transitional between Great Basin sagebrush steppe and Mojave Desert creosote bush scrub. It is similar to the *Grayia-Lycium* community that has been described for (and thought to be restricted to) southern Nevada by Beatley (1975), except that *Atriplex polycarpa, Eriogonum fasciculatum* subsp. *polifolium,* and *Haplopappus cooperi* are additional codominants. The senior author anticipates repeated sampling on these permanently located plots every 5 years.

The Great Basin area of California has received so little phytosociological attention that it has been called a "forgotten ecological province" (Young et al. 1977); yet, it covers about 2% of the state's area. Major communities include sagebrush scrub or steppe, shadscale scrub, and blackbrush scrub. The southern portion of this province is particularly complex where it abuts the Mojave Desert (Randall 1972, Vasek and Barbour 1977, Thorne et al. 1981, Taylor, unpub. BLM reports). It was our objective to begin a long-term study of vegetation dynamics in this southern region. This paper presents only initial data on the range of community variation, which may be due to such factors as grazing, geologic substrate, slope aspect, and topographic or soil surface roughness.

METHODS

Study area. The area selected for sampling includes all of the Alabama Hills and part of a bajada just to the west, altogether covering an area of about 30 sections (80 km^2). The Alabama Hills extend about 15 km along a southeast-to-northwest axis that centers on 36°37′N and 118°05′W, only 2–3 km west of Lone Pine, Inyo County. They rise from a basal elevation of 1160 m to peaks of 1700 m and are of Jurassic age. The westerly $^4/_5$ is granitic and the easterly $^1/_5$ is metavolcanic.

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Sampling on the adjacent bajada to the west centered on the 1560 m contour. The bajada is composed of Pleistocene and Recent granitic alluvium from the east flank of the Sierra Nevada Mountains. Soils tend to be coarse-textured entisols, inceptisols, or aridisols; Alabama Hills sites in addition may be strewn with large boulders on the surface.

The nearest weather station is at Independence, 26 km north of Lone Pine at an elevation of 1200 m (Anonymous 1981). Mean annual precipitation is 138 mm, 70% of which falls during the fall and early winter (October through February). Mean temperatures are: January, 6°C; July, 27°C; annual, 16°C. There are more than 170 frost-free days, and temperatures below −10°C are rare. Maximum summer temperatures are rarely above 42°C.

Sampling procedures. A total of 29 potential sampling locations were established at the intersections of section lines, thus placing them systematically 1 mile (1.6 km) apart in a grid pattern. In this paper, we summarize data from 24 of those locations, excluding five because of highly atypical situations: sites of road and residence construction, seeps and springs, altered by type conversion activities. Each location was a circle 30.5 m in diameter (0.07 ha in area). Within each circle, all woody species and cacti were counted, and canopy dimensions (length, width, height) of every individual were measured. Canopy volumes were later calculated, using a circular cone as a model (length and width were averaged to estimate the circle's diameter). Although a circular cone does not approximate the shape of all canopies, we feel justified, at this initial stage of the study, to use it uniformly for all species. Presence of some herbaceous perennials (e.g., *Stipa*) was noted but not quantified; annuals and perennial seedlings were ignored due to variation in time of sampling, which extended throughout 1980. The sites are permanently marked so the senior author can repeat the measurements every 5 years.

Notes were made on the intensity of cattle grazing, based on a knowledge of land use history and field evidence (but see Results and Discussion section), soil surface roughness (extent of boulders, topographic diversity), presence of lichens and moss, soil surface texture, slope angle and aspect, presence of daily or seasonal shade, geologic substrate (granitic or metavolcanic), extent of rodent activity, and plant phenology. Plant nomenclature follows Munz and Keck (1959). A more complete species list and quantification of field data can be obtained from the senior author.

Data analyses. Summary tables were prepared for each site, listing absolute density, relative density, absolute canopy volume, and relative canopy volume for each species. We believe that canopy volume can convey a picture of overstory dominance superior to that from percent canopy cover.

Polar ordination of the sites was performed by a computer program (ORDIFLEX release B, program CEP-25B, in the Cornell Ecology Programs series) provided by H. G. Gauch, Jr., of Cornell University. The program calculated indices of similarity (IS) for every pair of sites, weighting species presence by absolute density with Motyka's modification of Sorensen's formula (Mueller-Dombois and Ellenberg 1974):

$$IS = \frac{(2)(M_{min})}{M_{site\ 1} + M_{site\ 2}}$$

M is absolute density for any species; M_{min} is the minimum density of every species common in both sites, summed for all species, $M_{site\ 1}$ is the sum of all species densities in site 1; $M_{site\ 2}$ is the sum of all species densities in site 2. Rare species, occurring on fewer than three sites, were omitted from the analysis. The program then used the IS values to calculate an index of difference (ID) between every pair of sites, where: $ID = 1.0 - IS$. A two-dimensional polar ordination was performed on the matrix of ID values, using automatic endpoint selection for both axes.

We recognize that polar ordination is not universally considered to be the best vegetation analysis technique (see for example, Whittaker 1978). However, it is a simple, straightforward means of illustrating stand relationships; its biases and distortions are not critical at this initial stage of vegetation description.

RESULTS AND DISCUSSION

General vegetation. Although the Alabama Hills region has been mapped as a sagebrush scrub or steppe by both Küchler (1977) and Matyas and Parker (1979), the actual vegetation is something quite different. According to Küchler (1977) and the Regional Ecology Group (1981), California sagebrush vegetation is moderately open (about 15% cover), dominated by evergreen shrubs up to 1 m tall (in particular by *Artemisia tridentata*), with an admixture of deciduous shrubs and below them a seasonal 5–15% cover by graminoids, forbs, and winter annuals. Cacti are uncommon.

Alabama Hills vegetation, by contrast, is dominated by a collection of partly or completely drought-deciduous sub-shrubs less than 0.5 m high. *Artemisia tridentata* was found on only five of the 24 sites. There were four species of cactus, and these occurred in 15 of the 24 sites. Altogether, 43 woody and succulent taxa were recorded, a higher species richness than one would expect from sagebrush scrub or steppe. Table 1 summarizes the eight leading dominants, based on relative canopy volume averaged over all 24 sites. Although *Atriplex polycarpa* and *A. confertifolia* have the highest values in that list, they are not dramatically larger than the next several species on the list; thus one could conclude that this regional community exhibits dominance by at least a handful of species with 60–70% constancy (presence).

TABLE 1. LEADING DOMINANTS (BASED ON PERCENT RELATIVE CANOPY VOLUME) AVERAGED FOR ALL 24 STANDS. Species are listed in descending order, down to an arbitrary limit of 6% relative canopy volume. For comparative purposes, the *Grayia-Lycium* transitional community of southern Nevada (Rickard and Beatley 1965) has been summarized in the right-hand column; those data are in percent relative cover.

Alabama Hills			*Grayia-Lycium*	
Species	Volume	Stands present	Cover	Species
Atriplex polycarpa	13	15	—	
Atriplex confertifolia	12	15	5	*Atriplex confertifolia*
Ephedra nevadensis	9	19	4	*Ephedra nevadensis*
Eriogonum fasciculatum	9	15	—	
Grayia spinosa	8	17	39	*Grayia spinosa*
Lycium andersonii	7	18	19	*Lycium andersonii*
Haplopappus cooperi	6	11	—	
Hymenoclea salsola	6	19	2	*Hymenoclea salsola*
Others, to match *Grayia-Lycium* associates:				
Eurotia lanata	1	13	11	*Eurotia lanata*
Atriplex canescens	<1	2	4	*Atriplex canescens*
Tetradymia axillaris	1	2	4	*Tetradymia axillaris*
	—	—	3	*Acamptopappus shockleyi*
Coleogyne ramosissima	<1	2	3	*Coleogyne ramosissima*
Artemisia spinescens	1	14	3	*Artemisia spinescens*

If this regional community does not fit well into the sagebrush scrub category, neither does it fit well into other Great Basin Californian types, such as blackbrush scrub, shadscale scrub, or saltbush scrub, as recently reviewed by Vasek and Barbour (1977). Blackbrush (*Coleogyne ramosissima*), shadscale (*Atriplex confertifolia*), and saltbush or allscale (*Atriplex polycarpa*) are all in the Alabama Hills (Table 1), but none shows the dominance it characteristically exhibits in its own type. Shadscale stands sampled by Billings (1949) in southern Nevada exhibited 44% average relative canopy cover by *Atriplex confertifolia* (range of 11–98%); this contrasts with only 12% relative canopy volume of shadscale in our stands. Furthermore, the second most abundant shrub in the shadscale vegetation sampled by Billings was *Sarcobatus baileyi* (28% relative cover), which was absent from the Alabama Hills. The third most abundant shadscale scrub species was *Artemisia spinescens* (17% relative cover), which was much less important in the Alabama Hills (1% relative canopy volume, Table 1).

Saltbush scrub in California (Vasek and Barbour 1977) typically not only contains *Atriplex polycarpa* and *A. confertifolia,* present in the Alabama Hills, but usually also the more narrowly halophytic succulents *Allenrolfea occidentalis, Nitrophila occidentalis, Salicornia subterminalis, Suaeda* species, and *Sarcobatus vermiculatus,* all of which are absent from Alabama Hills study sites. Saltbush scrub is usually an edaphically defined community, on saline soils, and the mere presence of *Atriplex* species in the Alabama Hills is not sufficient to place our sites within that community.

Even though many species are shared with the blackbrush community (e.g., *Artemisia tridentata, Atriplex confertifolia, Dalea fremontii, Ephedra nevadensis, Eriogonum fasciculatum, Gutierrezia microcephala*; see Cronquist et al. 1972), *Coleogyne* here had less than 1% relative canopy volume, far from the overwhelming dominant it usually is in a typical blackbrush community. Neither does this community closely resemble the mixed desert scrub described by Thorne et al. (1981) and Randall (1972) for the eastern Mojave Desert of California. That mixed community shares only $^1/_3$ of its genera with our vegetation; it appears to be floristically much richer, it lacks clear dominants, and it contains a greater diversity of life forms, in comparison with our vegetation. A few of our most bouldery sites (C, O, and Q are described in the Ordination section of this paper) do resemble this mixed scrub in habitat and composition, but the majority of our sites differ from it.

In our opinion, the regional Alabama Hills vegetation can best be described as a variant of the *Grayia spinosa-Lycium andersonii* community described in southern Nevada by Beatley (1975) and Rickard and Beatley (1965). They referred to this community as transitional between Great Basin sagebrush scrub and Mojave Desert creosote bush scrub, lying on non-saline, gentle slopes at middle elevations of 1200–1500 m. Species richness exceeds that of shadscale and sagebrush communities, but is less than that of creosote bush scrub. Beatley (1975) wrote that the *Grayia-Lycium* community was restricted to southern Nevada.

Five of the eight leading dominants of Alabama Hills vegetation are typical associates or dominants of the *Grayia-Lycium* community (Table 1). Of the 11 species Rickard and Beatley (1965) reported for that community, 10 were found in the Alabama Hills, although their relative importances were not always comparable. Specifically, Alabama Hills vegetation showed less dominance by *Grayia, Lycium,* and *Eurotia,* and added three new elements: *Atriplex polycarpa, Haplopappus cooperi,* and *Eriogonum fasciculatum* subsp. *polifolium,* the first two being restricted in range to California.

Ordination. The polar ordination resulted in a wide dispersion of stands in two-dimensional space (Fig. 1), with little indication of clusters of stands. This may indicate that there are quite a few discrete habitats, each supporting its own community variant, and that the intensity of sampling was not sufficient to replicate these. Our limited environmental data, however, suggest that much of the horizontal and vertical spread can be correlated with geologic substrate and degree of present grazing intensity. Lightly grazed stands on granitic material

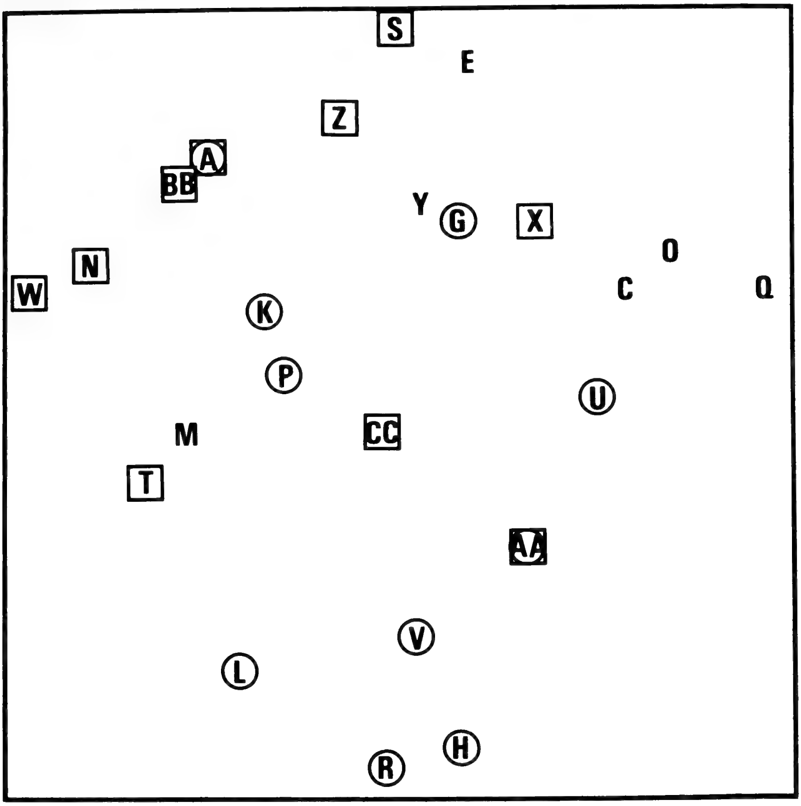

FIG. 1. Polar ordination of 24 stands. Stand names are coded by letters. Boxed stands are on metavolcanics, circled stands are moderately to heavily grazed, open stands are on granitics and are lightly grazed or ungrazed.

are largely in the upper right quadrant; heavily grazed stands are largely in the lower half of the figure; stands on metavolcanic material are largely in the upper left quadrant.

Topographic roughness may be secondarily important in determining community composition. For example, sites C, O, and Q on the right side of the figure are all on bouldery, uneven terrain that experiences shade at some time of the day or year. Mosses and lichens were common. Vascular dominants in those three sites were somewhat different from those shown in Table 1 for all sites: *Haplopappus cooperi, Ephedra viridis, Chrysothamnus teretifolius, Senecio douglasii,* and *Stephanomeria pauciflora*. It is possible that a careful consideration of other site features would also show some correlation with community variation, but we believe that the number of stands is currently too few to warrant such an analysis.

TABLE 2. AVERAGE DENSITY AND CANOPY VOLUME FOR SPECIES ON 10 "GRAZED" AND 14 "UNGRAZED" PLOTS. Relative values are not shown. Only species recorded on three or more grazed and three or more ungrazed plots are included. All volumes are approximated by a cone. One asterisk = statistically different at the 0.05 level, two asterisks = 0.01 level, three asterisks = 0.001 level, t-test.

	Density (plants/700 m^2)		Volume (dm^3/700 m^2)	
Species	Grazed	Ungrazed	Grazed	Ungrazed
Ambrosia dumosa	10*	113*	76*	644*
Artemisia spinescens	117	76	216	146
Atriplex confertifolia	132	164	1383	1532
Atriplex polycarpa	34	30	2873	1798
Chrysothamnus teretifolius	19	7	652	56
Ephedra nevadensis	52***	5***	3245**	507**
Eriogonum fasciculatum	80	114	434	1131
Eurotia lanata	37	33	160	162
Grayia spinosa	76	27	1963	1383
Gutierrezia microcephala	42	36	185	90
Haplopappus cooperi	275**	21**	1764**	277**
Hymenoclea salsola	115**	35**	1450	776
Lepidium fremontii	33	22	252	87
Lycium andersonii	30	11	1890	1182
Lycium cooperi	1	4	101	1439
Machaeranthera (Xylorhiza) tortifolia	21	54	50	87
Stephanomeria pauciflora	33**	98**	174*	857*
Total	1108	849	16,867	12,152

Effect of grazing. Our ordination indicated that grazing intensity by livestock is correlated with major stand-to-stand variation. While we cannot here demonstrate a causative relationship, vegetation in the Great Basin province in general has undergone much change over the past century due to over-grazing and the introduction of exotic, aggressive plant species (Young et al. 1972, 1975). Consequently, we analyzed species preference for "grazed" (heavily to moderately grazed, based on subjective criteria) and "ungrazed" (lightly grazed to ungrazed) plots in Table 2. Our 24 plots were nearly evenly divided between these two categories, 10 heavily to moderately grazed and 14 lightly grazed to ungrazed.

Of 17 taxa that occurred in at least six plots (three grazed, three ungrazed), only five showed statistically significant differences in absolute density and/or absolute canopy volume. Grazing appeared to depress *Ambrosia dumosa* 8–11-fold and *Stephanomeria pauciflora* 3–5-fold. Grazing appeared to stimulate *Ephedra nevadensis* 6–10-fold, *Haplopappus cooperi* 6–13-fold, and *Hymenoclea salsola* 2–3-fold. The relative canopy volume of *Lycium cooperi* was depressed 8-fold by grazing (0.05 level, not shown in Table 2). All other differences for absolute or relative values were statistically insignificant at the 0.05 confidence level. Surprisingly, total density and canopy volume were greater on grazed sites.

We must emphasis that the above differences have to be carefully interpreted, and their relationship to grazing is not absolutely clear. The history of grazing in the area during this century is complex, and grazing intensity may certainly have varied from site to site over time. Some sites may have been heavily grazed in the past to such an extent that species composition has not yet recovered, despite absence of grazing in recent decades. Some sites may be lightly grazed because of unique substrate or topographical features which make them inaccessible, but it is such physical features which promote or depress the cover of certain plant species and not the presence or absence of grazing.

ACKNOWLEDGMENTS

We thank Drs. Dean Taylor and Frank Vasek for their careful, critical reading of an earlier version of this manuscript.

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(Received 23 Dec 1981; revision accepted 31 May 1982).

NOTEWORTHY COLLECTIONS

NEW MEXICO

ARENARIA STRICTA Michx. subsp. TEXANA (Robins.) Maguire (CARYOPHYLLACEAE).—Torrance Co., 2.1 km e. of Negra, rocky outcrop (T5N R13E S12), 1950 m, 6 Jun 1977, *Wagner & Sabo 3053* (RM, UNM) (Det. and confirmation of extension of extension by R. Hartman, RM, 1981).

Significance. First report for NM, range extension of at least 250 km from high plains of TX.

GALIUM EMERYENSE Demp. & Ehrend. subsp. EMERYENSE (RUBIACEAE).—San Juan Co., The Hogback, ca. 13 km e. of Shiprock and ca. 5 km nne. of Hwy 550 (T30N R16W S19), 1650 m, 13 May 1977, *Wagner & Sabo 2880* (UC) (Det. L. Dempster, UC, 1981).

Significance. First report for NM, range extension ca. 130 km se. from San Juan Co., Utah. This specimen is atypical in that it has leaves similar to *G. coloradoense* Wright, which presumably was involved in the formation of *G. emeryense* (Dempster, pers. comm. 1981).

LEPIDIUM OBLONGUM Small (BRASSICACAE).—Bernalillo Co., ne. of Pajarito on e. side of Rio Grande (T9N R2E S19), 15 Aug 1976, *Wagner & Cole 2349* (MO) (Det. R. Rollins, GH, 1981).

Significance. A range extension nw. from Chaves Co., NM, ca. 270 km.—WARREN L. WAGNER, Missouri Botanical Garden, PO Box 299, St. Louis 63166. (Received 14 May 1982)

NOTES AND NEWS

A MALE STERILE MORPH IN *Lycium fremontii* (SOLANACEAE) FROM BAJA CALIFORNIA SUR.—Hitchcock (Ann. Missouri Bot. Gard. 19:179–360, 1932) recognized that *Lycium fremontii* Gray is an unusually variable species. In describing *L. fremontii* he noted (p. 294) "The flowers are strikingly dimorphic, one type having a tubular corolla, which is but one and one half the length of the calyx, the other extreme having a funnelform corolla fifteen millimeters in length, the tube being much flared at the summit, and the anthers frequently but partially developed." He suggested that the difference may be due at least in part to the age of the branches: flowers from old branches usually are reduced in size, whereas the leaves and flowers of young twigs are twice their size. Apparently the functionality of gynoecia and androecia was not determined. Herbarium specimens examined by Hitchcock were from Arizona and California in the United States and Sonora and Baja California Sur, Mexico.

I made collections of *Lycium fremontii* in Baja California during January 1981 at Punto Conejo, an area sporadically inundated during recent geological times, situated 160 km north of the Cape on the Pacific side of the 1200 km-long peninsula. In the southern half of the Peninsula the shore line has retreated and advanced repeatedly during the Pleistocene and recent times (Durham and Allison, Syst. Zool. 9:47–91, 1960). Among conspicuous plants in the area are *Machaerocereus gummosus* (Engelm.) Britt. & Rose, *Bursera hindsiana* (Benth.) Engelm., *Fouquieria diguetii* (Van Tiegh.) Jtn., *Opuntia cholla* Weber, *Simmondsia chinensis* (Link) Schneider, *Stegnosperma halimifolium* Benth. The study area is in a shallow arroyo at Pto. Conejo from 90 to about 200 m inland from the beach. While collecting other shrubby species common in the area, I noticed two types of flowers of *Lycium fremontii*. Individual plants possessed one floral type only.

Flowers from plants of one morph consistently had included stamens, exserted stigma, and short corolla tubes that were noticeably constricted a few mm above the corolla base (Fig. 1-1). Plants of the other morph had larger flowers with only the stamens exserted in the throat of the long corolla tube (Fig. 1-2). The only *Lycium* populations in the study-area were of the two morphs and a very distinct second species, *L. richii* Gray (*L. brevipes* sensu Wiggins) growing nearby. Individuals of the two morphs were growing one to several meters apart and plants of both morphs were equally robust. They were easily identifiable as *L. fremontii*. Plants were in full flower and flowers were abundant on both morphs but the second morph had fewer fruits.

Two to four flowers from each of four different plants were prepared for pollen viability tests using Alexander's acid fuchsin-malachite green stain (Stain Technol. 44: 117–122, 1969). Anthers from the morph with included stigmas produced abundant pollen and 96% of the grains were filled. Stamens of the flowers with exserted stigmas were less than half the size of those of the other morph. No pollen was found in any of the anthers of 20 flowers of the morph having stigmas exserted. In order to provide a comparison with a different species of *Lycium* occurring adjacent to the study area, flowers of *L. richii* Gray were examined. Percent filled grains was between 85% and 98%. The latter species consistently had exserted stigmas and these were bilobed and as broad as the exserted stigmas of *L. fremontii*. Included stigmas of *L. fremontii* were narrow, and not bilobed.

Two distinct morphs of *L. fremontii* coexist at Pto. Conejo, Baja California Sur. Because the plants with small anthers formed no pollen at all, although producing fruit, these plants were male-sterile. The other morph produced apparently viable pollen but the degree of female-sterility of this morph is unclear. As mentioned, stigmas remained unlobed and very few fruits were evident. A single fruit with seeds was found on one plant. Lloyd terms plants whose ovular contribution is small as inconstant males rather than hermaphrodites (Lloyd, New Phytol. 71:1181–1194, 1972). No Solanaceae are known to be heterostylous (Ganders, New Zealand J. Bot. 17:607–636, 1979). Symon (The biology and taxonomy of the Solanaceae, p. 384–397, 1979) employs the term stylar hetero-

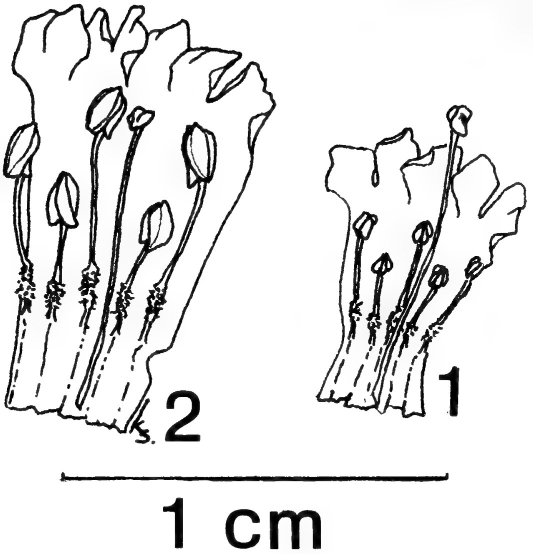

FIG. 1. Line drawings of flowers from the two morphs of *Lycium fremontii*. (1) morph with stigma exserted and stamens with included small anthers (*Gilmartin 2845,* WS), (2) morph with stigma included and anthers in the throat of the corolla (*Gilmartin 2844,* WS).

morphy for *Solanum* species with 2 morphs in which the short styled flowers are female-sterile.

Further studies are required to determine the percentage of flowers that are female-sterile, populational proportion of individuals that are functionally female, and the proximate cause of female sterility individual flowers of the pollen producing morph. While, to date, Pto. Conejo is the only place where I have noted the two morphs of *L. fremontii,* I suspect that a search of other areas where the species occurs may reveal them elsewhere in the Cape Region of the Peninsula, e.g., Bahia de los Muertos.

Support for this project was provided by the Center for Field Research. The help of the following expedition members is acknowledged: D. Gilmartin, E. Malmgren, R. Malmgren, L. McNeel, C. Mapes, B. Simons, M. Simons, and C. Wagner. Line drawings were rendered by K. Simmons.—A. J. GILMARTIN, Ownbey Herbarium, Department of Botany, Washington State University, Pullman 99164. (Received 21 Jan 1982; revision accepted 31 May 1982.)

NOTEWORTHY COLLECTIONS

CALIFORNIA

BRICKELLIA KNAPPIANA E. Drew (ASTERACEAE).—Inyo Co., n. Kingston Range, 0.16 km n. of Crystal Spring (T20N R9E S25 projected), 1170 m, 14 May 1980, *Stone 151* (CAS, RSA). Four widely scattered populations known from the Kingstons, in cyn. bottoms on dolomite or granite. Plants were always found among populations of *B. multiflora* and either *B. californica* or *B. desertorum,* suggesting a hybrid origin for *B. knappiana* and the need for a more detailed study of these taxa.

Significance. Currently under review for listing as threatened or endangered (US Fish & Wildlife Service, *Federal Register* 45:82482, 15 Dec 1980).

SELINOCARPUS NEVADENSIS (Standl.) Fowler & Turner (NYCTAGINACEAE).—Inyo Co., extreme ne. Kingston Range, fractured shale outcrop 0.16 km sw. of saddle between peaks 4037 and 4439 (T20N R10E S22 projected), 1250 m, 30 May 1980, *de Nevers 358* (CAS, RSA) (Det. by R. F. Thorne).

Significance. First report from California.—STEVE CASTAGNOLI, GREG DE NEVERS, and R. DOUG STONE, Kingston Range Resource Survey, Environmental Field Program, Univ. California, Santa Cruz 95064. (Received 1 Jul 1982)

PHACELIA VALLICOLA Congdon. ex Brand (HYDROPHYLLACEAE.)—Placer Co., ne. end of Ralston Ridge, 0.4 km s. of the forest service road (below highest point of ridge), 1550 m, 28 May 1978, *Stebbins and Smith 7898* (DAV); El Dorado Co., in rocks beside staircase e. of Jaybird Powerhouse (T11N R13E S33), 900 m, 17 Jun 1978, *Lee 78F-669-1* (DAV); steep se.-facing slope, 0.5 km w. of dam at Loon Lake (T13N R11E S7), 1950 m, 18 Jun 1978, *Lee 78F-670-1* (DAV).

Significance. Previously known only from Mariposa and Tuolumne Cos., CA, a range extension of ca. 100 km. Considered rare but not endangered by CNPS (Smith et al., CNPS Spec. Publ. 1, ed. 2 1980). The locations of these collections suggest that populations of *P. vallicola* are scattered throughout the area.—GREGORY J. LEE, Dept. of Botany, Univ. California, Davis 95616. (Received 1 Mar 1982)

ANTENNARIA FLAGELLARIS (A. Gray) A. Gray (ASTERACEAE).—Lassen Co., near old gold mining town of Hayden Hill, ca. 7 km se. of hwy. 139 on Hayden Hill Rd. (T36N R9E Sl s.½ne.¼), 1735 m, 27 May 1981, *Schoolcraft 410* (UC, DAV) (Confirmed by G. L. Stebbins and J. Strother).

Significance. First known collection in CA, extending the range ca. 320 km s. of its previously known s. extension in se. OR. This is the only known population in CA and covers only about 0.1 km^2.

CAULANTHUS MAJOR (Jones) Pays. (BRASSICACEAE).—Lassen Co., near top of Fredonyer Pk. at ne. end of Eagle Lake (T33N R12E S26 sw.¼), 2400 m, 21 Jul 1980, *Prendusi 30* (UC) (Determined by Arthur Kruckeberg).

Significance. Range extension of ca. 160 km n. from previously known occurrences in Washoe Co., NV. The Fredonyer Peak population is small, but larger, more extensive occurrences of the plant were discovered in the summer of 1982 in the Fort Sage Mts. of CA (also in Lassen Co. and ca. 80 km n. of the Washoe Co. populations).—GARY D. SCHOOLCRAFT, Bureau of Land Management, PO Box 1090, Susanville, CA 96130. (Received 15 Aug 1982)

MOENCHIA ERECTA (L.) Gaertn., Mey. & Schreb. (CARYOPHYLLACEAE).—Butte Co., along edge of unimproved dirt road ca. 200 m se. of the Oak Grove Cemetery, ca. 1.2

km se. of Hurleton, ca. 19.3 km e. of Oroville (T19N R5E S23 ne.¼sw.¼), 5200 m, 4 May 1980, *L. Ahart 2192* (CHSC, CAS, NY) (Determined by J. T. Howell).

Significance. First record for California; possibly second record for the New World. This collection extends the known range of the species s. ca. 330 km of its nearest known location in Jackson Co., OR (Peck, M. E. 1961. Man. higher pl. Oregon).—MARY S. TAYLOR, PO Box 1686, Chico, CA 95926 and LOWELL AHART, Rt. 2, Box 2715, Oroville, CA 95965. (Received 25 Feb 1982)

REVIEW

Atlas of United States Trees. Volume 6. *Supplement*. By ELBERT L. LITTLE, JR. USDA Misc. Publ. 1410: i–v, 1–31, 3 base maps, 36 maps. US Government Printing Office, Washington, DC. 1981. No price listed.

The final slender volume of Little's *Atlas* closes a 10-year project of publishing maps that show the full distributions of all native continental U.S. trees. Together with Little's *Checklist,* the *Atlas* volumes have brought to a close the major dendrological activities of the U.S. Forest Service, and with Little's retirement, the title of Chief Dendrologist has disappeared from the Forest Service's rolls. The crowning achievement of the last Chief Dendrologist's career was built on a foundation begun 70 years ago by G. B. Sudworth, the Forest Service's first dendrologist. Of the almost 700 species mapped in the *Atlas,* the *Supplement* includes maps of 36 species, but only one of these, *Juniperus erythrocarpa* Cory, shares the 1:10,000,000 base map uniform throughout the majority of the series. The other 35 species are the hawthorns accepted as distinct in the *Checklist,* although many other authors would not be so conservative. Their distribution is indicated only by dots in states and provinces. This treatment is disappointing since willow and juneberry species, which also show considerable taxonomic difficulties, are mapped in confident detail in other volumes of the series. However, the hawthorn maps are based primarily on literature citations, not on specimens, just as the accepted hawthorns and synonymy of the *Checklist* derive primarily from regional treatments rather than from overall personal study. Although lacking detail and not particularly informative, the maps generally accord with the more detailed ones presented by Tom Elias in his recent tree manual. Finally, Volume 6 presents indices to all species maps (duplicating material in the *Checklist*) and a list of all base maps for the whole series.

Nothing in Volume 6 makes me change the generally positive view of the series that I presented in a review of the preceding volumes in *Systematic Botany* (3:327–328), although the faults remain. For example, the errors in scale and presentation of the overlay maps included in Volume 1 are addressed but not corrected in the introduction to Volume 6. Furthermore, the introduction to this volume contains one paragraph that represents the biggest disappointment of the whole series: there is no plan for any new editions. The Forest Service apparently believes, and here I sense that Little shares my disappointment, that the *Atlas* and *Checklist* are complete, the final word in American dendrology. Little has accomplished a labor of love, but it is far from final. There are innumerable small errors of detail in the maps (some surprisingly large, such as the broad southern Ontario range of *Quercus prinus* L. adopted for Volume 1 from Hosie's *Native trees of Canada,* when the species apparently does not grow naturally in Canada), and Little can only suggest that such corrections be sent to state herbaria. In addition, the actual presentation of the maps could be greatly improved. The lack of commitment to further work in this field by the Forest Service is depressing because it is the only organization with the national base and resources needed to accomplish the task of revision. Rather than ending the program, the Forest Service should extend it to mapping the ranges of Hawaiian trees and of naturalized tree species, to documenting changes in distribution since the contact time chosen as a baseline, to incorporating the abundance of tree species throughout their ranges, and to adding at least some shrubby species, perhaps in interdepartmental cooperation with the Soil Conservation Service, the Bureau of Land Management, the National Park Service, and other agencies concerned with management of federal and state lands. In the *Atlas,* Little and his collaborators have given us the most extensive suite of detailed, large-scale distribution maps for any group of organisms in North America. They are useful, not only to biogeographers and other biologists, but also to land managers and many other segments of American society. Although trees are the most conspicuous organisms, and thus the easiest to map, these maps pose a challenge to the biological community to provide comparable detail for other organisms. Since the federal government has abandoned responsibility in this area, who will shoulder the burden and follow the trail that Little has set for us?—JAMES E. ECKENWALDER, Department of Botany, University of Toronto, Toronto, Ontario, Canada M5S 1A1.

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THE ROLE OF FOUR MACROPHYTE SPECIES IN THE REMOVAL OF NITROGEN AND PHOSPHORUS FROM NUTRIENT-RICH WATER IN A PRAIRIE MARSH, IOWA

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ABSTRACT

Precipitation, runoff, and drainage supplied about 1.5 metric tons of NH_4-N, 4.1 metric tons of NO_3-N, and 0.09 metric tons of PO_4-P to Eagle Lake in 1976. Shoots of *Typha glauca, Carex atherodes, Sparganium eurycarpum,* and *Scirpus validus* had accumulated 18.0 metric tons of N and 1.8 metric tons of P at peak standing crop in late July. During decomposition, shoots of all four species lost organic matter faster than P, and lost P faster than N. *Carex, Typha,* and *Scirpus* litter were more effective in retaining or accumulating N and P than was *Sparganium* litter.

INTRODUCTION

Prairie pothole marshes extend from central Iowa, through southwestern Minnesota and the Dakotas, and into central Canada (Shaw and Fredine 1956), a part of the North American prairie known as the Pothole Region. The landscape is gently undulating glacial till with numerous poorly drained depressions (potholes). When the first settlers traversed the prairie more than a century ago, marshes were abundant. Today, however, most prairie wetlands have been drained. For instance, less than 10% of the presettlement wetland acreage in Iowa remains.

Prairie pothole marshes range in size from less than one to more than 1000 ha and generally are dominated by a mixture of emergent macrophyte species (van der Valk and Davis 1978a). These marshes typically undergo vegetation changes in response to drought cycles of 5- to 20-year duration (Weller and Spatcher 1965; van der Valk and Davis 1976, 1978b, 1979, 1981). There is no indication that they are undergoing succession toward a more mesophytic state.

Because many prairie glacial marshes are in areas now devoted to intensive agriculture, they often receive runoff that is rich in N and P. High levels of these nutrients can be particularly troublesome in streams and lakes, but when agricultural runoff passes through a marsh, water quality often is improved. Phosphorus is precipitated from the water column, and NO_3^- is denitrified in the anaerobic substrate (see

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MADROÑO, Vol. 30, No. 3, pp. 133–142, 15 July 1983

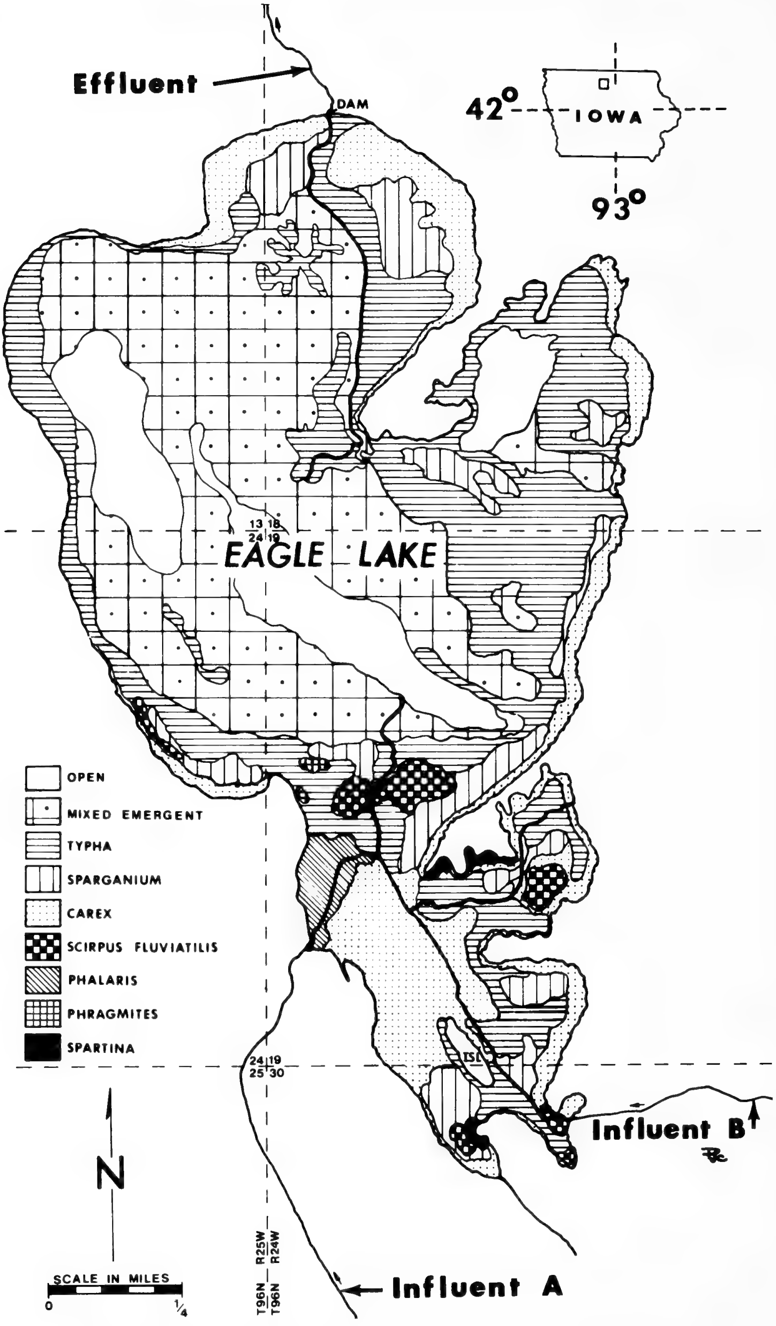

FIG. 1. Influent and effluent points and 1976 vegetation cover at Eagle Lake, Iowa. The Mixed Emergent zone was dominated in 1976 by *Scirpus validus*.

Good et al. 1978, Greeson et al. 1979, for reviews of N and P cycling in freshwater wetlands).

The purpose of this paper is to examine the roles played by *Typha glauca, Sparganium eurycarpum, Carex atherodes,* and *Scirpus validus* in N and P removal from agricultural runoff passing through a large prairie pothole marsh, Eagle Lake.

Study Site

Eagle Lake (Fig. 1) is located in north-central Iowa and is owned and managed by the Iowa Conservation Commission. It has a surface area of 365 ha and receives runoff from a basin of 2562 ha (measured from aerial photographs). Water depth rarely exceeds 1 m and is controlled by a dam at the northern end of the lake.

Surface and drain-tile runoff enters the lake at its southern end and along its eastern shore. A morainal ridge along the western shore limits flow into the marsh from that direction. Flow-weighted averages of influent N and P over a 4-year period (1976 to 1979) were 0.2 ppm NH_4-N, 13.0 ppm NO_3-N, and 0.23 ppm PO_4-P (Davis et al. 1981).

North-central Iowa has a continental climate. Average temperatures in January are $-7°$ to $-9°C$ and in July are 23° to 24°C (Shaw and Waite 1964). Average annual precipitation at Eagle Lake is ca. 802 mm (determined from records at Britt, Iowa, the nearest U.S. Weather Station). Approximately half of this falls in April, May, and June. In 1976, spring precipitation was normal, but a summer drought resulted in decreased water level. By mid-September, the marsh was dry.

The vegetation of Eagle Lake is dominated by the four emergent macrophytes discussed in this study (Fig. 1). Vegetation dynamics have been studied by Currier et al. (1978) and van der Valk and Davis (1978a, 1979, 1981).

Methods

The Eagle Lake basin comprises two drainages, one 992 ha and one 1570 ha. The smaller drainage was monitored for flow and water quality, but the larger basin was monitored for water quality only. Flow from the ungauged drainage was assumed to be proportional to the gauged drainage on an area basis; i.e., ×1.58. This is a reasonable assumption, because the soil type is the same; and topography, cropping practices, and drainage systems are similar in the two watersheds. Because there was no effluent from the lake in 1976, only water quality was monitored in the stagnant water behind the outflow dam.

Water samples were collected at the two influents (Fig. 1) and from the standing water behind the dam every other day during the spring, summer, and fall. During storms, samples were collected every 4 hrs. Samples were collected in polyethylene bottles and frozen until they could be analyzed. A Technicon Autoanalyzer II system was used to analyze for NH_4-N and NO_3-N. The alkaline phenol method was used for NH_4-N analyses, and NO_3-N analyses were done according to the cadmium reduction method. The ascorbic acid reduction method of Murphy and Riley (1962) was used to analyze for PO_4-P. Levels of detection were 0.02 ppm for NH_4-N, 0.05 ppm for NO_3-N, and 0.005 ppm for PO_4-P. The nutrients deposited with precipitation were computed from precipitation data for Britt, Iowa, five miles west of Eagle Lake and from inorganic N and P analyses of precipitation from two other Iowa studies (Tabatabai and Laflen 1976, Baker et al. 1978).

Approximately 300 quadrats (1 m^2) were established in a stratified random pattern and were harvested over a 10-day period in late July and early August of 1976. Shoots were clipped at ground level and separated by species. Samples were returned to the laboratory, oven-dried at 80°C for 48 hrs, and weighed to the nearest gram. Total biomass for each species was calculated by adding the individual quadrat biomass data and extrapolating to the total area of the marsh (Currier et al. 1978).

On 31 July, three shoot samples were collected in homogeneous, monodominant stands of each of the four macrophyte species. Shoots of all ages were removed from an area 50 × 50 cm. These were returned to the laboratory, oven-dried at 80°C for 48 hrs, subsampled, and ground in a 40-mesh Wiley mill. Subsamples of each species were combined and mixed for nutrient analysis which was performed at the WARF Institute, University of Wisconsin–Madison. Total N was determined by semi-microkjeldahl procedures, and P was determined by multispectral analysis (Genson et al. 1976). Absolute quantities of N and P were estimated by multiplying the total biomass of each macrophyte species in late July and early August by the percentage N or P in tissues collected on 31 July.

Changes in biomass and N and P content of decomposing litter were studied by using standard litter bag techniques. Samples of senescent 1975 shoots were collected in November 1975 and oven-dried at 80°C. For each species, subsamples of 20 to 30 g were placed in each of 12 fiberglass mesh bags (1 mm). Three of these bags were selected randomly as controls. The other nine were deployed on the marsh bottom in stands of the same species on 24 November 1975. Three randomly selected bags were retrieved from the marsh on 28 August 1976, 19 September 1977, and 15 September 1979. In the lab the tissues were washed gently in distilled water and extraneous plant and animal tissue was removed. Further sample preparation and nutrient analysis were the same as for shoot tissues.

RESULTS

In 1976, Eagle Lake received 575 mm of precipitation (72% of 10-year average). Inputs of NH_4-N, NO_3-N, and PO_4-P in precipitation and in the two principal influents are illustrated in Fig. 2. Precipitation

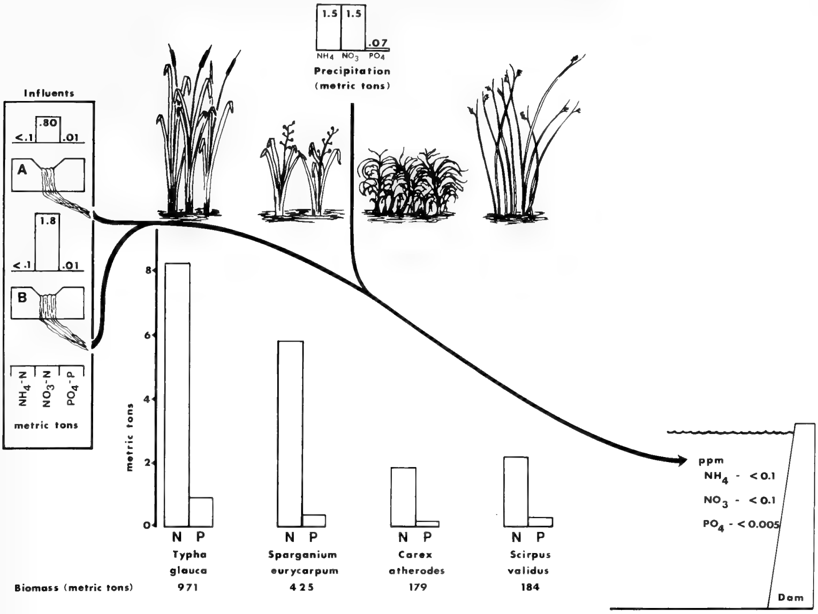

FIG. 2. Water quality and biomass, N, and P content of emergent macrophyte shoots at peak biomass at Eagle Lake in 1976.

contributed 1.5 metric tons of NH_4-N to the marsh, whereas less than 0.1 metric ton entered in each of the influent ditches. Precipitation also contributed 0.07 metric ton of PO_4-P, compared with a combined total of about 0.02 metric ton in the two influents. But the situation with NO_3-N was quite different. Precipitation supplied 1.5 metric tons of NO_3-N, but the two principal influents supplied a total of 2.6 metric tons. Concentrations of NH_4-N and NO_3-N in the stagnant water near the outlet usually were less than 0.1 ppm, and PO_4-P concentration was usually less than 5 ppb.

At peak crop in late July and early August, shoot tissues of the four dominant emergent macrophytes contained 18.4 metric tons of N and 1.8 metric tons of P. Stems of *Typha glauca* contained 8.2, *Sparganium eurycarpum* 5.8, *Scirpus validus* 2.2, and *Carex atherodes* 1.8 metric tons of N; and 0.9, 0.4, 0.3, and 0.2 metric tons of P, respectively. Sampling peak standing crop provides a reasonable estimate of net above-ground primary production in *Typha* and *Sparganium* but underestimates net primary production in *Carex* by 22% and in *Scirpus* by more than 15% (van der Valk and Davis 1978a). Therefore, our estimates of N and P content of *Carex* and *Scirpus* stem tissues are conservative.

TABLE 1. BIOMASS AND NITROGEN AND PHOSPHORUS CONCENTRATIONS OF DECOMPOSING SHOOTS OF FOUR EMERGENT MACROPHYTE SPECIES AT EAGLE LAKE, IOWA. Tissues were enclosed in 1-mm mesh fiberglass litter bags. * Corrected for biomass loss according to Boyd (1970b).

	Biomass (dry weight)		Nitrogen		Phosphorus	
	Grams (SD)	% remaining (SD)	% dw	% remaining*	% dw	% remaining*
Typha glauca						
Nov. 1975 (controls)	30.0	100	0.46	100	0.06	100
Aug. 1976	15.3 (1.1)	51 (3.5)	0.87	96	0.09	77
Sep. 1977	5.4 (1.2)	18 (4.2)	1.64	64	0.11	33
Sep. 1979	3.6 (1.3)	12 (4.0)	1.57	44	0.12	24
Carex atherodes						
Nov. 1975	30.0	100	0.34	100	0.05	100
Aug. 1976	22.5 (4.1)	75 (5.1)	0.34	75	0.09	135
Sep. 1977	15.3 (3.3)	51 (15.3)	0.97	146	0.08	82
Sep. 1979	4.5 (1.3)	15 (4.4)	1.55	68	0.15	45
Sparganium eurycarpum						
Nov. 1975	20.0	100	0.56	100	0.09	100
Aug. 1976	6.8 (2.4)	34 (11.9)	1.60	97	0.24	91
Sep. 1977	2.4 (0.9)	12 (4.7)	1.02	22	0.08	11
Sep. 1979	1.8 (0.9)	9 (4.9)	1.94	31	0.18	18
Scirpus validus						
Nov. 1975	30.0	100	0.36	100	0.06	100
Aug. 1976	7.5 (1.7)	25 (5.7)	1.52	106	0.17	71
Sep. 1977	2.6 (1.5)	9 (4.9)	1.11	28	0.07	11
Sep. 1979	3.1 (1.6)	10 (5.5)	2.62	73	0.19	32

Table 1 compares the biomass, nitrogen, and phosphorus content of stem tissues after 277, 664, and 1391 days of decomposition in mesh bags. After 1391 days, biomass had decreased more than phosphorus, and phosphorus had decreased more than nitrogen in all four species. This pattern was especially pronounced in *Typha, Carex,* and *Scirpus* tissues. After 277 days, *Carex* P content actually had increased by 35%, and after 664 days the *Carex* N content was nearly 50% higher than it had been at the beginning of the study. *Scirpus* tissues were also very effective in retaining or accumulating N and P. Indeed, N levels in these tissues increased by 6% in the first 9 months of decomposition. Following a marked decline in N and P levels after 664 days, these levels recovered substantially. After 1391 days N and P levels in *Scirpus* tissues were 73 and 32% of 1975 levels. Decomposing *Sparganium* tissues were much less efficient at retaining N and P after the first year. By the end of the second year, loss of N was nearly equal to biomass loss, and loss of P exceeded biomass loss. Recovery during the third and fourth years was minimal.

DISCUSSION

In a four-year study of water chemistry at Eagle Lake, Davis et al. (1981) found that this marsh functioned as a major sink for inorganic N and a minor sink for inorganic P. They suggested that the biotic communities in the marsh are important in uptake and release of nutrients in water passing through the marsh; the marsh was far less efficient as a nutrient sink during the cool early spring than it was in the warmer months of the growing season.

Data presented in this paper demonstrate that in 1976 emergent macrophytes (*Typha, Sparganium, Carex,* and *Scirpus*) accumulated a considerable amount of N and P in their shoot tissues during the growing season. Some of this N and P was mobilized from N and P stored in rhizomes; Davis and van der Valk (in press) found that approximately 40% of N and P accumulation in *Typha* shoots was mobilized from N and P reserves in the rhizomes. Even if we subtract 40% from our shoot N and P figures, we still find that these four macrophytes accumulated more than twice the amount of N and 10 times the amount of P that entered the marsh in precipitation, drainage, and runoff combined. But these plants extract N and P primarily from the substrate interstitial water (Bristow and Whitcombe 1971, Valiela and Teal 1974, Klopatek 1978). Therefore, uptake of N and P by emergent macrophytes would not appreciably reduce surface water N and P concentrations.

During the summer, some shoot N and P is translocated to belowground tissues and stored (Bayley and O'Neill 1972, Davis and van der Valk in press), translocated to inflorescences (Boyd 1970a), leached or excreted, or removed by grazing animals, primarily muskrats. In years when precipitation is normal or nearly normal, leaching and grazing would tend to increase N and P in surface water. But, in 1976 leaching and grazing losses were minimal because of the drought. Most of the nontranslocated N and P remained in the shoot tissues until these tissues died in September.

Dead shoot tissues of *Typha, Carex, Scirpus,* and *Sparganium* require several to many years to decompose fully. As decomposition proceeds, tissue N and P are released gradually (Davis and van der Valk 1978a,b; Boyd 1970b) into the water where they may be taken up by plants or microorganisms, precipitated, chemically transformed (i.e., nitrified, denitrified), or flushed from the marsh (van der Valk et al. 1981). Under anaerobic conditions in the substrate, release of tissue N and P via decomposition is probably not total, especially in *Typha* (Davis and van der Valk 1978a,b) and *Carex.* A certain amount of residual shoot tissue N and P will persist after the litter has been converted completely to organic soil.

Decomposing macrophyte litter is colonized by populations of microorganisms that use it as an energy substrate (Mason and Bryant 1975, Mason 1976, Coulson and Butterfield 1978, and others). When N and P concentrations in the litter tissue are too low to support these microorganism populations, the microorganisms extract N and P from the marsh water. Brinson (1977) estimated that litter tissue C:N and C:P ratios of 16 and 200, respectively, are necessary to support microorganism populations and allow for complete decomposition. Davis and van der Valk (in press) found that C:N and C:P ratios for fresh *Typha* litter at Eagle Lake in October 1975 were 132 and 703, respectively. Neely (1982) found that fresh *Sparganium* litter at Eagle Lake had C:N and C:P ratios of 76 and 570, respectively. Although we have no data on C concentrations in fresh *Carex* and *Scirpus* litter, C:N and C:P ratios were undoubtedly higher than 16 and 200, respectively. Therefore, microbial uptake of N and P was largely responsible for the fact that decomposing tissues of all four species lost N and P at a slower rate than they lost biomass. Differences in the C:N and C:P ratios also explain the fact that litter from species with a high content of structural tissue in their shoots (*Typha, Carex, Scirpus*) were more effective in retaining and accumulating N and P than was litter of *Sparganium* which has little structural tissue.

In conclusion, we suggest that because, in most years, conditions within the litter layer support the growth of microorganism populations that extract both N and P from enriched surface water, support the growth of denitrifying bacteria, and retard the mineralization of macrophyte tissue N and P, this compartment is the major sink for N and P at Eagle Lake. By contrast, the macrophyte shoot compartment is at best a minor sink for N and P. The principal contribution of macrophyte production seems to be that it is the source of fresh litter each year.

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A NEW SPECIES OF LOMATIUM (UMBELLIFERAE) FROM WYOMING

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ABSTRACT

A new species of *Lomatium* from Park County, Wyoming is described and illustrated. **Lomatium attenuatum** is distinguished by its inconspicuous involucel, elongate pedicels, and glabrous fruit with only 2 commissural vittae. It is compared with *L. cous* and other species, but its relationships are unclear.

Lomatium attenuatum Evert, sp. nov.

Herba perennis, brevicaulis 10–25 cm alta, plus minusve scaberula, e radice palari incrassata. Folia, 3-pinnata; laminae ovatae 2–11 cm longae, 1.5–10 cm latae; divisionibus ultimis linearibus, 2–5 mm longis, 0.5–1.5 mm latis; petioli 1.5–5 cm longi. Pedunculi 1–4, 10–15 cm longi. Radii fertiles 5–8 patentes, 3–5 cm longi. Involucellum absens vel 1–6 bracteolis attenuatis inconspicuis. Umbellulae ca. 15 floribus. Pedicelli fructificantes 3–10 mm longi. Petala et antherae flavae. Fructus oblongus-ellipticus, 5–8 mm longus, 3–5 mm latus, alae angustae, 0.5–0.75 mm latae; vittae prominentes, in intervallis 1, ad commissuras 2 (Fig. 1).

Plant perennial, short-caulescent, with only 1 or 2 cauline leaves, more or less scaberulous, (7–)10–25 cm tall, from an elongated thickened taproot and also occasionally from a several-branched caudex; leaves petiolate, 3-pinnate or ternately 3-pinnate, blades 2.0–11 cm long, 1.5–10 cm wide, ovate in outline, the ultimate divisions linear to oblanceolate, 2–5 mm long, 0.5–1.5 mm wide, obtuse to somewhat acute and mucronulate; petioles 1.5–5 cm long, the dilated and scarious sheathing extending to the middle or above; peduncles 1–3(–4), scaberulous, exceeding the leaves in fruit, 10–15 cm long; involucre usually absent but occasionally 1 inconspicuous, filiform bract present; fertile rays 5–8, spreading, angled, unequal, (1.5–)3–5 cm long in fruit; sterile rays 4–8, spreading, 3–10 mm long in fruit; involucel absent or of 1–6 inconspicuous linear-lanceolate, attenuate, non-connate bractlets, 1–4 mm long; umbellets ca. 15-flowered, only 2–6 developing into fruit; pedicels 3–10 mm long in fruit; petals 1.5 mm long including the incurved apex, yellow, obovate, glabrous; sepals inconspicuous; anthers ca. 0.5 mm long, yellow; styles 1–1.5 mm long, spreading or reflexed; ovaries glabrous to slightly scaberulous; fruit oblong-elliptic, glabrous, glossy, 5–8 mm long, 3–5 mm wide, the wings ca. 0.5–0.75

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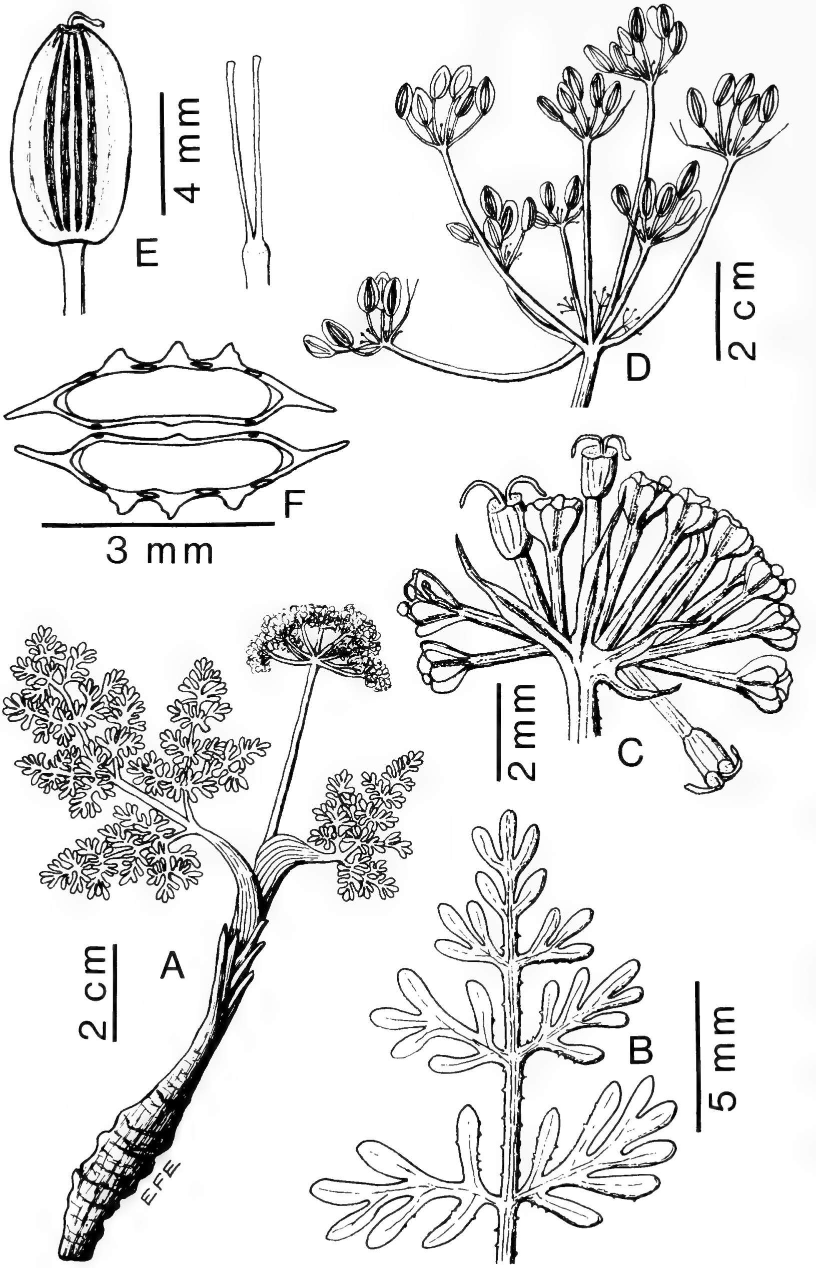

FIG. 1. *Lomatium attenuatum*. From *Evert 1756*. A. Flowering habit. B. Leaflet dissection C. Flowering umbellet. D. Fruiting umbel. E. Mature fruit and carpophore. F. Fruit transection.

mm wide, narrower than the body; oil tubes prominent, 1 in each interval, 2 on the commissure; carpophore bipartite.

TYPE: USA, WY, Park Co., Absaroka Range on ridge e. of Elk Fork Cr., ca. 1.6 km s. of Hwy 14, T52N R106W SW ¼ S29, 1876 m; open, dry, rocky soil with *Antennaria umbrinella, Haplopappus acaulis, Phlox hoodii,* and *Oryzopsis hymenoides,* 19 May and 26 Jun 1980, *E. F. Evert 1756* (Holotype: RM; isotypes: MO, NY, UC, MOR).

PARATYPES: USA, WY, Park Co., Absaroka Range along Sweetwater Creek Rd. ca. 1.6 km n. of Hwy 14, T52N R106W, NW ¼ S16, 1860 m, 20 Jun 1975, *Evert 811* (RM); Shoshone Canyon, just below Buffalo Bill Dam, T52N R103W S1, 1616 m, 29 May 1980, *Hartman and Dueholm 11409* (RM); on s. slopes of Pat O'Hara Peak, ca. 29 km nw. of Cody, T54N R104W S15 SW ¼, 2745 m, 16 Jul 1981, *Evert 3179* (RM); sw. side of Rattlesnake Mtn. ca. 13 km w. of Cody T53N R103W S35 NE ¼, 2623 m, 17 Jul 1981, *Evert 3203* (RM); on ridge above Cougar and Pagoda Creeks, ca. 7 km s. of Hwy 14, T51N R106W, S10 SW ¼, 2623 m, 22 Jul 1981, *Evert 3278* (RM).

Habitat and distribution. Open, dry, rocky areas in lithosols derived from volcanic material or limestone at elevations of 1616–2745 m in or along the border of the Absaroka Range, Park Co., Wyoming.

Leaves appear with the flowers in mid-May to mid-June depending on elevation; mature fruit is produced about 4 weeks later. Derivation of epithet is from the Latin in reference to the bractlets of the involucel.

Lomatium attenuatum was first collected by the author in 1975 during floristic studies of the North Fork Shoshone River drainage in northwest Wyoming. It was thought at the time that it might be an undescribed variety, with abbreviated involucel, of the widespread and variable *L. cous* (S. Wats.) C. & R. complex, including *L. circumdatum* (S. Wats.) C. & R. and *L. montanum* C. & R., of Cronquist (1961). However, subsequent collections indicated that it was evidently an undescribed species. *Lomatium attenuatum* does resemble the *L. cous* complex in habit, leaf dissection, and fruit size, shape and texture, but differs in its greater over-all scabrosity, inconspicuous involucel, elongate pedicels, and distribution of vittae on the fruit. Although it is probably most closely related to the *L. cous* complex, *L. attenuatum* also resembles *L. vaginatum* C. & R. in its overall scabrosity and elongate pedicels and *L. canbyi* C. & R. in its similar leaf dissection, involucel, and elongate pedicels; but it differs from the former in fruit size, distribution of vittae, and leaf dissection and from the latter in flower color and in the lack of a globose, tuberous root. It appears that the exact relationships of *L. attenuatum* with other *Lomatium* species are unclear.

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MIMULUS HYMENOPHYLLUS (SCROPHULARIACEAE), A NEW SPECIES FROM THE SNAKE RIVER CANYON AREA OF EASTERN OREGON

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ABSTRACT

Mimulus hymenophyllus, a new perennial species recently discovered growing on canyon walls in eastern Wallowa County, Oregon is described and illustrated. The new taxon appears morphologically and ecologically closest to *M. jungermannioides*, an allopatric species occurring to the west in the Columbia Basin. *Mimulus hymenophyllus* also shows affinities to *M. moschatus*, *M. floribundus*, and *M. arenarius* through similarities in the nature of the specialized glandular pubescence and the distinctive calyx structure. Based on these characters it is placed with this species group in the sect. *Paradanthus*.

Extreme northeastern Oregon is one of the botanically least explored areas of the western United States. Of particular interest within this region is the rugged corridor of ridges and canyons immediately west of the Snake River in Wallowa County, paralleling the Idaho border from the Wallowa Mountains north to the Washington state line. During a recent collecting trip here an undescribed, perennial species of *Mimulus* was discovered growing in diffuse sunlight in the moist cracks of deteriorating basalt cliffs. This fragile monkeyflower is the only member of its genus whose known geographic range is confined to Oregon, although it would not seem unreasonable to expect that future field work may uncover it in similar habitat in adjacent Idaho as well.

Mimulus hymenophyllus Meinke, sp. nov.

Herbae perennes, pubescentes, viscido-villosae; caulibus infirmis, 0.5–2.5 dm longis, suberectis, ramis paucis, internodis longis; foliis caulium paucis, oppositis, tenuibus, late lanceolatis vel ovatis, denticulatis, 1.0–3.5 cm longis, petiolo lamina plerumque longiore, divaricato; pedicellis axillaribus, tenuibus, reflexis aut ascendentibus; calyce in statu florifero (2.5–)3.5–5.5(–6.0) mm longo, in statu fructifero late campanulato, infirme angulato, 4.0–7.0 mm longo, dentibus ciliatus, 0.5–1.2 mm longis, aequalibus, late triangularibus, acutis; corolla flava, infundibulari, (15–)18–28 mm longa, calyce 3–4 plo longiore, tubo angusto, exserto, labiis plus minusve inaequalibus, patulis; staminibus stylo brevioribus, inclusis, glabris; stylo fere glabro, incluso, labiis stigmatis ±aequalibus; capsula inclusa, subglobosa; seminibus

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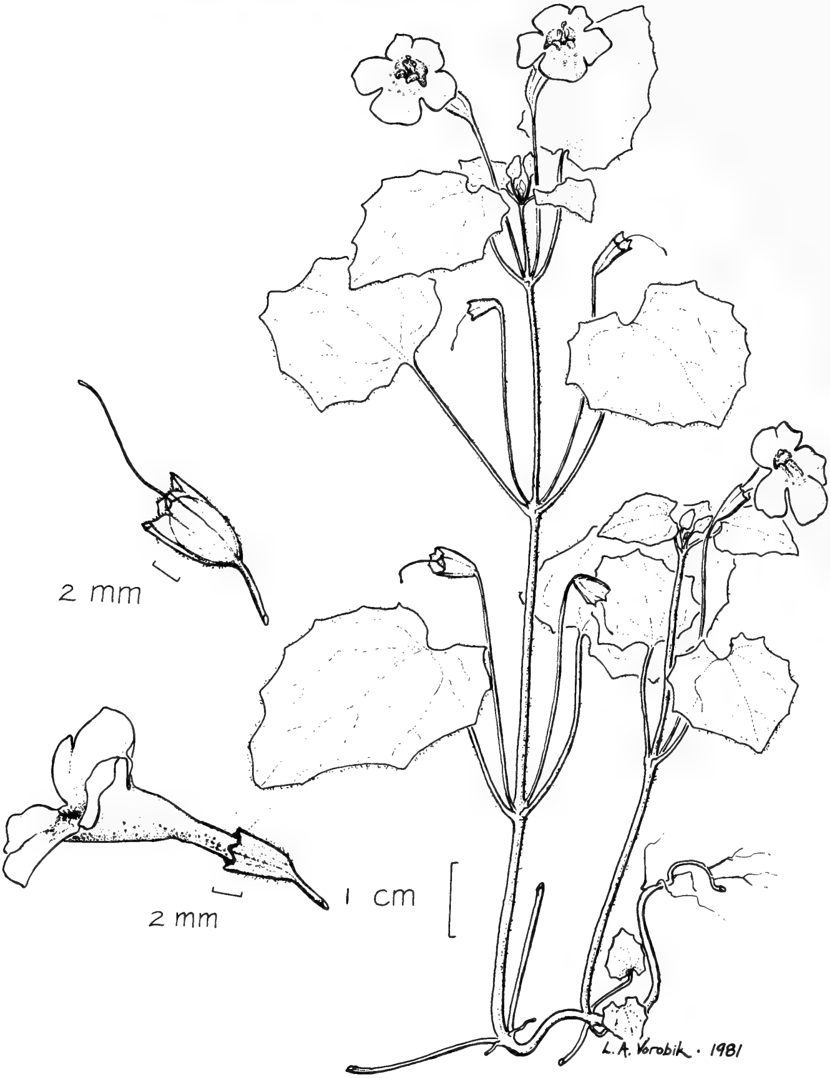

FIG. 1. *Mimulus hymenophyllus* Meinke. A. Habit. B. Flower, depicting relationship of calyx and corolla length. C. Fruiting calyx, enveloping mature capsule.

(0.5–)0.65–0.85 mm longis, late oblongis, longitudinaliter rugatis (Fig. 1).

Delicate perennial herb, typically growing in masses, prostrate to suberect, sparsely glandular-villous with slimy-viscid transparent hairs less than 0.8 mm long; stems few to several, fragile and thin, 0.5–2.5 dm long, winged, arising from numerous reddish-orange capillary rhizomes, sparingly branched throughout, with long internodes; leaves few, cauline and basal, generally 3–7 opposite pairs per primary stem; leaf blades thin, filmy, broadly lanceolate to ovate, acute, subpalmately veined, 1.0–3.5 cm long and equally wide or slightly less, shallowly denticulate to nearly entire, broadly triangular at the base and tapering or occasionally cordate; petioles of cauline leaves equal to or usually exceeding the leaf blades, generally less than the internodes, diverging, prominently winged; flowers in axillary pairs; pedicels narrower than the petioles, slightly winged at the base, reflexed or usually ascending, ranging from 0.5–1.8 times the petiole length but seldom exceeding the blades; calyx green, the tube narrowly triangular and evidently angled, acute at the base or slightly rounded, with scattered glands on the angles, calyx in its entirety (2.5–)3.5–5.5(–6.0) mm long at anthesis, moderately inflated in fruit, becoming campanulate but not lengthening significantly, up to 7.0 mm long and nearly as wide; calyx teeth equal, 0.5–1.2 mm long, about half again as broad, deltoid and abruptly acute in flower, rounded and mucronate in late fruit, with simple acerose eglandular cilia on the margins; corolla funnelform, weakly bilabiate with an open orifice, (15–)18–28 mm long (3–4 times the length of the calyx), light yellow with scattered red or purplish dots on the throat and lower lobes, puberulent externally with a tuft of thickened yellow hairs on the inner lower lip, the tube half again as long as the calyx, the throat moderately flaring, the lobes short and spreading, typically entire or apically notched; stamens glabrous, included, ½–¾ the length of the corolla; style glabrous or with a few hairs, included, exceeding the stamens; stigma lips ±equal and rounded, glabrous or not; capsule essentially glabrous, oval to rounded, the tip abruptly apiculate to shallowly retuse, barely included in the calyx tube at maturity, 3.0–6.0 mm long and 2.5–5.7 mm wide, short stipitate, the placentae firmly adherent; seeds ovoid to oblong, blunt, longitudinally wrinkled, (0.5–)0.65–0.85 mm long, 25–70(–95) per capsule; pollen grains large, tricolporate with semitectate, microreticulate exines, diameter (mean, followed parenthetically by range) of polar axis 41.4 (34.0–46.1) μm, equatorial axis 44.4 (37.5–49.2) μm.

TYPE: USA, Oregon, Wallowa Co., loosely erect or hanging from seasonally moist basalt cliffs with sw. exposures, mostly in partial shade or occasionally full sunlight, on e. side of Horse Cr., ca. 12 km s. of the Imnaha R. and ca. 21 km w. of the Snake R. (T1N R49E S7), 1075 m, 2 Jul 1980, *Meinke & Kennison 2656* (Holotype: OSC; isotypes: ID, NY, ORE, UC, US, WS, WTU).

PARATYPES: USA, Oregon, Wallowa Co., along Horse Cr. (T2N R48E S36), 900 m, 20 Jun 1979, *Leary & Leary 3312* (OSC); Horse Cr., ca. 14 km s. of the Imnaha R., 1150 m, 26 Jun 1979, *Meinke, Leary, & Bafus 2365* (OSC).

Mimulus hymenophyllus is restricted, insofar as is currently known, to the deep canyons of Horse and Cow Creeks in southeast Wallowa County, Oregon at altitudes from ca. 850 to 1300 m. Populations of the species are scattered on steep cliffs of gray basalt with western or southwestern aspects, occurring within narrow, isolated bands of *Pseudotsuga menziesii-Pinus ponderosa* forest maintained by the northerly downward flow of cool air from the Wallowan uplands. Additional associate species include *Holodiscus discolor, Symphoricarpos albus, Berberis repens, Ribes velutinum, R. aureum, Penstemon wilcoxii, P. triphyllus, Glossopetalon nevadense* var. *stipuliferum, Floerkea proserpinacoides, Sedum leibergii, Thelypodium laciniatum,* and *Cystopteris fragilis.* There are several other similar drainages in the area which although unexplored are anticipated to shelter populations of *M. hymenophyllus* as well.

Flowering is initiated in late April and continues more or less continuously through August or early September, depending on elevation and available moisture. Capsules first mature in late May or early June.

Mimulus hymenophyllus apparently is most closely related to *M. jungermannioides* Suksdorf (sect. *Paradanthus*), a localized perennial endemic to basalt outcrops in the Columbia River Basin of north-central Oregon and reputedly adjacent Washington (Pennell 1951, Cronquist 1959). The two species possess lax habits of similar form and size, both being adapted to crevices in steep, basalt cliffs overlooking riparian habitats. In addition, their pubescence type, shape and venation of the leaf blades, and calyx construction are essentially identical. There are a number of marked morphological and ecological differences between the taxa, however, amply justifying separation at the species level. These data are outlined in Table 1.

The known populations of *M. hymenophyllus* and *M. jungermannioides* are widely separated geographically (Meinke, unpubl. data). Their respective narrow distribution patterns suggest that they are probably glacial relicts, but their evolutionary relationship to each other and related elements within sect. *Paradanthus* have yet to be assessed. The relatively scant seed production, large seed size, and "gigas" pollen grains of *M. hymenophyllus,* the latter feature the largest reported for the section (Argue, unpubl. data) are reminiscent of a polyploid condition (Argue, pers. comm.; Stebbins 1971). Chromosome counts, however, remain to be completed for both species.

In her monograph of the genus *Mimulus,* Grant (1924) allied *M. jungermannioides* with *M. moschatus* Dougl. ex Lindl. and *M. floribundus* Dougl. ex Lindl., two polymorphic species widespread in western North America, and *M. arenarius* Grant, a regional endemic of the central Sierra Nevada in California. *Mimulus hymenophyllus* displays strong affinities with this assemblage also, all of the species sharing a similar symmetrical calyx shape and structure as well as an

TABLE 1. MORPHOLOGICAL AND ECOLOGICAL DISTINCTIONS BETWEEN *M. hymenophyllus* MEINKE AND *M. jungermannioides* SUKSDORF.

Character	*M. hymenophyllus*	*M. jungermannioides*
Morphology		
Reproduces vegetatively from subterranean buds	No	Yes
Pubescence	Sparse, hairs all less than 0.8 mm	Moderate to very heavy, many hairs 1.0–1.5 mm
Fruiting pedicels	0.5–1.8 times petiole length	(2.5–)4–15 times petiole length
Calyx length	3.5–5.5 mm in flower, barely longer in fruit	5.0–9.0 mm in flower, up to 12.5 mm in fruit
Corolla length	18–28 mm, 3–4 times calyx length	14–20(–24) mm, 1.8–3 times calyx length
Capsule	3.0–6.0 mm long, rounded to ovate, mucronate	5.0–9.0 mm long, elliptic to lanceolate, attenuate
Seeds	0.65–0.85 mm long, 25–70(–95) per capsule: $\bar{x} = 45$	0.35–0.5 mm long, 75–200 per capsule: $\bar{x} = 135$
Pollen grain diameter ($\bar{X}$):		
Polar axis	41.4 μm	31.0 μm
Equatorial axis	44.4 μm	34.4 μm
Ecology		
General habitat	Within mesic coniferous forest type	Within xeric sagebrush-bunchgrass type
Elevational range	Ca. 850–1300 m	Ca. 95–370 m

unusual sticky or slimy glandular vesture on the vegetative parts. The significance of this exudate, which varies in its degree of copiousness from species to species, has not been determined. Recent pollen analysis of the genus (Argue 1980, and unpubl. data) tends to support this proposed alliance. Palynological studies also indicate, in support of Pennell (1951), that a reevaluation of the broad species concept, which is generally accepted today for *M. moschatus,* might be appropriate. Pennell advocated taxonomic recognition of several morphogeographic phases of *M. moschatus,* in spite of relatively broad zones of intergradation. A revival of this interpretation founded on current evidence would probably have implications in future evolutionary studies of *M. hymenophyllus* and its relatives. It is suspected that *M. hymenophyllus* and *M. jungermannioides* are common derivatives of one of these forms of *M. moschatus,* possibly splitting from that entity as a single unit and then diverging later under local ecological pressure. Preliminary phytogeographic research (Meinke, unpubl. data) suggests that a north to south migration was responsible for current distribution patterns of the two species, leading to speculation that their common hypothetical ancestor is or was indigenous to eastern Washington.

Mimulus hymenophyllus is noteworthy in that it is the single member of its large genus that may be endemic to Oregon. Although it has been recorded from only a few small populations, it exists in remote country far from significant disturbing influences. Development of this area in the forseeable future by government or private interests appears very unlikely. Therefore, despite its overall rarity and limited occurrence within its range, this species should not be considered threatened or endangered at this time. Periodic monitoring of its populations is recommended.

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NECTAR SUGAR COMPOSITION IN SOME SPECIES OF AGAVE (AGAVACEAE)

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Abstract

The nectar sugar composition of 19 species in the genus *Agave* was determined by high-performance liquid chromatography and found to be variable among species. Eleven species produced hexose-rich nectars with small amounts of sucrose, four species produced nectars that contained hexoses only, and four species produced sucrose-rich nectars. Known pollinators and visitors of four species are compared to expectations based on sugar composition.

The sugar composition of floral nectars is known to vary among species (Wykes 1952, Percival 1961), and coevolutionary relationships have been found between the proportions, or ratios, of different sugars and the kinds of pollinators attracted (Baker and Baker 1979, Spira 1981, Stiles 1976). However, it has also been suggested that some plant taxa are bound by "phylogenetic constraint" and do not develop the clear pollination syndromes seen in others (Baker and Baker 1979). Therefore, each study of plant-pollinator relationships will require knowing the overall capacity of the taxon under consideration to respond to evolutionary pressures. In addition, quantitative determinations of nectar sugars seem a prerequisite to more comprehensive and detailed theories of coevolution. The genus *Agave* has received recent attention as a model of plant-pollinator coevolution (Howell 1974; Schaffer and Schaffer 1977, 1979; Howell and Roth 1981), but few data are available on the nectar sugars within this genus. Our study examined the nectars of ecologically diverse species to determine if the nectar sugar composition varies among the taxa (perhaps reflecting different pollinators) or is relatively constant (perhaps indicating phylogenetic constraint).

Materials and Methods

In most cases, flower clusters of appropriate age were collected in the field or botanical garden. They were washed carefully with a stream of deionized water, gently shaken dry, and left indoors overnight to

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produce nectar. The nectar was then removed with a micropipette and frozen until anlaysis. Samples from the Huntington Botanical Garden were collected, dried, and mailed to us in vials.

Sugars were identified and quantified by high-performance liquid chromatography (HPLC). A Waters Associates liquid chromatograph with a refractive index detector and Alltech Model 600NH column was used. The solvent was an acetonitrile : water (80:20 v/v) system at a flow rate of 2.0 ml/min. For calibration, regressions based on the response peak heights to standard sugar solutions were established. Quantities of each sugar in the nectar samples were determined by comparison to the calibrations and expressed as relative percent by weight. Injection volumes were 5–25 μl in 5 μl increments for calibrations and 10–25 μl in nectar samples.

RESULTS AND DISCUSSION

Substantial differences exist in the proportions of sugars in the nectars of the taxa examined (Table 1). Eleven of the 19 species had nectars of the sFG type of Percival (1961), meaning that the nectars were rich in fructose and glucose with small amounts of sucrose. Four were of the FG type of Percival with only fructose and glucose. Two were the SFG type with nearly equal proportions of the sugars, and two were sucrose rich, the Sfg type. The first three types (FG, sFG and SFG) fall within the "sucrose poor" or "hexose rich" category of Baker and Baker (1979) because the ratio of sucrose to hexose is less than 0.5 in all of them. The Sfg nectars are in the "sucrose rich" category of Baker and Baker (1979) because this ratio is between 0.5 and 1.0. The agave samples have hexoses (fructose and glucose) in relative balance, with a tendency toward slightly higher concentrations of glucose. One species, *A. schottii* contained detectable quantities of maltose.

These data are also shown in Fig. 1, a ternary diagram well suited to illustrating systems with three components that sum to 100%. The data of Van Handel et al. (1972) for a broad spectrum of species from several families are shown for comparison. While none of the agaves we have examined so far is sucrose-dominated, the wide range of differences among the species supports the conclusion that the genus is without phylogenetic constraint.

The data suggest the probability of variation among pollinators or communities of pollinators, in habitats where agaves are found. Pollinator differences seem likely, because the species examined occur from sea level in arid and tropical Mexico to temperate grasslands and coniferous forests at elevations of up to 2200 m in the United States. That environment markedly affects the types of potential pollinators is well established (Arroyo et al. 1982, Primack 1978, Moldenke 1976, Pojar 1974, Cruden 1972, Downes 1965, Mani 1962).

TABLE 1. NECTAR SUGARS IN THE GENUS *Agave*. F indicates fructose, G glucose, S sucrose, M maltose, and R is the ratio of sucrose (plus maltose) to fructose plus glucose. HGB is the Huntington Botanical Garden, and DBG the Desert Botanical Garden. Locations in parentheses are the sources or type localities of garden plants. Replicates from the same locality were taken from different plants.

#	Species	Locality and elevation	% F	% G	% S	% M	R
Subgenus *Agave* (paniculate)							
1	*neomexicana*	Sacramento Mts., Otero Co., NM, 2250 m	46	54	0	0	0.0
2	*neomexicana*	Franklin Mts., El Paso Co., TX, 1200 m	40	60	0	0	0.0
3	*parryi*	Pinos Altos, Grant Co., NM, 2250 m	46	54	0	0	0.0
4	*shrevii*	HBG (type: Sierra Canelo, Chih., Méx.)	44	56	0	0	0.0
5	*fenzliana*	Revolcadero, Dgo., Méx., 1900 m	42	56	2	0	0.02
6	*chrysantha*	DBG (Pinal Co., AZ)	43	54	3	0	0.03
7	*chrysantha*	DBG (Pinal Co., AZ)	43	50	7	0	0.08
8	*zebra*	DBG (Sierra Viejo, Son., Méx., 700 m)	36	59	5	0	0.05
9	*mckelveyana*	DBG (Burro Ck., Yavapai Co., AZ, 700 m)	37	56	7	0	0.08
10	*palmeri*	Portal, Cochise Co., AZ, 1460 m	36	56	8	0	0.09
11	*palmeri*	Florida Mts., Luna Co., NM, 1580 m	52	36	12	0	0.14
12	*americana*	cult., El Paso Co., TX	39	49	12	0	0.14
13	*havardiana*	Chisos Mts., Brewster Co., TX, 1800 m	44	43	13	0	0.15
14	*pacifica*	Rio El Fuerte, Sin., Méx., 100 m	37	46	17	0	0.20
15	*colorata*	San Carlos, Son., Méx., 100 m	30	42	28	0	0.39
Subgenus *Litteae* (spicate)							
16	*utahensis*	Clark Mts., San Bernardino Co., CA, 1700 m	50	50	0	0	0.0
17	*pedunculifera*	El Palmito, Sin., Méx., 1875 m	40	51	9	0	0.10
18	*lechuguilla*	El Paso, El Paso Co., TX, 1120 m	40	50	10	0	0.11
19	*bracteosa*	HGB (type: Monterrey, N.L., Méx.)	47	21	32	0	0.47
20	*schottii*	22 km e. Douglas, Cochise Co., AZ, 1200 m	22	35	41	2	0.75
21	*toumeyana*	Sunflower, Maricopa Co., AZ, 1100 m	27	32	41	0	0.69
22	*toumeyana*	Sunflower, Maricopa Co., AZ, 1100 m	25	31	44	0	0.79

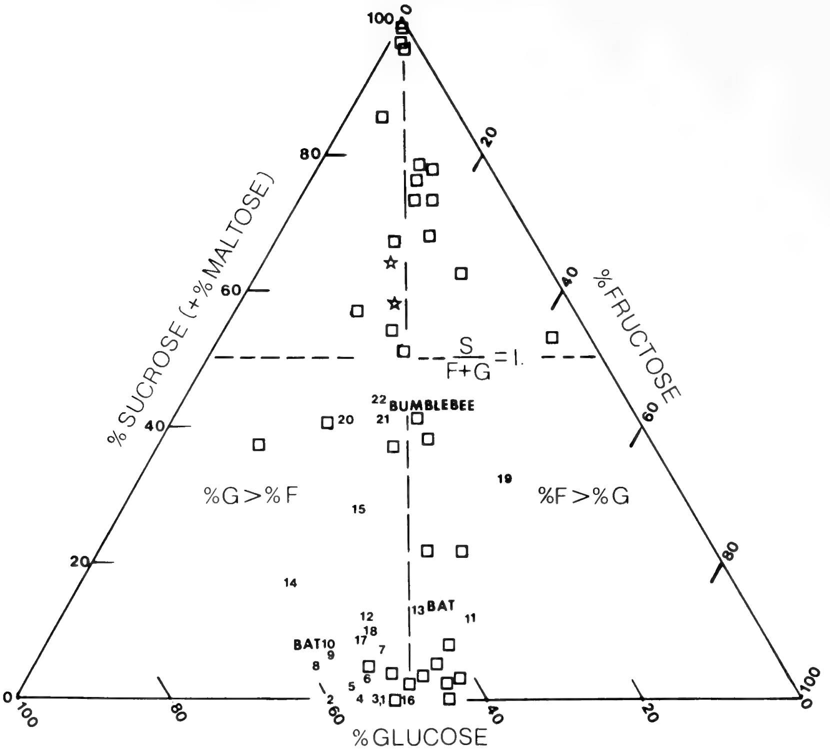

FIG. 1. Ternary diagram showing the distribution of sucrose (plus maltose), glucose, and fructose in floral nectars. Numerals indicate the *Agave* samples listed in Table 1, with two bat-pollinated taxa indicated. Open boxes are floral nectars from the survey of Van Handel et al. (1972), and the stars show two honeybee-pollinated plants (Bailey and Fieger 1954).

The pollination ecology of only two of the sucrose-poor species (*A. palmeri* and *A. havardiana*) is known in any detail. Baker and Baker (1979) suggest that the pollinators of species with sucrose-poor nectars are likely to be passerine birds, bats, flies, and some bees. Bats do exploit the nectar of *A. palmeri* (Howell and Roth 1981, Schaffer and Schaffer 1977) and *A. havardiana* (J. Kuban, pers. comm.). Other animals known to visit *A. havardiana* are passerine birds and hummingbirds (Allen and Neill 1979, Neill and Allen 1979), as well as many bees and other insects. Preliminary results of pollinator studies in *A. havardiana* indicate that bats and passerine birds are the most important pollinators, and that bees and hummingbirds are probably not of major significance (J. Kuban, pers. comm.). Although hummingbirds generally prefer sucrose-rich nectars, they also commonly utilize the nectars of sucrose-poor species in the mountains of Texas

(Allen and Neill 1979, Neill and Allen 1979), New Mexico (pers. obs.), and Durango (pers. obs.). Cruden (1972) notes that hummingbirds are much more common in the mountains of Mexico than at low elevations. In addition, Crosswhite and Crosswhite (1981) and Moldenke (1976) report that several species of hummingbirds visit *Agave* flowers. Perhaps the large quantity of nectar available is more important to hummingbirds than taste, as suggested by Stiles (1976).

Though most agaves have open flowers in which nectar is readily available to any visitor, *A. schottii* and *A. toumeyana* have tubular flowers. These species produce sucrose-rich nectars. Baker and Baker (1979) have stated that hummingbirds, hawkmoths, butterflies, and some bees prefer such nectars. Schaffer and Schaffer (1977) found that *A. schottii* and *A. toumeyana* were pollinated by carpenter bees (*Xylocopa*) and bumblebees (*Bombus*) and that bats are not important pollinators of *A. schottii* in southern Arizona. Schaffer and Schaffer (1977) pointed out that photographs of bats visiting these flowers (McGregor et al. 1962, Cockrum and Hayward 1962) were taken under artificial conditions using caged animals.

We found no evidence that nectar sugar composition is related to phylogeny, at least at the subgeneric level. Indeed, the subgenus *Litteae* contains nectars at the extremes of the genus (Table 1). It does seem that nectars of open-flowered species have very little or no sucrose, whereas higher sucrose levels are found near sea level and/or farther south. Further work is needed to determine whether this observation is real or an artifact of small numbers of species from lowland and or tropical areas.

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REPRODUCTIVE POTENTIAL OF BROMUS MOLLIS AND AVENA BARBATA UNDER DROUGHT CONDITIONS

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ABSTRACT

In California annual grasslands, flowering and seed set occur during spring when soil water conditions change rapidly due to increased plant growth, high evapotranspiration, and infrequent rainfall. This study simulated short drought periods and an early onset of summer drought to determine possible drought effects on seed production and population carry-over of *Bromus mollis* and *Avena barbata*. Drought treatments diminished seed production, but some germinable seeds were produced under severe conditions. Drought effects carried over to the next generation because stressed plants produced smaller seeds that produced smaller seedlings.

Annual species comprise from 50% to more than 90% of the foliar cover in California annual grasslands. Most of them are introduced annuals, having come from other parts of the world with Mediterranean climates. Success of the alien species has been attributed to abundant seed production (Biswell and Graham 1956), ability to survive summer drought as seed (Bartolome 1976), and ample seed production, even under heavy grazing pressure (Heady 1961).

Major and Pyott (1966) and Bartolome (1979) showed that a majority of the viable seeds produced each spring by winter annuals germinate the following autumn; seed reserves are small as a result. This means that the plants must produce seeds nearly every year. Seed production data have been reported by several workers in the California annual grassland (Papanastasis 1973, Biswell and Graham 1956, Batzli and Pitelka 1970, Holland 1974), but the numbers vary considerably from site to site and year to year. Environmental conditions in California and their direct effects on annual grass reproduction have rarely been reported, making it difficult to compare seed production data. Moreover, knowing the total number of seeds produced is not as important as knowing whether enough germinable seed is produced to carry the vegetation through another year.

In California annual grasslands, flowering and seed set occur in the annuals during spring when soil water conditions change rapidly because of increased plant growth, high evapotranspiration, and infre-

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quent rainfall (Evans et al. 1975). Although seed production insufficient to maintain populations of the alien species has not been observed (Biswell and Graham 1956, Heady 1961), reproduction is probably influenced by spring weather conditions (Ewing 1981). Newman (1967) studied the effects of spring drought periods on reproduction of *Aira praecox* in Great Britain and demonstrated that a short spring drought period did not reduce seed production or seed weight. Only severe drought (soil matric potential below an estimated threshold of −30 bars) caused noticeable differences in inflorescence emergence, seed formation, and seed weight. He concluded that *Aira praecox* is drought resistant beyond what is necessary to reproduce successfully.

Short drought periods during the winter-spring growing season and an early onset of summer drought were simulated in this study to determine possible drought effects on seed production and population carry-over of alien annuals in California annual grasslands.

METHODS

Facility. Twelve plywood boxes, 60 × 60 × 60 cm, were filled with a pale brown, medium-textured, and slightly acidic Laughlin (fine-loamy, mixed, mesic Ultic Haploxeroll) soil from an annual grassland, oak-savannah range site at the Hopland Field Station, Mendocino County, California. Drainage was provided through a 10-cm layer of washed gravel under the soil and holes in the bottoms.

After fall germination of winter annuals in the field (14 September 1978), 10-cm deep slabs of sod from the same site were removed and set on top of the soil. Each of the twelve experimental units had continuous plant cover with typical botanical composition for the beginning of the growing season at Hopland.

The experimental units were transported to a field laboratory at the Gill Tract in Albany, California, where a clear plastic shelter with open sides was constructed above them to intercept precipitation. Temperatures under the rain shelter tracked outside temperatures, never varying by more than 1°C. Spectroradiometer readings indicated a complete light spectrum passed through the plastic, though the intensity at all wavelengths was reduced by about 25%. Three gypsum resistance blocks were placed at each of three soil depths, 9, 20, and 40 cm, in each experimental unit to measure soil matric potential.

Soil water regime treatments. Beginning 29 October 1978, three treatments were applied to randomly selected experimental units in 4 replications. Soil matric potential was measured three times weekly, and water was applied to bring the soil to field capacity each time gypsum blocks indicated an average −1, −7, or −15 bar matric potential at the 20 cm depth, for the three treatments, respectively. The treatments closely simulated field conditions recorded by Evans et al. (1975). After 15 March 1979, two of the four replicates for each treatment were allowed to dry, simulating an early end of the winter rainy season. The remaining two replicates continued under the original treatments until 19 May 1979, when the plants began to senesce.

Plant sampling. On 11 November 1978, five plants each of *Bromus mollis* and *Avena barbata* were marked in each experimental unit. Maturing panicles on the marked plants were enclosed in translucent paper bags on 12 May 1979 to collect developing seeds.

The collected seeds were counted, weighed, and then stored in the laboratory until 11 December 1979, when seeds from each plant were germinated separately in greenhouse flats. A mixture of sand and peatmoss (U.C. soil mix) was used as a germination substrate, with sand sprinkled over the seeds. Distilled water was applied as needed until 20 March 1980. As seedlings emerged, they were counted and discarded; emergence was taken as a measure of successful germination.

In June 1979, fifty seeds of each species were selected at random from each water regime treatment. Average seed weight was recorded before sowing the seeds in boxes with slanted plate glass fronts. Plant height and root length were measured five days after germination. Rooting space was limited so three groups of seeds were planted sequentially in the boxes: all the −15 bar treatment seeds were grown together, followed by the −1 bar treatment seeds, and then the −7 bar treatment seeds. Comparison of seedling top and root growth was made only among seedlings growing in the same box and the same trial.

In the text, a significant difference is indicated when sample means, by an F-test, have a less than 5% probability of being equal ($p < 0.05$). A highly significant difference occurs when $p < 0.01$. Bars in histograms topped with the same letter are probably not different ($p < 0.10$).

RESULTS

Seed production. When water was available throughout the growing season, maximum seed production for *B. mollis* occurred under the −1 bar treatment (Fig. 1A). The −7 bar conditions reduced seed production, which was further reduced by the −15 bar regime. Water withheld after 15 March sharply reduced *B. mollis* seed production from that in the −1 and −7 bar "dried late" treatments. The decrease appeared to be much less under the −15 bar conditions. On the average, the number of seeds produced by plants in the "dried early" treatments were significantly fewer than those produced in the "dried late" treatments. *Avena barbata* responded similarly to the water regime treatments (Fig. 1A). When water was available throughout the growing season, maximum seed production occurred under the −1 bar treatment. Seed production was reduced by the −7 bar regime and further reduced under the −15 bar conditions. Early depletion of

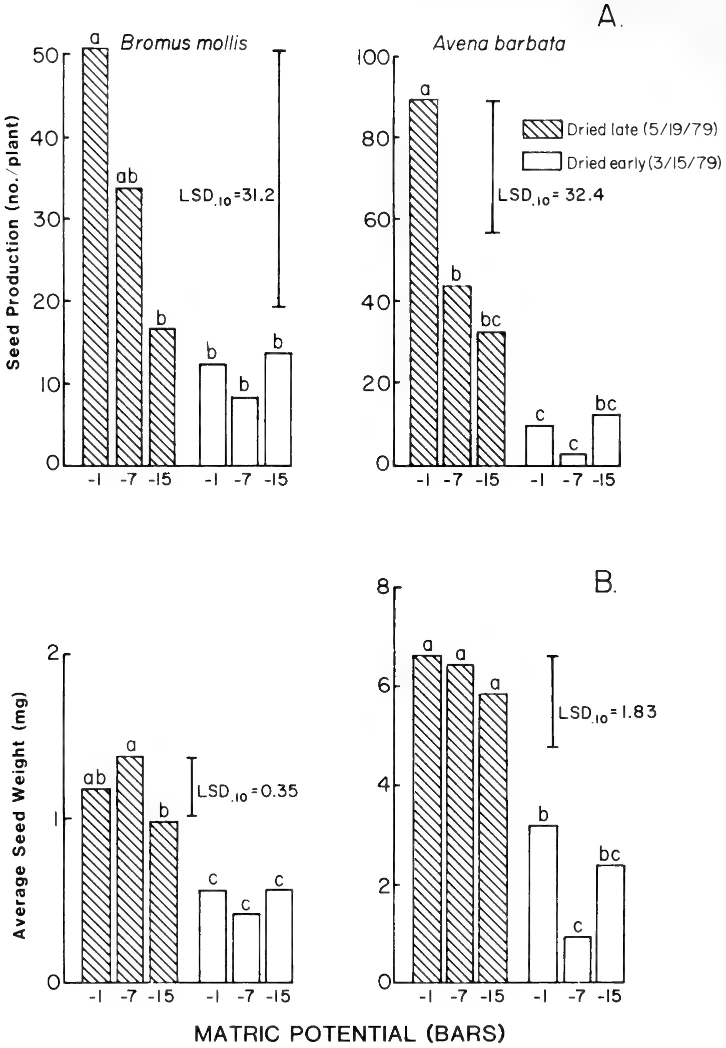

FIG. 1. Number and average weight of seeds (florets) produced by *Bromus mollis* and *Avena barbata* plants dried early or late and growing in three soil water regime treatments (−1, −7, −15 bars). Bars labeled with the same letters are not significantly different at the 10% level.

available soil water (no water after 15 March) greatly reduced seed production in all treatments and, again, the least decrease occurred in the −15 bar treatment. Differences between the "dried early" and "dried late" treatment groups were highly significant.

Seed weight. The effect of periodic drought during the growing season on average *B. mollis* seed weight is not clear (Fig. 1B). A slight reduction was observed under the −15 bar treatment. Although seed numbers were reduced, average seed weight was relatively uniform if water was applied until 19 May. A significant reduction in seed weight occurred when water was withheld after 15 March, the average seed weight being 55% less. *Avena barbata* seed weights were relatively uniform with periodic drought during the growing season (Fig. 1B) even though seed numbers were reduced. Seed weights did not differ among treatments when water was available through 19 May, but significant differences occurred when the soil dried early. On the average, withholding water after 15 March reduced seed weight by 79%.

Reproductive potential. Periodic drought during the growing season did not affect germination rate of *B. mollis* seeds (Fig. 2A). About 50% germination occurred in seeds produced by plants growing in both the −1 and −15 bar treatments if water was available through 19 May. Only prolonged spring drought resulted in significant germination rate reductions. While moderate decreases in germination rate may have occurred under the more intense drought treatments, neither periodic drought during the growing season nor early depletion of soil water reserves significantly reduced the percentage of *A. barbata* seeds that germinated (Fig. 2A).

The reproductive potential of a plant is more accurately represented by the number of germinable seeds produced. Periodic drought during the growing season reduced reproductive potential of *B. mollis* (Fig. 2B). Plants undergoing the −1 bar treatment produced more germinable seeds than plants undergoing the −7 bar and −15 bar treatments. A highly significant reduction occurred when water was withheld after 15 March, and the reproductive potential of plants in the −15 bar treatment was reduced by 41%. For the −7 bar and −1 bar treatment plants, 93 and 85% reductions occurred, respectively. Though not all marked *B. mollis* plants reproduced, at least some germinable seed was produced in each experimental unit. Reproductive potential of *A. barbata* was also reduced by periodic drought during the growing season (Fig. 2B). Plants growing under the −1 bar treatment produced many more germinable seeds than plants growing in the −7 bar and −15 bar treatments. Withholding water after 15 March further reduced reproductive potential and was probably more critical because a 71% reduction occurred in plants already receiving the −15 bar treatment. Early depletion of soil water reserves significantly reduced reproductive potential, 96 and 90% in the −7 bar and −1 bar treatments, respectively. Nevertheless, some germinable *A. barbata* seed was produced regardless of soil water conditions.

Second generation seedlings. Seeds produced by plants grown under the various soil water regimes were planted to determine whether

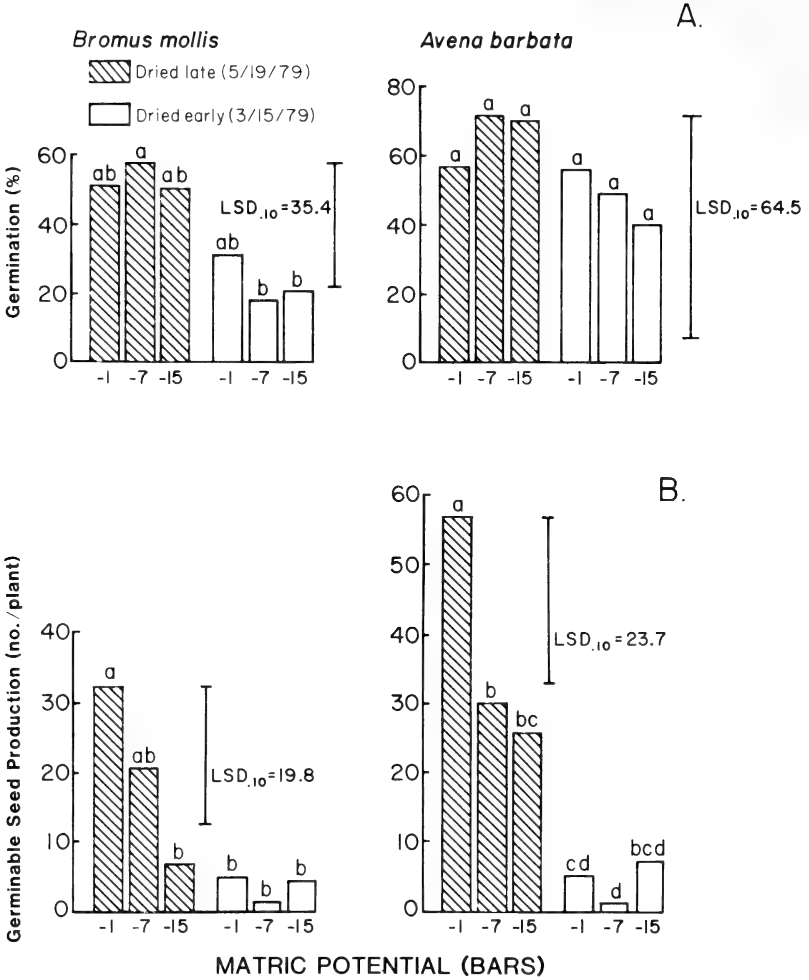

FIG. 2. Germination rate and number of germinable seeds produced by *Bromus mollis* and *Avena barbata* plants dried early or late and growing in three soil water regime treatments (−1, −7, −15 bars). Bars labeled with the same letters are not significantly different at the 10% level.

the subsequent generation of seedlings reflected stress on parent plants. Average weight was lower for seeds taken from "dried early" treatments (Table 1). In all instances, smaller seeds from stressed parent plants produced significantly smaller seedlings. For example, *B. mollis* plants receiving the −15 bar treatment produced seeds weighing on the average 2.2 mg if water was applied through the spring. Five day

TABLE 1. AVERAGE WEIGHT OF SEEDS PRODUCED BY PLANTS GROWING IN SIX SOIL WATER REGIME TREATMENTS AND SUBSEQUENT SEEDLING SIZE (5 DAYS AFTER GERMINATION). "Early" means water withheld after 15 March; "Late" means water applied until 19 May.

Treatment	Ave. seed weight (mg)	Ave. seedling height (mm)	Ave. root length (mm)
Bromus mollis			
−1 bar early	1.5	26	40
−1 bar late	2.4	34	58
−7 bars early	1.5	20	34
−7 bars late	2.5	28	52
−15 bars early	1.2	19	60
−15 bars late	2.2	40	94
Avena barbata			
−1 bar early	6.4	53	65
−1 bar late	8.5	62	84
−7 bars early	6.7	38	64
−7 bars late	10.8	47	80
−15 bars early	5.8	45	98
−15 bars late	7.8	57	130

old seedling height from those seeds averaged 40 mm and root length averaged 94 mm. *Bromus* plants receiving the −15 bar treatment and early spring drought produced seeds weighing 1.2 mg on the average (46% reduction). Seedling height from those seeds averaged 19 mm (52% reduction) and root length averaged 60 mm (36% reduction). Water stress decreased reproductive output of plants growing under all water regimes. Water stress on the parent plant also decreased seedling size of the next generation.

DISCUSSION

Reproductive output of *B. mollis* and *A. barbata* was reduced by periodic drought during the growing season. Maximum seed production occurred only when water was readily available over the entire growing season. A simulated end of the rainy season in mid-March greatly reduced seed production but never completely suppressed it. Given the data of Evans et al. (1975) showing only rare soil water potentials below −10 bars, in many annual grassland areas it is unlikely that drought conditions occur that would completely interrupt or stop seed production.

Bromus mollis and *A. barbata* are ideally suited to the Mediterranean climate in California because they survive the dry summer season as seeds. They are also suited because even under extreme drought conditions, at least a few germinable seeds are produced to carry the species through the summer.

When plants experienced short drought periods during the growing season, seed numbers were reduced but seed weights and germination rates stayed relatively uniform. Stressed plants allocated energy to fewer seeds and maintained reproductive efficiency of those seeds. Only when drought stress was severe and prolonged during spring did seed weights and germination rates decline.

Drought stress resulted in smaller as well as fewer seeds, and smaller seeds produced smaller seedlings. Seedlings from small seeds may be at a competitive disadvantage in a mixed stand (Black 1958). Through changes in seed production, seed size, and seedling vigor, there is a possibility that annual vegetation reflects not only the current year's growing conditions but also the previous years'. Future experiments with annual grassland species and communities should take this into account, especially when seeds of unknown origin are used.

One of the problems encountered in evaluating the data was tremendous variation in the number of seeds produced by a single plant. While this type of variation is distressing for the researcher, it may well be adaptive for the species, enabling at least some members of the population to survive year-to-year environmental variation.

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CHANGES IN MORPHOLOGICAL CHARACTERISTICS OF PINUS ENGELMANNII OVER AN ELEVATIONAL GRADIENT IN DURANGO, MEXICO

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ABSTRACT

Needle number per fascicle has been used to distinguish two varieties of pine (*Pinus engelmannii* Carr., and *P. engelmannii* var. *blancoi*). This character, along with needle length and the number of rows and number of stomates per mm of row, was studied in pines growing over an elevational gradient in Durango, Mexico. Differences in needle number per fascicle were found to represent clinal variation within the species: a gradual increase in needle number occurred with altitude and age. Seeds from 5-needled pines, grown for 21 months in the laboratory under dry conditions, confirmed this by producing predominantly 3-needled seedlings.

INTRODUCTION

In the genus *Pinus* there are many examples that exhibit variation in needle number over environmental gradients. *Pinus monophylla* is described as having predominantly 1, but sometimes 2 needles per fascicle (Shaw 1909). Recently Trombulak and Cody (1980) reported an increase in needle number per fascicle for *P. monophylla* with increase in elevation in the New York Mountains of California. This suggests clinal variation of the character along a moisture and temperature gradient. Dodge (1963) reported an increase in needle number per fascicle from the high elevational or northern *P. ponderosa* var. *scopulorum* to the mid-elevational *P. arizonica* Engelm. in the mountains of southeastern Arizona. He used this result along with other characteristics to conclude that *P. arizonica* Engelm. is a variety of *P. ponderosa, P. ponderosa* var. *arizonica.* Haller (1965) made a similar claim for *P. ponderosa* var. *scopulorum, P. arizonica,* even *P. durengensis,* and described a clinal increase in needle number per fascicle with decreasing latitude in the Sierra Madre Occidental of northwestern Mexico.

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In this study we examine some of the characteristics of *Pinus engelmannii* over an elevational gradient in the Sierra Madre Occidental of Durango, Mexico. Shaw (1914) reduced this species to synonymy under *P. ponderosa*. Martinez (1948) reconsidered Shaw's work, rejected this designation, and recognized two varieties: the typical form in Mexico, *P. engelmannii* Carr., and *P. engelmannii* var. *blancoi*. He assigned Shaw's *P. engelmannii* to the latter variety. Martinez distinguished the two varieties of *P. engelmannii* on the basis of needle numbers per fascicle; *P. engelmannii* var. *engelmannii* Carr. is described as having 3 or 4 needles and sometimes 5, whereas *P. engelmannii* var. *blancoi* exhibits 3 (very rarely 4 or 5). Other characteristics are described as being relatively similar or exhibiting great overlaps. The geographical ranges of the two varieties overlap greatly as well. Both are sympatric throughout the Sierra Madre Occidental, particularly in the states of Durango and Chihuahua (Martinez 1948, Mirov 1967). Foresters in this region identify individuals at high elevations as var. *engelmannii* and those at low elevations as var. *blancoi*. Our question is a straightforward one: Are there two distinct varieties of this species or do the characteristics of *P. engelmannii* vary clinally in response to environmental changes over an environmental gradient?

Study Sites and Methods

Ascending the eastern slopes of the Sierra Madre Occidental in Durango, Mexico, gradual changes in the plant associations are observed beginning with those species typical of warm Chihuahuan desert to those associated with mixed grassland, chaparral, and broad-sclerophyll forest and ending finally in open ponderosa-pine like forests (Oosting 1956). A series of four study sites was established over the 230 m elevational range of *Pinus engelmannii* along Mexico Highway 40. The sites were evenly distributed (77 m elevational intervals), beginning beside the Rio Mimbres at the lower edge of the distribution of *P. engelmannii* and ending at Los Cumbres, its upper limit (Table 1).

At each site 10 adult individuals (defined as having trunk diameters greater than 16 cm at base) and 10 juveniles (trunk diameters less than 5 cm at base and less than 1 m in height) were selected randomly. For each individual 10 fascicles were picked randomly and needle length and needle number per fascicle were determined. Average needle number per fascicle and average needle length were calculated for each individual. From one needle on each tree the number of stomate rows was counted, and from one row on this needle the number of stomates per mm of row was determined. Means and standard errors for each parameter were then calculated for adult and juvenile classes at each site. Student's t-test was used to determine statistical significance of differences in means of adults and juveniles within a site and within

TABLE 1. CHARACTERISTICS OF STUDY SITES ALONG AN ELEVATIONAL GRADIENT ON THE EASTERN SLOPES OF THE SIERRA MADRE OCCIDENTAL IN DURANGO, MEXICO.

Elevation (m)	Site	Aspect	Predominant vegetation
2177	Rio Mimbres	West-facing	Open chaparral with scattered *Pinus* and *Quercus*
2254	Santa Barbara	Flat	Pastureland with scattered *Pinus*
2331	Unnamed	South-facing	Chaparral and open scrubland with *Quercus* and some *Pinus*
2408	Los Cumbres	Flat or north-facing	Open woodland with *Pinus* and *Quercus*

classes between sites. Due to the large number of tests performed, we decided to accept $p < 0.01$ as our level for rejecting the null hypothesis of no difference between means.

A sample of seeds was gathered from 5-needled members of the Los Cumbres population and grown in 3-inch diameter pots under bright sunlight and dry conditions in Claremont, California, from August 1978 to May 1980. The number of needles per fascicle in the secondary bundles were counted and each individual was categorized as exhibiting solely 3, 4, or 5 needles per fascicle, or some combinations of 3, 4, and 5 needles per fascicle.

RESULTS

The means and standard errors of the four parameters measured are given in Table 2 for each age class and site.

TABLE 2. MEANS AND STANDARD ERRORS FOR NEEDLE NUMBER, LENGTH, AND STOMATES FROM ADULT AND JUVENILE *Pinus engelmannii* OVER AN ELEVATIONAL GRADIENT IN DURANGO, MEXICO.

Elevation (m)	Class	Needle number	Needle length (cm)	No. of rows of stomates	No. of stomates per mm of row
2177	Adult	3.11 ± 0.04	25.75 ± 0.93	21.90 ± 1.31	13.00 ± 0.02
	Juvenile	2.85 ± 0.09	22.39 ± 1.23	19.10 ± 1.09	12.30 ± 0.69
2254	Adult	3.42 ± 0.16	27.97 ± 0.69	23.50 ± 1.18	13.10 ± 0.28
	Juvenile	3.02 ± 0.05	20.29 ± 1.26	19.20 ± 0.94	12.50 ± 0.31
2331	Adult	3.74 ± 0.14	22.65 ± 0.95	17.80 ± 1.18	12.10 ± 0.53
	Juvenile	3.40 ± 0.12	19.28 ± 0.89	18.10 ± 1.22	11.80 ± 0.39
2408	Adult	4.14 ± 0.17	25.71 ± 0.80	18.60 ± 0.86	12.30 ± 0.50
	Juvenile	3.27 ± 0.11	18.71 ± 0.80	18.20 ± 0.51	11.80 ± 0.42

TABLE 3. COMPARISON OF MEAN VALUES USING STUDENT'S T-TEST FOR NEEDLE NUMBER PER FASCICLE OF *Pinus engelmannii* WITHIN AGE CLASSES AND BETWEEN SITES OVER AN ELEVATIONAL GRADIENT IN DURANGO, MEXICO. Values in table are t's. * $p < 0.01$. Diagonal line from A to B separates juveniles (left) from adults (right).

	Elevation (m)	A	2177	2254	2331	2408	
Juveniles	2177			1.87	4.21*	5.81*	Adults
	2254		1.79		1.48	3.05*	
	2331		3.69*	2.08		1.78	
	2408		2.98*	3.03*	0.81		

B

Both adult and juvenile trees exhibit significant differences in needle number per fascicle with altitude (Table 3). Adult needle number increases from predominantly 3 needles per fascicle at 2177 m to more than 4 needles per fascicle at 2408 m (Fig. 1). Although the increase is consistent, adjacent sites are not far enough apart to produce statistically significant differences. However, sites 140 m or more apart do exhibit significant differences. For juveniles a similar pattern exists, except that maximum needle number per fascicle occurs at 2331 m (Fig. 1). Comparing age classes, the greatest difference in needle number per fascicle occurs at the highest site (2408 m), where adults have significantly more needles per fascicle than do juveniles (Table 4). Adults also tend to have more needles per fascicle at the lower sites but the differences are not significant.

Needle lengths of adults are significantly shorter at 2331 m than at the other three elevations (Table 5). The longest needles are at the 2254 m site (Santa Barbara). For juveniles, needle lengths decrease slightly with increased altitude, but the differences are not significant. Within elevational sites, adult needle length is 11–37% greater than that of juveniles.

For adults, the number of rows of stomates is significantly greater

TABLE 4. COMPARISON OF MEAN VALUES USING STUDENT'S T-TEST FOR NEEDLE CHARACTERS OF *Pinus engelmannii* BETWEEN ADULTS AND JUVENILES WITHIN SITES OVER AN ELEVATIONAL GRADIENT IN DURANGO, MEXICO. Values in table are t's. * $p < 0.01$.

Elevation (m)	Needle number	Needle length	No. of rows of stomates	No. of stomates/ mm of row
2177	2.70	2.18	0.40	0.92
2254	2.39	5.34*	0.18	1.45
2331	1.84	2.59	2.86	0.46
2408	4.24*	6.20*	1.64	0.77

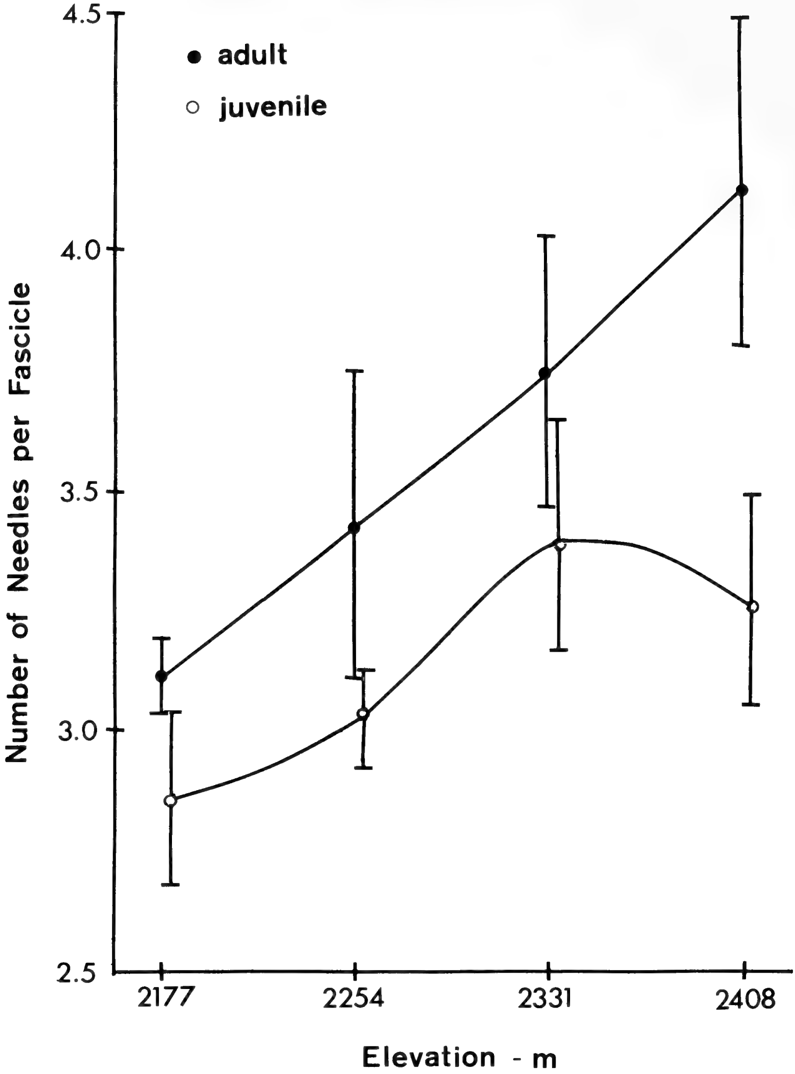

FIG. 1. Average number of needles per fascicle in adult and juvenile *Pinus engelmannii* over an altitudinal gradient. Error bars represent 2 × standard error.

at 2254 m than either of the two higher sites. With juveniles, no significant differences in this character are found between sites. Comparison of adult and juvenile pines also reveals no significant difference in number of stomate rows at any elevational site. Likewise the number of stomates per mm of row did not differ significantly, either

TABLE 5. COMPARISON OF MEAN VALUES USING STUDENT'S T-TEST FOR NEEDLE LENGTH OF *Pinus engelmannii* WITHIN AGE CLASSES AND BETWEEN SITES OVER AN ELEVATIONAL GRADIENT IN DURANGO, MEXICO. Values in tables are t's. * $p < 0.01$. Diagonal line from A to B separates juveniles (left) from adults (right).

	Elevation (m)	A	2177	2254	2331	2408	
Juveniles	2177			1.92	2.33	0.03	Adults
	2254		1.19		4.54*	2.15	
	2331		2.04	0.65		2.47	
	2408		2.51	1.06	0.48		
						B	

between adults and juveniles at any site, or with altitude for a given age class.

Seedlings of *Pinus engelmannii* Carr. grown from the seed of 5-needled individuals of the 2408 m population under hot, dry conditions predominantly have 3 needles per fascicle; of fifty plants only one had 5-needled fascicles and even then, only in some fascicles (Table 6).

DISCUSSION

The major character distinguishing *Pinus engelmannii* var. *engelmannii* from *P. engelmannii* var. *blancoi* is needle number per fascicle. Our measurements indicate that this character varies clinally with elevation from the Rio Mimbres (2177 m) to Los Cumbres (2408 m), and that both adults and juveniles exhibit significant increases with increasing elevation. Needle number increases with elevation more markedly in adults than in juveniles, so that at the highest site (2408 m) a significant difference between age classes occurs. These differences appear to be a response to changing moisture levels experienced over the mountainside; where more soil moisture is present, needle number per fascicle is greater.

TABLE 6. INDIVIDUAL NEEDLE COUNTS AND % OCCURRENCE FOR SECONDARY FASCICLES ON SEEDLINGS OF 5-NEEDLED *P. engelmannii* ADULTS IN THE LOS CUMBRES POPULATION (2408 M) GROWN UNDER DRY CONDITIONS AT CLAREMONT, CALIFORNIA.

Needle number in fascicles	Number of individuals	% occurrence of individuals
3 only	33	66
4 only	9	18
5 only	0	0
3, 4	7	14
3, 5	1	2
4, 5	0	0

Since *P. engelmannii* occupies the lower and middle slopes of the Sierra Madre, it experiences quite dry and hot conditions at desert edge but encounters increasing levels of precipitation and cooler temperatures with increasing elevation. Juveniles of *Pinus engelmannii* appear to suffer more from drought stress than do adults. This is presumably because juvenile root systems have not developed sufficient size or depth to protect them during dry periods (Ledig, Clark, and Drew 1977; Yeaton 1978). In contrast, adult trees have larger root systems that potentially have access to soil moisture sources unavailable to juveniles. Juveniles may respond to drought stress during development by maintaining lower needle numbers per fascicle and shorter needle length, thereby reducing their relative transpirational surface area. Adult trees respond to increased water availability by producing more and longer needles per fascicle, hence increasing their photosynthetic surface area. The results of growing seedlings from seeds of 5-needled individuals support our contention that differences in needle number reflect developmental responses on the part of the individual.

The pattern of increasing precipitation and lower temperatures with increasing elevation is typical of, at least, the lower and middle elevations of all mountain ranges (e.g., MacArthur 1972). It should be noted that in high mountain ranges a point is reached at which rising, cooling air is no longer saturated with moisture and the amount of precipitation begins to decrease with increasing elevation. This means that on very high mountains the highest levels of precipitation will be found at intermediate elevations. This fact explains Dodge's (1963) observation that needle number per fascicle in *P. ponderosa* decreases with increasing elevation in the high mountains of southeastern Arizona. It also explains another interesting and apparently similar situation seen in *P. hartwegii,* a timberline species that has an elevational range of over 1000 m and is restricted to the higher elevations of the Transverse Range in Mexico. This species shows a gradual decrease in needle number per fascicle with increasing elevation, as the species ranges into zones with decreased precipitation and increased winter drought stresses. For example, on Tláloc Mountain, in the state of México, needle number per fascicle for adults of *P. hartwegii* decreases from an average of 3.52 at 3230 m to an average of 3.0 at 3530 m (R. I. Yeaton, unpubl. data). Juveniles from the same elevational range decrease from an average of 3.11 to 2.99 needles per fascicle. These observations are rather similar to those reported here for *P. engelmannii*; increased precipitation is again associated with increased needle number per fascicle.

This study indicates that the two varieties of *Pinus engelmannii* represent the extremes of clinal variation within the species. We now pose a second question that is not as simple to answer. In regions of the northern hemisphere such as Mexico, where there is a wide range of environmental conditions imposed upon members of the genus *Pi-*

nus, how do the characters used traditionally to distinguish varieties and species (e.g., needle number per fascicle, needle length, internal needle structure, bark and cone characteristics, and even phytochemistry), respond developmentally to diverse environmental conditions? It seems to us that they may vary a great deal and in their variation contribute much confusion to the taxonomy and the understanding of the evolutionary history of this genus.

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ACACIA PACENSIS (LEGUMINOSAE: MIMOSOIDEAE), A NEW SPECIES FROM BAJA CALIFORNIA SUR, MEXICO

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ABSTRACT

Acacia pacensis Rudd & Carter is described as new from México. It is known thus far only from the vicinity of La Paz, Baja California Sur and the adjacent islands in the Gulf of California, Isla Espíritu Santo and Isla Partida Sur.

Several unidentified and misidentified collections of *Acacia* from the vicinity of La Paz, Baja California Sur, México, and adjacent islands in the Gulf of California have been found to represent a new species, described in this paper as *Acacia pacensis* Rudd & Carter.

The earliest extant specimen of this *Acacia,* which we have chosen as the type, was collected by T. S. Brandegee near La Paz and cited originally as "*Acacia* ? sp." (1891, p. 134); and later (1892, p. 221) as *Acacia constricta* Benth. He commented, "also found by Mr. Bryant on Espiritu Santo Island." Unfortunately, Bryant's collections were lost in the 1906 San Francisco earthquake and fire (Wiggins 1980, p. 42). A later collection from La Paz, made by Marcus E. Jones in 1930, was misidentified as "a pretty Prosopis (?)" (Jones 1933–1935, p. 99). Incidentally, Jones' notebook gives Oct. 3, 1930 as the date but the herbarium specimen at UC bears the date Oct. 4, 1930. More recently, in 1981, Turner and Burgess found the species in that same locality. All other known specimens are from the two offshore islands, Isla Espíritu Santo and Isla Partida Sur. In 1921, I. M. Johnston found a "globose shrub 12–25 dm high, frequent in gravelly soil near the ocean at Candeleros Bay on Espíritu Santo island (4073) . . . The fruit necessary for positive identification is lacking. The relationship of the plant seems to be with *A. constricta* Benth. It differs from that species . . . in its stout, short, unbracted peduncle. It probably is the same as the unexamined Bryant plant reported by Brandegee. The island plant is probably an unnamed form" (Johnston 1924, p. 1032). Most of the more recent collections have been referred to *A. constricta* Benth.

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Acacia pacensis Rudd & Carter

Frutices usque ad 2.5 m alti; spinae stipulares aciculares, 1–1.5 mm longae; folia 3–4 cm longa, pinnarum paribus 2–6, foliolarum paribus (3–)4–10, foliolis ellipticus, 1–3 mm longis, 0.5–1 mm latis, glabris vel nonnumquam margine ciliatis vel glanduliferis, nervo medio centrali vel plus minusve excentrico; inflorescentiae capitatae, diam. 6–8 mm, floribus flavidus, 3 mm longis, pedunculo apice bracteato; legumina elongata, indehiscentia, stipite ca. 5–10 mm comprehendente 6–15 cm longa, 5–7 mm lata, ad apicem versus attenuata, inter semina plus minusve constricta; seminibus brunneis, ca. 8–13(–15) (Fig. 1).

Acaciae constrictae simulentes utcunque *A. cochliacanthae, A. pennatulae, A. macracanthae, A. schaffneri,* et *A. farnesianae* affinis.

Shrubs, to about 2.5 m tall; trunk dark gray, to about 8 cm diam.; young stems brown or reddish-brown, pubescent with minute crispate hairs, glabrescent with age; stipular spines straight, to about 1–1.5 cm long, 1–1.5 mm diam. at base, terete, acicular, whitish or brown; leaves to about 3–4 cm long with 2–6 pairs of pinnae, the rachis puberulent bearing a minute, raised, cupular gland between the terminal pair of pinnae, sometimes also between some lateral pairs and, occasionally, on the petiole slightly above midpoint; leaflets (3–)4–10 pairs, elliptic, obtuse or sometimes acuminate with a glandular tip, asymmetrical at the base, 1–3 mm long, 0.5–1 mm wide, glabrous or sometimes ciliate or minutely glandular along the margin, the venation inconspicuous, the midvein central or slightly excentric; inflorescences essentially capitate, 6–8 mm in diameter, summibracteate, i.e., bracteate at the apex of the peduncle, the bracts sometimes caducous, the receptacle usually with minute glands; bractlets at base of flowers about 0.5 mm long, spatulate; flowers yellowish, 3 mm long, glabrous; calyx about 1 mm long with teeth slightly glandular; corolla 2 mm long; stamens 3 mm long; peduncle 5–15 mm long, minutely pubescent; fruit elongate, straight or slightly curved, indehiscent, about 6–15 cm long including stipe about 5–10 mm long, 5–7 mm wide, attenuate at the apex, septate, slightly constricted between the seeds, bright red when fresh, blackish with age, lightly pubsecent with subappressed hairs, about 5–13(–15)-seeded; seeds dark brown, lenticular to subovoid, 5–8 mm long, 4–5 mm wide, 1.5–3 mm thick, the areole lighter in color, about 3-mm long, 1.5–2 mm wide.

TYPE: México, Baja California Sur, La Paz, 1 Nov 1890, *T. S. Brandegee 190* (Holotype: UC 81017).

PARATYPES: México, Baja California Sur, coast e. of La Paz, 4 Oct 1930, *M. E. Jones 27268* (UC), as *27168* (BM); west-facing hillside above small bay, 0.5 mi n. of Pichilinque Ferry, low, open scrub, 19 Oct 1981, *R. M. Turner & T. L. Burgess 6190* (ARIZ, SFV, UC); 1.0 mi n. of Pichilinque Ferry, rocky breccia hillside e. of Bahía de La Paz, 19 Oct 1981, *Turner & Burgess 6192* (ARIZ, SFV, UC, others to be distributed). Isla Espíritu Santo, Candeleros Bay, 9 Jun 1921, *I. M. Johnston 4073* (CAS); Ensenada de la Ballena, 21 Apr 1962, *Wiggins 17853* (DS); 4 Apr 1981, *Rudd 3610* (SFV, UC); without exact locality, elev. 50 m, 27 Mar 1971, *Hastings 71-179* (SD). Isla Partida Sur, near n. end, rocky slope near beach, ca. 5 m elev., 20 Apr 1962, *Moran 9606* (SD, US); near summit of pass leading to dry lake, ca. 62 m elev., 24 Jun 1964, *Wiggins 19110* (DS); without exact locality, 22 Nov 1973, *Orr s.n.* (UC).

Superficially, *A. pacensis* does resemble *A. constricta,* both species having small leaflets, yellowish flowers in capitate inflorescences, straight spines, and long, narrow pods. However, as pointed out by Johnston, *A. pacensis* lacks the medibracteate peduncles characteristic of *A. constricta* and its relatives (Bentham 1875, p. 446, 513). Another difference is in the structure of the pods. Those of *A. constricta* are dehiscent, and the inner surface of the valves (pericarp) has a ribbon-like, continuous, sclerenchymatous band parallel to the longitudinal axis of the valve. In *A. pacensis,* the pods are indehiscent with parenchymatous tissue forming septa between the seeds. The seeds of *A. constricta* are mottled-gray with lighter-colored areoles, i.e., the area on each face bounded by the pleurogram, a crack in the testa (Gunn 1981, p. 920; Polhill et al. 1981, p. 6). The seeds of *A. pacensis* are dark brown with lighter-colored, relatively larger areoles.

More closely related to *A. pacensis,* apparently, are such species as *A. cochliacantha* (*A. cymbispina*), *A. pennatula, A. macracantha, A. schaffneri,* and *A. farnesiana,* all of which are fairly similar vegetatively, have summibracteate peduncles, capitate inflorescences, and indehiscent pods with pulpy, parenchymatous valves, and are more or less septate between the seeds (Bentham 1875, p. 446, 499 ff.). All have spines that are essentially straight, not recurved or unguiculate. Of these species, *A. cochliacantha* and *A. farnesiana* are known from Baja California, the others only from the mainland.

Key to *Acacia pacensis* and related species in Baja California

Pods linear or elongate, dehiscent or indehiscent, 3–7 mm wide; peduncles medibracteate or summibracteate; flowers essentially glabrous; stipular spines slender, straight, terete.

  Peduncles medibracteate, i.e., bearing several minute bractlets at about midpoint; pods dehiscent, continuous within, not septate, constricted between the seeds, glabrous, often lustrous at maturity; seeds gray-mottled. .... *A. constricta* Benth.

  Peduncles summibracteate, i.e., bearing bractlets at the apex, immediately below the flowering head; pods indehiscent, septate, slightly constricted between the seeds, puberulent with subappressed hairs; seeds dark brown, not mottled. .... **A. pacensis** Rudd & Carter

FIG. 1. Holotype of *Acacia pacensis* Rudd & Carter.

Pods oblong, 9–25 mm wide, indehiscent; peduncles summibracteate; flowers puberulent, at least at tip of calyx and corolla lobes; stipular spines terete or flattened, concave-boat-shaped.

Spines terete, acicular; pods turgid, sessile with seeds usually irregularly imbedded in parenchymatous tissue. .... *A. farnesiana* (L.) Willd.

Spines flattened, concave-boat-shaped; pods compressed, stipitate, with seeds regularly aligned. .... *A. cochliacantha* Humb. & Bonpl. ex Willd.

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SUAEDA ESTEROA (CHENOPODIACEAE), A NEW SPECIES FROM ESTUARIES OF SOUTHERN CALIFORNIA AND BAJA CALIFORNIA

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ABSTRACT

A new species, **Suaeda esteroa,** is described from estuaries of southern California and Baja California, Mexico. Although numerous collections of this plant have been made during the last century, it has been confused previously with four other species of the genus. Most frequently, *S. esteroa* has been identified as *S. californica* var. *californica,* a plant restricted to the coast of central California. These two taxa are distinct morphologically, ecologically, and geographically. Recognition of *S. esteroa* as a species restricted to estuaries of southern California and Baja California emphasizes further the floristic difference between estuaries occurring to the north and south of Point Conception, Santa Barbara County. A key to the coastal central and southern California species of *Suaeda* is provided.

Taxonomy of *Suaeda* Forsk. ex Scop. (Chenopodiaceae), a genus restricted to saline or haline, primarily wetland soils, has been problematical for many years. In southern California, *Suaeda* has been considered to include anywhere from 3 species containing 7 taxa to 7 species containing 9 taxa (Watson 1874, 1880; Jepson 1914, 1923; Standley 1916; Abrams 1944; Munz 1959, 1974; Mason 1969; Hopkins and Blackwell 1977). The various treatments have differed not only on the assignment of rank, but also on the geographic limits of the taxa. The causes of inconsistencies among treatments of the genus can be attributed to several factors: material of each taxon, including type specimens, has not been available to or examined by all researchers; some species are quite variable morphologically; specimens are difficult to identify when pressed and dried; herbarium material often lacks important characteristics of the plants; and some researchers have made limited or no observations on the plants in their native habitats. One result of the varied interpretations of *Suaeda* in the taxonomic literature is the misapplication of names by biologists when preparing manuals, monographs, floras, and lists.

While conducting inventories of vascular plants from estuarine wetlands in southern California, the authors made numerous collections

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of *Suaeda*. Included among these is a new species, which in previous reports has been confused with other species of the genus.

Suaeda esteroa Ferren & Whitmore, sp. nov.

Plantae glaber, perennis, suffruticosus. Caules decumbens ad erectus, plerumque ramosissimus in inflorescentia, rami erectus. Folia linearis, ascendens, pagina adaxialis planus, pagina abaxialis convexus, sessilis, usque 6 cm longa, virens et plerumque non glaucus; plus lata basi folia, bractiformis, et abbreviatus (0.5–2 cm longa) in inflorescentia. Flores perfectus vel interdum unisexualis, 1.5–3 mm lata, (1–) 3–5 in uterque glomerulus ex axillae bractiformis folia in inflorescentia definate, subtendus a 1–5 bracteolae inaequalis, integromarginatus, scariosus; perianthium lobi 5, carinatus et cucullatus, cum appendices membranous marginatus, unus lobus magus quam alius lobi; staminea 5; styli (2–)3 partitum, glabrous, linearis. Fructifer calyces 2.5–3.5 mm lata. Semina horizontalis in ovarium, irregulariter biconvexus, fere orbicularis, porphyreus, nitens, 0.8–1 mm crassus, 1–1.3 mm latus, 1.2–1.5 mm elatus, pericarpium facile amotus (Fig. 1).

Plants glabrous, perennial, from several oblique to horizontal, generally shallow roots; axis up to 60 cm long, average ca. 40 cm. Stems decumbent to erect, suffruticose, up to 2 cm in diameter at base, straw-colored, often with exfoliations, usually much branched in inflorescence, branches erect and with short sharp alterations in course of axis in mature inflorescence. Leaves linear, ascending, entire-margined, acute-tipped, usually falcately curved, plane adaxially, convex abaxially, sessile, up to 6 cm long, succulent, green, yellow-green, or pale glaucous green, occasionally reddish; withering to straw color and becoming deciduous or persisting as vascular strands towards base of mature plant; broader at leaf base, bract-like, and shorter (0.5–2 cm long) in the inflorescence. Flowers perfect or occasionally unisexual, 1.5–3 mm broad (fresh material), (1–)3–5 per glomerule from bract-like leaf axils of well-defined inflorescence, subtended by 1–5 unequal, entire-margined, scarious bractlets; perianth lobes 5, carinate (keeled) and cucullate (hooded), with membranaceous marginal flanges; stamens 5; styles (2–)3-parted, glabrous, linear. Fruiting calyces 2.5–3.5 mm broad (fresh material). Seeds horizontal in ovary, irregularly biconvex, nearly orbicular, reddish-brown, shiny, 0.8–1 mm thick, 1–1.3 mm broad, 1.2–1.5 mm tall, pericarp easily removed.

TYPE: USA, California, Ventura Co.: clay substrate of salt marsh, vicinity of mean high tide along creek adjacent to n. shore, e. arm of Mugu Lagoon; ca. 0.1 km w. of Rt. 1 and 2 km se. of Las Posas Rd., Pacific Missile Testing Center, Pt. Mugu Naval Air Station; 34°06′15″N, 119°05′W; 10 Sep 1980, *S. A. Whitmore & W. R. Ferren 2343* (Holotype: UCSB; isotypes: CAS, GH, MEXU, RSA, SD, UC, US).

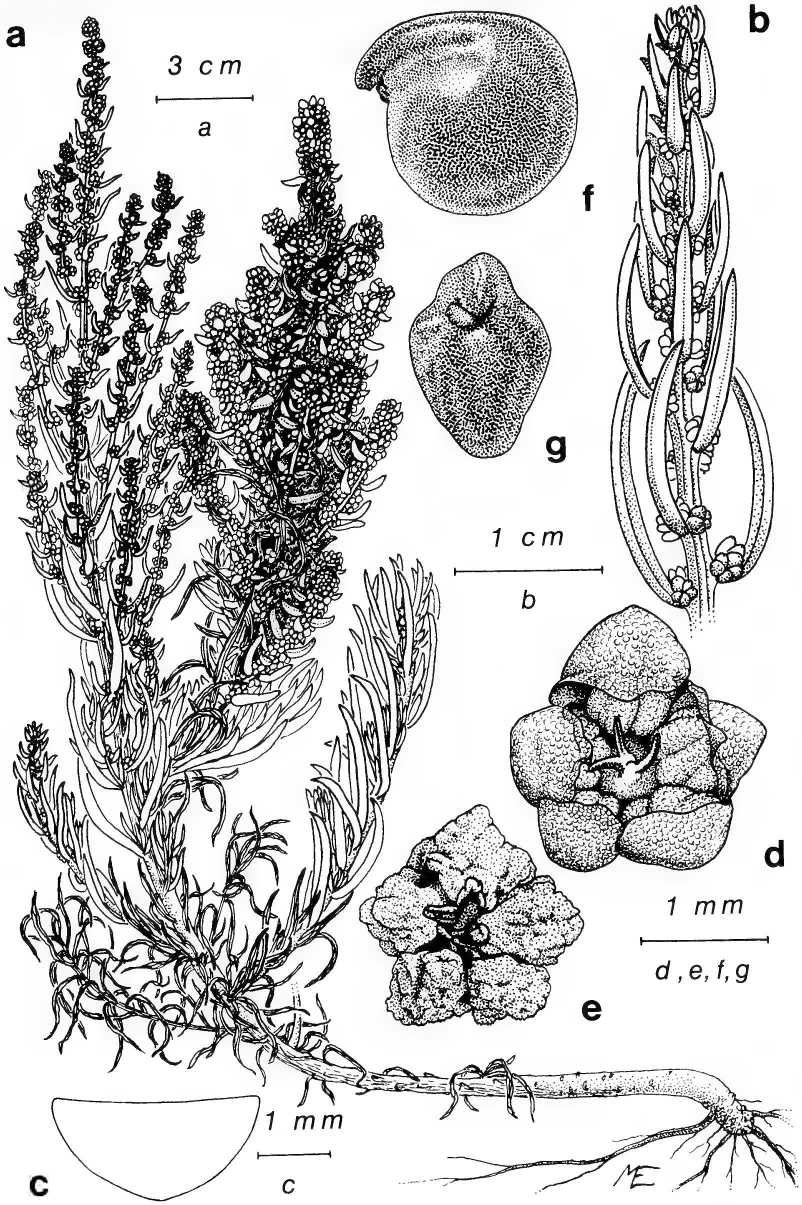

FIG. 1. *Suaeda esteroa*. a. Habit. b. Branch of inflorescence. c. ×-section of leaf. d. Pre-anthesis flower, fresh material. e. Pre-anthesis flower, herbarium material. d. Seed, orbicular outline. g. Seed, irregularly biconvex view.

PARATYPES: Mexico, Baja California Norte: Laguna Mormona, 16 Sep 1970, *Neuenschwander 7* (RSA, SD); San Quintin Bay, 17 Jan 1973, *Moran 19468* (SD); Laguna Manuela, 25 Jan 1972, *Moran 19073* (SD); Bahia de los Angeles, 24 Nov 1973, *Mudie 1061* (SD); Baja California Sur: Scammon's Lagoon, 9 Jan 1973, *Anderson 3227* (RSA); Abreojos Lagoon, 20 Apr 1972, *Mudie 759* (SD); Estero de la Laguna, 25 Apr 1972, *Mudie 804* (SD); El Coyote Lagoon, 22 Apr 1972, *Mudie 768* (SD); Estero Salinas, 22 Nov 1946, *Wiggins 11489* (UC); Puerto Chale, 2 May 1972, *Mudie 855* (SD); USA, CA, Los Angeles Co.: Long Beach, 12 Jul 1900, *Jones s.n.* (POM); Anaheim Landing, 10 Jul 1930, *Fosberg S3179* (LAM); San Pedro, 6 Sep 1904, *Abrams 4195* (DS, POM); Orange Co.: Balboa Beach, 10 Feb 1924, *Peirson 4535* (RSA); Bolsa Bay, 25 Jul 1970, *Henrickson 5029* (RSA); Newport Backbay, 27 Aug 1980, *Ferren 2333 & Whitmore* (UCSB); Seal Beach, 19 Sep 1925, *Jones s.n.* (POM); Surfside, 28 Sep 1957, *Raven 11383* (CAS); San Diego Co.: Chula Vista, 25 Jul 1938, *Keller s.n.* (POM); Coronado, 29 Apr 1919, *Cooper 306* (JEP); San Diego, Mar 1875, *Cleveland s.n.* (SD); Imperial Beach, 28 Oct 1938, *Purer 7889* (SD); National Ranch, 5 Jan 1884, *Cleveland s.n.* (SD); Silver Strand, 7 May 1938, *Gander 5488* (SD); Santa Barbara Co.: Goleta, 21 Oct 1964, *Pollard s.n.* (CAS, LAM, SBBG); Ventura Co.: Pt. Mugu, 4 Oct 1959, *Raven & Thompson 14609* (RSA, CAS).

Suaeda esteroa is confined to estuaries of southwestern North America from Goleta Sough, Santa Barbara County, California, south at least to Almejos Bay, Baja California Sur, Mexico (Fig. 2). It grows frequently in clay, silt, and sand substrates just above mean higher high water level of salt marshes. These upper marshlands are classified as Irregularly Flooded Estuarine Emergent Wetlands of the California Province (Cowardin et al. 1979). *Suaeda esteroa* is one of several plants in southern California and Baja California that characterize the lower portion of this wetland. Based on the occurrence of *S. esteroa,* the entire upper marsh, located between mean higher high water and extreme high water, has been called the Suaedetum flora assemblage or Upper Littoral Zone (Stevenson and Emery 1958; Henrickson 1976). Plants commonly associated with *S. esteroa* in this zone in California include *Batis maritima* L. (in lower areas), *Cuscuta salina* Engelm., *Distichlis spicata* (L.) Greene var. *spicata, Frankenia grandifolia* Cham. & Schlecht. var. *grandifolia, Jaumea carnosa* (Less.) Gray, *Limonium californicum* (Boiss.) Heller, *Monanthochloe littoralis* Engelm., *Salicornia virginica* L., and *Triglochin concinna* Davy. var. *concinna.* In the lower limits of its growth in intertidal zones *S. esteroa* occurs rarely in the Regularly Flooded Estuarine Emergent Wetland (Cowardin et al. 1979), associated with *Batis maritima, Salicornia bigelovii* Torr., *S. virginica,* and *Spartina foliosa* Trin.

Suaeda esteroa was apparently collected for the first time in 1875 in the vicinity of San Diego, California (*Cleveland s.n.* (SD)). Although

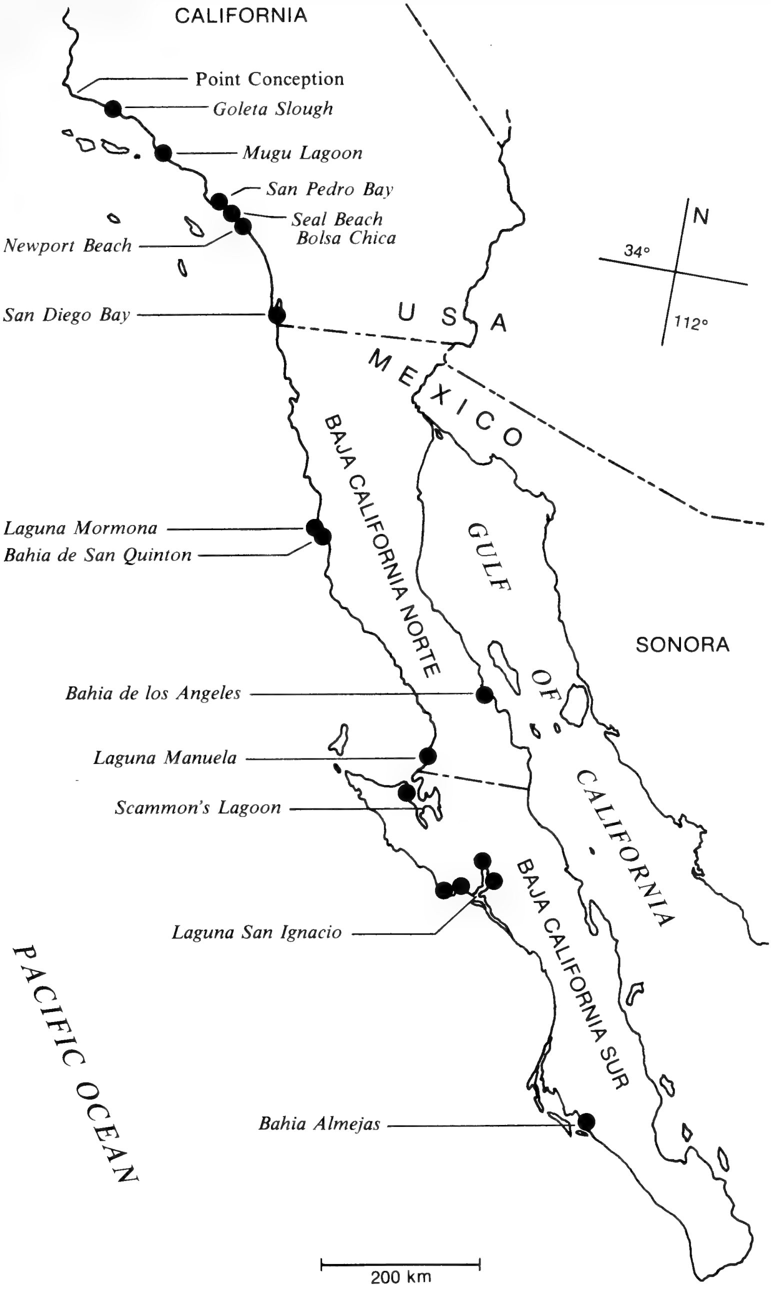

FIG. 2. Distribution of *Suaeda esteroa* based on herbarium specimens. Each dot may represent numerous collections or several adjacent localities.

there are numerous 20th century collections made throughout its range, previous investigators have referred the plant to one of four species of the genus: *S. californica* Wats. var. *californica, S. calceoliformis* (Hook.) Moq., *S. moquinii* (Torr.) Greene, or *S. fruticosa* (L.) Forsk. The latter is a plant of European coastal salt marshes and does not resemble *S. esteroa.* Using various manuals and floras (e.g., Munz 1959, 1974) collectors have named the great majority of specimens of *S. esteroa* as *S. californica* var. *californica,* a plant restricted to the coast of central California. Similar to *S. esteroa,* this plant appears glabrous, and is green (usually not glaucous) and perennial. Unlike *S. esteroa* it has cucullate or rounded (not cucullate and carinate) perianth parts; stigmas pubescent and subtended by a fleshy ring (not glabrous and without a ring); black (not reddish-brown) seeds; flowers in axils on branches and main stems (not restricted to inflorescence); leaves that are not reduced significantly in the inflorescence and are short petiolate or narrowed at the base; and stems that divide at or near the base of the plant often producing a multistemmed, spreading, shrubby habit rather than the decumbent or erect, single-stemmed habit of *S. esteroa.* Furthermore, *S. californica* var. *californica* occurs on coastal bluffs, beaches, berms, and margins of estuaries at elevations higher than the wetland type characterized by *S. esteroa.* At margins of estuaries it occurs in the vicinity of extreme high water and is one element of the Irregularly Flooded Estuarine Scrub/Shrub Wetland. Thus, the two taxa are distinct morphologically, ecologically, and geographically.

The inclusion of *S. esteroa* in *S. californica* var. *californica* has resulted in many reports of the latter plant from southern California. Literature in which plants of *S. esteroa* either are named *S. californica,* or have been included in this species in part, can be divided into three groups: taxonomic treatments (e.g., Standley 1916; Hopkins and Blackwell 1977); floras (e.g., Abrams 1944; Munz 1959, 1974; Shreve and Wiggins 1964; Raven and Thompson 1966; Mason 1969; Smith 1976; Wiggins 1980); as well as phytogeographical and ecological analyses (e.g., Purer 1942; Stevenson and Emery 1958; Vogl 1966; Warme 1971; Macdonald and Barbour 1974; Henrickson 1976; Macdonald 1977; Zedler 1977, 1982). Considerable information about *S. esteroa* is contained in these works. For example, Zedler (1977) reported elevational distribution data for plants fitting the description of *S. esteroa* from the Tijuana Estuary. She found that the plants occurred from about 3 to 13 dm above mean water level, with a peak occurrence (75%) at about 9 dm, where they also reached their greatest cover (ca. 20%). In the region of 9 to 10 dm above sea level she found that *S. esteroa, Frankenia grandifolia,* and *Monanthochloe littoralis* dominated the vegetation. Generally, reports of *S. californica* var. *californica* or glabrous *S. californica* from estuaries south of Point Conception, Santa Barbara County, have been based on plants of *S. esteroa.*

Recognition of *S. esteroa* as a species restricted to estuaries of southern California and Baja California emphasizes further the floristic differences between central and southern California coastal salt marshes. Macdonald and Barbour (1974), Henrickson (1976), and Macdonald (1977) have discussed in detail the environmental and floristic differences between these two groups of estuarine wetlands. They identified a series of plants that characterize or are restricted to each group. The occurrence of *S. californica* var. *californica* in coastal habitats of central California from San Francisco Bay Area south to Morro Bay, San Luis Obispo County, and the occurrence of *S. esteroa* in southern estuaries south of Point Conception, as described herein, are new examples of plants that do not overlap in range. Furthermore, as a result of the description of *S. esteroa,* recognition of the allopatric occurrence of *S. californica* var. *californica* and southern, pubescent, glaucous varieties (var. *pubescens* Jeps. and var. *taxifolia* (Standl.) Munz) provides a more realistic interpretation of infraspecific taxa than reported previously. *Suaeda esteroa* is added to *Monanthochloe littoralis* and *Batis maritima* as a plant restricted to southern estuaries; and both *S. esteroa* and *M. littoralis* reach their northwestern limits south of Point Conception at Goleta Slough.

Although several recent investigations (McNeil et al. 1977, Hopkins and Blackwell 1977, Bassett and Crompton 1978) have clarified some of the taxonomic and nomenclatural problems of North American species of *Suaeda,* various problems remain unresolved. Three problems in California that need work include identity and relationship of desert alkali flat plants, the relationships of infraspecific taxa of *S. californica,* and identity and relationships of these two groups when they occur sympatrically in coastal southern California and Baja California. In spite of these unresolved problems we think it is helpful to provide a key to the California species because of the addition of *S. esteroa* to the flora and the information provided recently by other researchers. However, we suggest that this key serve only as a general guide to the taxa until additional information is available.

Key to coastal central and southern California *Suaeda*

A. Perianth lobes corniculate (horned), unequal; plants annual, glabrous and usually glaucous; stems erect or decumbent, often with red stripes in maturity; leaves greatly reduced in inflorescence. Salt flats and disturbed, open, saline or haline soils; widespread in North America. .... *S. calceoliformis* (Hook.) Moq. [*S. depressa* (Pursh) Wats., including var. *depressa* and var. *erecta* Wats. (McNeill et al. 1977)]

A. Perianth lobes carinate (keeled) and/or cucullate (hooded) or rounded, unequal or equal; plants perennial, glabrous or pubescent, bright green or glaucous; stems erect, decumbent, or spreading; leaves greatly reduced in inflorescence or similar throughout.

B. Plants glabrous throughout, bright green, yellow green, or occasionally pale glaucous green; perianth lobes carinate and cucullate, unequal; stigmas glabrous, linear, without subtending structures; flowers (1–)3–5 per axil, confined to branches of well-defined inflorescence; bractlets entire-margined; seeds irregularly biconvex, reddish brown; leaves linear, sessile, plane adaxially, convex abaxially, greatly reduced in inflorescence; stems decumbent or erect, usually not divided near base; branches erect. Irregularly flooded, southern coastal salt marshes. .... *S. esteroa* Ferren & Whitmore

B. Plants appearing glabrous, or pubescent, glaucous or green; perianth lobes cucullate or rounded, usually equal; stigmas pubescent, linear-lanceolate and subtended by a fleshy columnar ring; flowers 1–9 per leaf axil; bractlets usually ciliate, laciniate, or denticulate; seeds regularly biconvex, black; leaves linear, petiolate or at least narrowed at base, terete, subterete, or flat, usually not strongly reduced in inflorescence; stems erect, decumbent, or spreading, usually divided near base; branches divergent. Coastal bluff scrub, beaches, and margins of salt marshes usually above extreme high water.

C. Flowers, including fruiting calyx, 1–2(–2.5) mm broad, usually 1–3 per leaf axil of branches and occasionally main stems; leaves, immature branches, and inflorescence appearing glabrous, or pubescent or puberulent; stems smooth, usually shiny; branches (fresh material) of inflorescence slender (ca. 1(–2) mm wide); leaves usually terete, subterete or flattened, occasionally reduced on branches of inflorescence. (Ventura Co.?) Orange Co. and south; also deserts and interior alkaline valleys. ... *S. moquinii* (Torr.) Greene [*S. torreyana* Wats., including var. *torreyana* and var. *ramosissima* (Standl.) Munz (Basset and Crompton 1978)]

C. Flowers, including fruiting calyx, 1.5–3(–4) mm broad, (1–)3–9 per leaf axil of branches and main stems; plants appearing glabrous, or pubescent; stems usually bearing knobby bases of deciduous leaves, frequently dull; branches (fresh material) of inflorescence stout (1–)2(–3) mm wide; leaves usually subterete, flat, or plane adaxially.

D. Plants green, appearing glabrous, or pubescent on immature branches and inflorescence. San Francisco Bay Area south to Morro Bay, San Luis Obispo Co. .... *S. californica* Wats. var. *californica*

D. Plants glaucous, occasionally nearly glabrous, to pubescent, puberulent, or densely villous on stems, leaves, and throughout inflorescence. Santa Barbara

Co. and south. ....
... *S. californica* var. *pubescens* Jeps. (as treated here, including var. *taxifolia* (Standl.) Munz. This complex is quite variable, poorly understood, and best treated as a single variety until additional work is done.)

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NOTES AND NEWS

Is *Dudleya parva* (Crassulaceae) Truly in San Luis Obispo County?—In describing *Dudleya bettinae,* Hoover (Leafl. W. Bot. 10:186–187. 1965) reported two small colonies of *Dudleya parva* Rose & Davidson near Morro Bay, San Luis Obispo County, California along San Bernardo Creek and near the mouth of Chorro Creek. The species was known previously from two localities in Ventura County. The seeming disjunction of over 300 km makes one wonder about the identity of the northern plant.

Herbarium specimens of the *Dudleya* from San Bernardo Creek (*Hoover 9101* CAS, DS, UC; *Nakai 614* CAS, LA, SD) seem similar to specimens of *D. parva* from Ventura County [(Conejo Grade, *Davidson 3535* (Bullard), (Isotype: UC); Arroyo Santa Rosa, *Moran 2066* (CAS, DS, UC); *Moran 3074* (DS, UC); *Nakai 611* (CAS, LA, SD)]: They differ in having a thicker caudex and narrower leaves. When living material is compared, they are quite different. In the description and illustrations published by Moran (Des. Pl. Life 20:137–140. 1948) and in wild and cultivated plants of *D. parva* from Arroyo Santa Rosa, the roots are constricted at irregular intervals; the caudex branches laterally, especially from the base; leaves are linear to oblanceolate, turgid though relatively flat, slightly glaucous, often tinged purple especially near the base, withering and deciduous by early summer. In the *Dudleya* from San Bernardo Creek, on the other hand, the roots lack constrictions; the caudex is somewhat thicker and branches "dichotomously"; leaves are linear, mostly terete, glaucous, withering (though often not completely) towards the middle of summer, after flowering, and remaining attached for a year or more. The differences between the two seem to show that the northern plant should not be referred to *D. parva,* a view also shared by Moran (Status Report of *Dudleya bettinae* in Inventory of Rare and Endangered Vascular Plants of California, California Native Plant Society Special Publication No. 1 ed. 2:18, 39 fn. 1980).

Hoover (1965) remarked that "the inflorescence and flowers of *D. bettinae* are virtually identical with those of *D. parva,* but the caudex and leaves are markedly stouter." Compared with herbarium and living material from the type and other localities of *D. bettinae* [Ridge one mi w. of Cerro Romauldo, *Hoover 7278* (Type: CAS; Isotype: RSA); *Nakai 615* (CAS, LA); Cayucos, *Moran 2277* (CAS, DS, SD, UC)] the San Bernardo Creek plant seems to be a dwarf form. In *Dudleya,* species with dwarf forms are not uncommon [*D. greenei* Rose, *D. cymosa* (Lemaire) Britton & Rose subsp. *gigantea* (Rose) Moran, *D. cymosa* subsp. *setchellii* (Jepson) Moran, *D. attenuata* (Watson) Moran subsp. *orcuttii* (Rose) Moran, etc.]. *Dudleya bettinae* and the San Bernardo Creek plant grow in similar substrates and exposures and flower at the same time. In an experiment utilizing a temperature and humidity regulated greenhouse to force rapid elongation of floral and vegetative parts of *D. bettinae* from the type and Cayucos localities, a closely related taxon, *D. abramsii* Rose subsp. *murina* (Eastwood) Moran, from Cuesta Canyon Park, San Luis Obispo County (*Nakai 616* CAS, LA, SD), *D. parva,* and the San Bernardo Creek plant, the San Bernardo Creek plant did not differ much from *D. bettinae* in both floral and foliage shape and size. Being only a few kilometers from the type locality of the species it resembles and exhibiting few taxonomic distinctions, except for its small size, this dwarf plant appears not to deserve taxonomic rank in the genus *Dudleya.* It would seem best, as Moran (1980) also believes, to refer the northern *D.* "parva" to *D. bettinae.*—Kei M. Nakai, 12717 S. Grevillea Ave., Hawthorne, CA 90250. (Received 8 Jan 1981; revision accepted 31 May 1982.)

A Disjunct Population of *Ribes sanguineum* (Grossulariaceae) in Idaho.—*Ribes sanguineum* Pursh. has not previously been reported from Idaho nor anywhere east of the Cascade/Sierra Cordillera (Vasc. Pl. Pacific NW Pt. 3, Hitchcock et al. 1961). A population of pink flowering currents has been known from the lower St. Maries River breaks in Northern Idaho since 1963 (Charles Scribner, pers. comm.). A fruitless search was made of the general area shortly thereafter. Years later, renewed interest in disjuncts prompted a letter to the local paper, and we were rewarded with a more precise location (Winifred Jensen, pers. comm.). The first collection of *Ribes sanguineum* was made from an isolated plant in May of 1975 (*M. Lazelle 7584,* IDF). Further investigation by the senior author in early June located eleven more living plants and several dead plants, all in a ½ km stretch of the same, steep-sided streambottom (*Johnson 75305,* IDF). In 1976 the authors carefully surveyed similar habitats in about 25 km² during the flowering period. We believe we now have circumscribed the population. Altogether, 65 living plants have been located, all in a 5 km² area of an unnamed tributary of Hell's Gulch (T46N R2W, Secs. 2, 3 and 35, B.M.) (*Ardema 76189, -101, -198, -232, -343, -344, -345,* all IDF).

The site is about 5 km north of the town of St. Maries, Benewah County, Idaho. The population inhabits a steep canyon cut through Columbia River basalts. Elevation ranges from 850 to 940 m, averaging some 45 m above valley bottom of the adjacent St. Maries River. Most of the area was burned in 1910 (probably re-burned later) and is now in a mosaic of dense pole-sized conifers, shrub patches and grassy balds. The habitat types undoubtedly include *Abies grandis*/ and *Thuja plicata*/*Pachistima myrsinites* (Daubenmire and Daubenmire, Wash. Ag. Expt. Sta. Tech. Bul. No. 60, 1968). Despite the restricted distribution, plants are found in a variety of habitats. Soils include thin rocky colluvium, basalt talus, and deep forest soils. Overstory shade ranges from open to 75% cover. More plants were on westerly aspects. The range of microhabitats coincides well with those taken from herbarium labels from collections west of the Cascades. Much of the area is grazed by cattle; it is deer winter range.

We postulate that one of the reasons this population of such a large and showy shrub has so long been undocumented is that the habitats and vegetative characteristics of *R. sanguineum* are very similar to those of the ubiquitous *R. viscosissimum* Pursh. Another factor is the inaccessibility; the entire population is on private land that is steep, uninviting, and unroaded. To determine if this population of plants escaped from cultivation we investigated every ranch and homesite for several kilometers below the site along the river valley and found no plants of *R. sanguineum*. There are no other homesites in or near the *Ribes* population. At least in the recent past there seems no immediate source of cultivated seed. Of course, past escapes from bird-disseminated seed could have made their way up this gulch and the population could have expanded in suitable habitat. But there are dozens of areas in northern Idaho, close to residences, where coastal habitats prevail, yet ten years of investigation on Idaho disjuncts has revealed no escaped *Ribes sanguineum*. We therefore believe this to be a natural but restricted relict population. Supporting the relict population hypothesis is the occurrence in the general area of other coastal disjuncts such as *Alnus rubra* Bong., *Physocarpus capitatus* (Pursh) Kuntze, *Dodocatheon dentatum* Hook., and *Berberis nervosa* Pursh. Daubenmire (Jour. Biogeo. 2:1–18, 1975) postulates that Pacific coastal disjuncts in the northern Rockies owe their existence to refugia that occur along the major canyons of the western slopes. The St. Maries River forms one of these canyons.

There seems no obvious reason why the population is so very restricted. Seed is produced (*Johnson 76496,* IDF), at least in some years, and after seed stratification seedlings were produced in cultivation. Perhaps most of a larger population of *Ribes sanguineum* was eliminated by white pine blister rust, introduced to this area about 1923. Red flowering current is only moderately susceptible to blister rust, and there is no record of *Ribes* plants having died from the disease (Raymond Hoff, pers. comm.). Perhaps a larger population was decimated by *Ribes* eradication practiced so vigorously in northern Idaho. Homer Hartman (pers. comm.), long connected with the eradication program, recalls that Hell's Gulch is a great distance from the nearest area where white pine was protected, hence *Ribes* were never purposefully eradicated from the lower St. Maries canyon habitats. Would heavy use by livestock or big game have decimated a larger population? The answer seems negative because *Ribes* species are notably unpalatable to big game, and we saw no indication of significant browsing on the plants in this population in spite of heavy grazing by cattle in the area. Furthermore, numerous gulches we investigated are too steep for cattle and don't appear ever to have been grazed.

Although no disjunct woody plants in northern Idaho are known to be so very restricted in distribution, herbaceous species such as *Viola sempervirens* Greene and *Thelypteris nevadensis* (Baker) Clute have been reported recently as coastal disjuncts of very limited range in the northern Rockies (Johnson and Steele, Northw. Sci. 52:3. 1978).

We present the following hypothesis to account for the elevational restriction of this disjunct population. The winter of 1972–73 had low temperatures with virtually no snow cover. *Ceanothus velutinus* Dougl. and *C. sanguineus* Pursh were killed to the snow level throughout Idaho by these conditions. We discovered many dead *Ribes sanguineum* plants during the survey work. It is quite possible that the dead *Ribes* plants were winter-killed. If this is true, then the restriction to a small midslope area of a steep canyon may result from these factors interacting: 1) an average snow depth sufficient to cover shrub crowns during lowest temperatures determines the lower elevational limits; 2) restricted growing season determines the upper elevational limits; 3) steep slopes provide excellent air drainage, preventing cold air pooling; 4) the heat sink properties of the canyon moderate temperatures.

We believe this population of *Ribes sanguineum* to be a natural Pacific coastal relict. This first report for Idaho is an eastward extension from the east slopes of the Washington Cascades of ca. 300 km. Herbaria searched: BOIS, CIC, ID, IDF, IDGH, NY, ORE, OSC, UC, US, WS and WTU. Duplicates deposited at ID, WS and WTU. *Ribes sanguineum* has been placed on the Idaho State list of threatened plants (Vasc. Pl. Spp. of Concern, FWR Exp. Sta. Bul. #34, Moscow, ID, June 1981).—FREDERIC D. JOHNSON and DOUGLAS S. ARDEMA, Forestry, Wildlife and Range Experiment Station, Univ. Idaho, Moscow 83843. Contribution No. 255. (Received 11 Dec 1981; revision accepted 20 Jun 1982.)

DISTRIBUTION OF *Polygala acanthoclada*.—*Polygala acanthoclada* is known from Utah, southwestern Colorado, northern Arizona, and southern Nevada, and has also been reported in California: Shadow Mountains (erroneous report based on a misidentified specimen) and New York Mountains of San Bernardino County; and Eagle Mountains of Riverside County.

We found a population of at least 300 plants in Lucerne Valley (San Bernardino County), 5 km east of Camp Rock Road along Old Woman Springs Road (S 20 T4N R2E), at an elevation of about 946 m. Our collection (*Sanders 2097*; 27 May 1981; UCR, RSA) documents a range extension of 225 km. The *Polygala* population is scattered on a flat sandy plain with individuals and small groups of plants interspersed within a creosote bush scrub matrix dominated by *Larrea tridentata, Ambrosia dumosa* and *Hilaria rigida*.

The Lucerne Valley habitat is very different from that reported elsewhere. The Eagle Mountain population occurs 0.5 km north of the Joshua Tree National Monument visitor center near Cottonwood Spring at an elevation of about 950 m. The *Polygala* population occurs on a gently rolling, sandy-gravelly, alluvial plain with individuals and small groups of plants interspersed within a mixed shrub vegetation, dominated by *Coleogyne ramosissima, Larrea tridentata, Tetracoccus hallii, Cassia armata,* and *Juniperus californica.*

The New York Mountain populations occur near Barnwell and in Keystone Canyon. Near Barnwell, at about 1500 m elevation, the topographic mosaic includes flat or gently tilted stony plains broken by ridges, washes, and their rocky slopes. The stony plains support a sparse "grassland" (5% cover) dominated by *Hilaria jamesii,* and sometimes *Gutierrezia microcephala.* The rocky slopes have less *Hilaria* and *Gutierrezia* but also include a sparse overstory (2% cover) of *Yucca brevifolia, Yucca baccata,* and *Juniperus osteosperma.* Plants of *P. acanthoclada* characteristically occur at the edges of the stony plains or along small washes and on rocky slopes.

In Keystone Canyon, *P. acanthoclada* occurs on steep, rocky slopes at an elevation of about 1708 m in a pinyon woodland about equally co-dominated by *Pinus monophylla, Juniperus osteosperma,* and *Quercus turbinella.* Plants of *P. acanthoclada* occur mostly in grassy openings among the trees and large shrubs.

In southern Nevada, *P. acanthoclada* is reported from Ash Meadows in Nye Co. (*J. C. and A. R. Roos 6144*), where it grows on alkali flats with *Chrysothamnus albidus* and *Atriplex confertifolia* at an elevation of 695 m.

Polygala habitats at Lucerne Valley, Cottonwood Spring, Barnwell, Keystone Canyon, and Ash Meadows are quite different from one another in terms of slope, substrate, vegetation density, and associated species. Consequently, knowledge of one habitat or locality does not help predict where other localities might be. Plants of *Polygala acanthoclada* are relatively few and inconspicuous. They are seldom collected, despite their highly accessible locations along well-traveled roads. Because of the apparent nonspecificity of its habitat, *Polygala acanthoclada* may yet be found in other Mojave Desert localities.—FRANK C. VASEK and ANDREW C. SANDERS, Dept. of Botany and Plant Sciences, Univ. California, Riverside 92521. (Received 28 Dec 1981; revision accepted 6 Jul 1982.)

JACKRABBIT HERBIVORY AND CREOSOTE BUSH (*Larrea*) REPRODUCTION.—Jackrabbits (*Lepus californicus*) evidently trim branches from the creosote bush, *Larrea tridentata* (D.C.) Cov. (Jaeger, J. Mammal. 19:187–188. 1948; Vorhies and Taylor, Univ. Arizona Agr. Exp. Sta. Techn. Bull. No. 49:471–587. 1933) but reports vary as to whether plant parts are actually ingested by the animals (Jaeger 1948; Hayden, J. Mammal. 47:42–46. 1966; Chew and Chew, Ecol. Monogr. 40:1–21. 1970).

Trimmed *Larrea* branches were observed lying at the bases of the shrubs during a recent study of Mojave Desert creosote bush (Boyd, M.S. thesis, Calif. State Polytechnic Univ., Pomona. 1979) near Barstow, California. Damage to the cut branches was detected only during flower production, when I observed that many of the flower buds had been eaten. This note reports my attempts to answer two questions regarding the observed browsing of *Larrea*: 1) Was *Lepus californicus* responsible for the damage? 2) Did the loss of reproductive units (flower buds, flowers, immature fruits) significantly decrease the reproductive output of creosote bush?

I established a 43 × 47.5 m quadrat within a relatively undisturbed *Larrea-Ambrosia* community (see Boyd 1979 for study site details). The pruned branches lying around each shrub were collected every 2–3 weeks from early April 1979 until mericarp dispersal began (late June 1979). I counted the number of cut pedicels and intact reproductive units on each branch. To determine whether the proportion of cut pedicels on the cut branches was different from that on unpruned branches, I removed one branch higher than 1.5 m above the ground from each of ten shrubs. The number of reproductive units was counted in the same way as with the pruned branches. Because the size of the animal pruning the branches is reflected in the heights of the cut branches, I measured the vertical distance from 773 freshly cut branches to the soil surface.

Although jackrabbits were not seen browsing *Larrea* shrubs on the site, two indirect lines of evidence point to their being responsible for the pruning. First, branches up to 5 mm thick were found cleanly sliced through. Examination of a mammal species list compiled for the site (Boyd 1979) reveals that *L. californicus* is the only browsing mammal present that has the jaw strength necessary to cut through a branch that thick. Second, the mean height of the cut branches was 52.5 ± 10.0 cm (S.D.), with a maximum height of 90 cm. Again, the only browsing mammal present of the appropriate size is *L. californicus*.

Pruned branches suffered a much greater loss of reproductive units than branches beyond reach of the rabbits. Of 863 reproductive units on the branches taken from heights greater than 1.5 m, only 0.35% had been destroyed. In contrast, branches gathered from the ground around the shrubs on the same day the high ones were collected had lost 84% of the 3708 reproductive units present.

Of the total number of reproductive units on the browsed branches (14,570), 89.4% were eaten by the rabbits. The average loss per shrub was 164 ± 245 (S.D.) reproductive units. The large standard deviation reflects the fact that a few shrubs lost no reproductive units while others lost up to 1220 during the monitored period.

Does the rabbit browsing significantly decrease the reproductive output of a *Larrea* population? Each shrub initiated an average of 5086 reproductive units (Boyd 1979). As the direct loss to jackrabbits is only 3.3% of this total, jackrabbit browsing causes a negligible reduction in the reproductive output of this *Larrea* population.

Although the direct loss is small, the pruning may indirectly affect *Larrea* reproduction. Loss of plant biomass can decrease reproductive output by way of resource limitation (Stephenson, Ecology 61:57–64. 1980). Of the 5086 reproductive units produced per shrub, 17% turned brown and died due to no apparent cause (Boyd 1979). These flower buds may have been aborted by resource limitation caused by the pruning activities of the jackrabbits. If so, the total loss of reproductive output caused by *L. californicus* may be large enough to affect *Larrea* reproduction.—ROBERT S. BOYD, Dept. of Botany, Univ. California, Davis 95616. (Received 8 Mar 1982; revision accepted 23 Aug 1982.)

NOTEWORTHY COLLECTION

MONTANA

ERIGERON FLAGELLARIS Gray (ASTERACEAE).—Lewis and Clark Co., lower Falls Cr. drainage (T18N R7W S34), 1500 m, 16 Aug 1980, *Lesica 1002* (MONTU, MONT, WTU). (Verified by J. R. Hill, WTU.)

Significance. First report for MT.

PAPAVER KLUANENSIS D. Löve (PAPAVERACEAE).—Carbon Co., Beratooth Mts., 1 km e. of Silverrun Pk. (T8S R18E S20), 3900 m, 15 Aug 1981, *Lesica 1784* (MONTU, MONT, WTU); Sundance Pass (T8S R17E S25), 3300 m, 15 Aug 1981, *Lesica 1791* (MONTU, NY, CO). (Verified by W. A. Weber, CO.)

Significance. First report for MT, a range extension of 200 km nnw. from the Big Horn Mts., WY.—PETER LESICA, Botany Dept., Univ. Montana, Missoula 59812.

REVIEWS

The Grasses of Baja California, Mexico. By Frank W. Gould and Reid Moran. Memoir 12, San Diego Soc. Natural History. 1981. 140 p.

This work is evidently Frank Gould's last agrostological publication, and appeared after his death, the manuscript being completed by Dr. Moran. The work includes a brief introduction to the phytogeography of Baja California, discussion of previous collectors, and several illustrations of grass structure. The system of classification used is basically that of Stebbins and Crampton. The work includes a modern segmented artificial key to genera which should be much simpler to use than the traditional Hitchcock keys. Rather full generic and species descriptions are given, as well as at least one illustration for each genus. The illustrations are mostly from previous publications, largely those of the Hitchcock group, as well as from Gould and Box and others. Some Spanish common names are stated and, regretfully, so are a certain number of the pedantic "standardized plant names" espoused by U.S. bureaucrats. "Woolspike balsam-scale," stated on page 130 for *Elyonurus barbiculmis* is one example. I don't believe that anyone could persuade a Mexican *paisano* or U.S. cowboy to use such monstrosities.

Descriptions of subfamilies and tribes are absent, although the work is arranged in a systematic order. The name "Eragrostoideae" should be replaced by the earlier "Chloridoideae" (Butzin, Wildenowia 7:116. 1973). There are few nomenclatural innovations with the exception of the use of the name *Dichanthelium* at the generic level, a treatment that some agrostologists feel is unrealistic. The binomial *Bromus unioloides* H.B.K. should be replaced by *B. catharticus* Vahl (Pinto-Escobar in Caldesia 11:54, 9–16). The common Para grass, given as *Brachiaria purpurascens* (Raddi) Henr. should be *B. mutica* (Forsk.) Stapf; the epithet *mutica* (1775) has nearly a 50-year priority over Raddi's *purpurascens* (1823). The text lists no bambusoid grasses, which may be due to the desert nature of much of the peninsula. It seems likely, though, that some cultivated bamboos would occur.—R. W. Pohl, Dept. of Botany, Iowa State Univ., Ames 50011.

A Flora of Waterton Lakes National Park. By Job Kuijt. 684 p. The University of Alberta Press, Edmonton, Alberta, Canada T6G 2E8. $15.00 paperback; $25.00 hardcover. ISBN 0-88864-065-X.

In an age of computers and genetic engineering, the production of a standard flora is still a good, solid achievement. Floras are the cornerstones of biogeography and systematics, and the cataloging process, begun in the 18th century, is still not completed. Each is a synthesis of invisible work by many people over many years: collections, illustrations, revisions, keys, and so on.

This flora represents the best of our taxonomic tradition and is a beautiful work. One might have thought that Job Kuijt, for all his efforts on loranths, viscads et al., would scarcely have found the time to produce a full-scale flora; though he acknowledges a debt to the earlier catalogues of August Breitung, credit for completion of the task must go to Kuijt. The families are sensibly arranged alphabetically, botanical terminology is simplified, and nearly every species is illustrated by a simple habit drawing done by the author (except for *Salix,* which is adapted from the work of T. C. Brayshaw).

Waterton Lakes National Park is in southern Alberta, directly north of Glacier National Park in the U.S. It covers 204 mi^2, and yet 55% of the flora of the entire province is represented within its boundaries. Part of the reason for this is probably the southern position of the park, compared with the increasingly depauperate northern Alberta and plains flora. But the park is so tiny compared to the rest of the province that this cannot possibly be a sufficient explanation. Kuijt mentions the enigmatic "botanical watershed" at ca. 50°N, and north of the park boundary, where species richness apparently decreases abruptly. An additional mystery is the significant number of species absent from the park but found to the north and south. Kuijt suggests that glacial history and the peculiar climatic conditions of the area may account for this disjunction without being able to explain why.

I would like to have seen a few more figures on the total flora of the park, the percent of endemism, and the floristic relationships included with the discussion of vegetation types and geology.

Because so many of the plants in the park also occur in south central Idaho, an area I know fairly well, I walked through a few of the keys and compared them with those in the Flora of the Pacific Northwest and the Intermountain Flora. They appear to be less technical in some respects but still are easy to follow. Difficult groups still yield difficult keys: *Carex* (70 spp.) and *Salix* (21 spp.). A master key to the families is given. Rounding off the treatments are a glossary, bibliography, and index to common and Latin names.—C. DAVIDSON, Idaho Botanical Garden, P.O. Box 2140, Boise 83701.

Imagenes de la Flora Quintanarroense. By OSWALDO TÉLEZ VALDÉS and MARIO SOUSA SÁNCHEZ. 224 p., 160 color photographs, 5 plates of line drawings. Centro de Investigaciones de Quintana Roo, S.A. and Instituto de Biología de UNAM. $800 pesos, plus postage. 1982. Paper.

This volume is the result of an investigation instigated to provide a better knowledge of the plant resources of Quintana Roo, Yucatan, México. Intensive field work, on the part of the authors and field assistants, was initiated in January 1980, and concluded in April 1981. This overview of the plants of the area treats 116 of the more than 1300 species reported for Quintana Roo. For each species, in addition to the scientific name and family, are included vernacular names, both Spanish and Mayan, when these are known. The text is comprised of adequate descriptions, general distributions, habitats in Quintana Roo, and uses. For certain species, biological aspects are also mentioned. The excellent color plates are an outstanding feature of the work, most of them taken by Biol. Téllez Valdés. For many species there is not only a close-up of the flower and/or fruit, but also of the habit and sometimes the habitat.

In addition to the major section devoted to the flora, the volume contains a chapter on vegetation types, as set forth by Miranda in his 1959 paper, "La Vegetación de la Peninsula Yucateca." This includes species lists for various vegetation types. The Glossary is accompanied by five pages of line drawings which serve to clarify certain terms. Literature cited and three indices (one to scientific names, one to common names, and the third to uses) conclude the volume.

Although this volume treats only a small portion of the plants of Quintana Roo, it gives an excellent image of the vegetation of this warm, subhumid part of Mexico. The coldest month is January, with an average temperature of 23°C; and the warmest months are July and August, with average temperatures of 27.8°C. Mean annual precipitation is 1300 mm. Inasmuch as many of the plants occur outside of Yucatan, the book has a wide potential use. It may be obtained from the offices of Centro de Investigaciones de Quintana Roo, S.A.: Puerto Morelos, Q.R., Apartado Postal 886, Cancun, Q.R. México, *or* Moctezuma No. 134, Colonia del Carmen, Delegación Coyoacán, México D.F. 04100, México.—ANNETTA CARTER, Dept. of Botany, Univ. California, Berkeley 94720.

Basin and Range. JOHN MCPHEE. Farrar, Straus and Giroux, New York. 1981. 216 p.

As a gift I received a volume with the textbookish title of *Basin and Range.* After reading the first chapter, which was an account of a young female geologist eyeballing strata exposed near a New York City roadcut while truckdrivers were tooting their horns at her, I was questioning how accurately the title reflected the contents of the book. Might this be an *avant-garde* girl-meets rock book? Something one should expect from progressive authors in the Big Apple? I was dismayed at this prospect because the Basin and Range Province is my favorite landscape. With uncharacteristic perseverance I read on, and I am delighted that I did.

John McPhee has written a reader-friendly book that makes angular unconformities fun. The book is a narrative account by a non-geologist of a trip across the U.S.A. on Interstate 80 in the accompaniment of an accomplished geologist. The actual trip occurred sometime in the late 1970s, but the author also describes imagined trips along the same route in the distant past as well as in the future. From this, one understands the literary licence taken in the first chapter: long ago as New York and North Africa separated from one another, block faulting wrinkled their rocky skins into a basin and range landscape in exactly the same manner as is happening or has happened in Nevada and Utah. This is learning made easy.

It is not all hard rock geology either. There are short and sweet discourses on such things as interactions of unconsolidated volcanic depositions and MX missiles, prominent geologists in the past and present, jibes at *Genesis,* local lore (e.g., dust plumes trailing speeding pickup trucks are known as Nevada door bells), and a host of other topics.

I cannot recommend this book for all ecologists, just for those who like to learn their geology in palatable doses, preferably after supper and with their feet up. And if you have ever worked in the Great Basin then you will be delighted with the book.—FRANK FORCELLA, CSIRO, Division of Plant Industry, Canberra City, A.C.T. 2601, Australia.

Flora of the Central Wasatch Front, Utah, 2nd Ed., revised by LOIS ARNOW, B. ALBEE, and A. WYCKOFF. XIV + 663 p. University of Utah Printing Service, Salt Lake City. 1980. Softbound $14.95.

This flora provides a complete treatment of the vascular plants of two counties (Davis and Salt Lake) in northern Utah. Although the area is small (ca. 100 mi^2), it supports a relatively rich flora of 1139 species (474 genera, 102 families). The flora is drawn from habitats that range from salt desert through saline marshes to foothill grasslands, montane forests and alpine herbland. Species included have all been collected in the area: there are no hypotheticals. The treatment is based on herbarium materials and intensive personal collecting by the authors. Full and original descriptions based on local materials are presented for all species except the grasses and sedges. Those taxa were not described because it was considered desirable to keep the book at a manageable size for field use. The keys, with few exceptions, are unambiguous and adequate to permit definite identification of most taxa considered. There are minor problems with single leads in the generic keys for Aceraceae and Apiaceae. Subspecific taxa are not considered in the keys, but where such taxa do occur in a species in our area, they are discussed in the species descriptions. Taxonomic problems with specific groups receive mature treatment throughout the book. There has been a generally successful attempt to bring the nomenclature up to date: synonyms in recent use are given after the correct names. Good habitat data are reported for all species. Families are alphabetically arranged, but a phylogenetic ordering of families (Cronquist's) is given in the preface. An illustrated glossary is included.

Perhaps one of the most significant contributions of this excellent work is its detailed consideration of introduced species that grow apart from cultivation. About 20% of the species treated are introduced. A number of the species are reported for the first time in Utah. Use of Old World herbarium materials and floras and correspondence with Old World authorities have permitted the authors to produce the first authoritative treatment of alien plants in the area. Places of origin and dates of introduction (when known) are given for the aliens.—K. T. HARPER, Dept. of Botany and Range Science, Brigham Young Univ., Provo, UT 84602.

ANNOUNCEMENT

A symposium on the "Biological Bases of Adaptation in Grasses" will be held during the annual meeting of the American Society of Plant Taxonomists and the AIBS in Grand Forks, North Dakota, August, 1983. The symposium will address the question "Why have grasses become one of the most successful plant groups?" A special emphasis will be placed on the evolutionary role of important features in grasses such as polyploidy, hybridization, modifications and specializations of various vegetative and reproductive structures, structural and physiological adaptations in grass leaves, and the evolutionary responses to herbivores. In addition, new fossil evidence will be used to interpret some paleobotanical aspects of grasses, particularly adaptations in reproductive bracts. The symposium will consist of an invited-speakers session on Tuesday afternoon, 9 August, and a contributed-papers session on Wednesday morning, 10 August. For further information contact Dr. Khidir W. Hilu, Department of Biology, V.P.I. and S.U., Blacksburg, VA 24061 or Thomas Soderstrom, Botany, Smithsonian Institution, Washington, D.C. 20560.

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All members of the California Botanical Society are allotted eight pages in MADROÑO over a two year period. Joint authors are each assessed the full page number. Beyond that number of pages a required editorial fee of $40.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

Contents, continued

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DISTRIBUTION OF SNOW AND ICE ALGAE IN WESTERN NORTH AMERICA

ROBERT A. WHARTON, JR.
National Aeronautics and Space Administration,
Ames Research Center, Moffett Field, CA 94305

WILLIAM C. VINYARD
Department of Biological Sciences, Humboldt State University,
Arcata, CA 95521

ABSTRACT

Twenty species of algae were identified in snow and ice collections from Alberta, California, Colorado, Montana, Nevada, Oregon, and Washington. Red resting spores of *Chlamydomonas nivalis,* zygotes of *Chloromonas brevispina* and *Chloromonas nivalis,* and cells of *Scotiella polyptera* were most frequently encountered. The following taxa are reported for the first time from snow and ice habitats in western North America: *Anabaena variabilis, Actinotaenium cucurbita* var. *attenuatum, Synedra mazamaensis, S. tabulata* var. *acuminata, Eunotia curvata* var. *curvata, Achnanthes flexella* var. *flexella, A. lapponica, Pinnularia hilseana* var. *hilseana,* and *Gomphonema acuminatum.* In addition *Cylindrocystis brebissonii* f. *cryophila* is first reported from Alberta, and *Raphidonema nivale* and *Chloromonas brevispina* from California.

Algae are commonly encountered on snowfields and/or glaciers in western North America. Distributional studies of snow and ice (=cryophilic) algae in western North America have included Alaska (Kol 1942), Arizona (Hoham and Blinn 1979), British Columbia (Kol 1964, Stein and Brook 1964), California (Thomas 1971, 1972; Wharton and Vinyard 1981), Colorado (Hoham and Blinn 1979, Stein and Amundsen 1967), Montana (Kol 1964, Garric 1965), New Mexico (Hoham and Blinn 1979), Oregon (Hardy 1966), Utah (Hoham and Blinn 1979), Washington (Garric 1965; Hoham 1971, 1975; Hoham and Mullett 1977, Hoham et al. 1979) and Wyoming (Garric 1965). Although several of these studies covered large geographic areas (e.g., Kol 1964, Garric 1965, Hoham and Blinn 1979), many snowfields and glaciers remain unsampled, particularly in more remote areas.

We report here the results of a study designed to define further the distribution of snow and ice algae in western North America. Specifically, snow and ice samples collected in Alberta, California, Colorado, Montana, Nevada, Oregon, and Washington were observed for algae.

METHODS

Samples of surface and subsurface snow, ice and meltwater were collected in clean vials. When possible, collections were observed mi-

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croscopically before preservation to detect motile forms. Samples were preserved with formalin and permanent slides made. These are presently stored in the herbarium of Humboldt State University. Field determinations of pH were made using pHydrion paper. Locations and elevations were determined using topographic maps and compass.

RESULTS

Table 1 presents habitat information for collection sites of snow and ice algae in western North America. Table 2 lists the algal taxa observed in snow and ice collections.

Alberta. Observations of sediment from small water-filled depressions (i.e., cryoconite holes) on Mt. Athabasca's North Glacier yielded 7 species of pennate diatoms. Also found in cryoconite were *Chlamydomonas nivalis, Chloromonas nivalis, Actinotaenium cucurbita* var. *attenuatum*. *Chlamydomonas nivalis* was observed as either green or red spherical, nonmotile cells. These cells usually had a gelatinous envelope with a smooth or scrobiculate wall. *Chloromonas nivalis* was observed as "ridged" zygotes. Collections of pink, dirty ice from the glacier's surface contained cells of *Chlamydomonas nivalis* and *Chloromonas nivalis* similar to those observed in cryoconite. Also found in surface ice were *Cylindrocystis brebissonii* f. *cryophila, Raphidonema nivale, Achnanthes flexella* var. *flexella, A. lapponica, Eunotia curvata* var. *curvata,* and *Synedra tabulata* var. *acuminata*.

California. Green or red motile and/or nonmotile cells of *Chlamydomonas nivalis* were present in all California collections except those from Summit Valley, Reflection Lake, and Roundtop Mountain. Both motile and nonmotile cells of *Chloromonas nivalis* were collected in snow at Summit Valley, Reflection Lake, Snow Camp Mountain, and near timberline at Cascade Gulch on Mt. Shasta. *Scotiella polyptera* was responsible for distinct orange and green snows on the north face of Roundtop Mountain. The upper orange layer contained what appeared to be zygotes (the cell type called *Scotiella polyptera*), and the lower green layer contained biflagellate cells which were associated with the *Scotiella polyptera* cell types. This species was also observed at Grove's Prairie. Zygotes of *Chloromonas brevispina* were observed in snow from Summit Valley. *Raphidonema nivale* was found in snow collections from Summit Valley and Roundtop Mountain.

Colorado. Red snow collections from near Vail Pass in Colorado yielded green and red nonmotile cells of *Chlamydomonas nivalis*.

Montana. Ice on the surface of Iceberg Lake contained *Anabaena variabilis*. Green or red, spherical, nonmotile cells of *Chlamydomonas nivalis* were observed in all collections from Montana. Zygotes of *Chloromonas nivalis* were present in snow and ice collections from

Mollman Pass, Garden Wall Ridge, and the surface of Sperry Glacier. Also, zygotes of *Chloromonas brevispina* were detected in snow on Garden Wall Ridge. *Cryocystis granulosa* was present in snow and ice at Mollman Pass, Iceberg Lake, Haystack Butte, and Garden Wall Ridge. Snow at Mollman pass contained *Raphidonema nivale.* The ice and snow of Iceberg Lake and Garden Wall Ridge provided *Ancylonema nordenskioeldii.*

Nevada. Snow collections from near Lamoille Lake in the Ruby Mountains contained green or red spherical, nonmotile cells of *Chlamydomonas nivalis.*

Oregon. Snow collections from near Crater Lake yielded red or green, spherical, nonmotile cells of *Chlamydomonas nivalis.* Also observed were zygotes of *Chloromonas brevispina* and cells of *Scotiella polyptera.*

Washington. Romeria elegans var. *navicola* was present in snow from Mt. Rainier. Green or red, spherical, nonmotile cells of *Chlamydomonas nivalis,* and zygotes of *Chloromonas nivalis* were found in all Washington collections. At Cascade Pass, red, spherical, nonmotile cells of *Chlamydomonas nivalis* were observed as "ablation residue" on soil or rocks around receding snowfields. Snowfields on Mt. Rainier contained *Scotiella polyptera* and *Raphidonema nivale. Raphidonema* was also observed at Cascade Pass. Collections from Mt. Adams provided *Cylindrocystis brebissonii* f. *cryophila.*

DISCUSSION

Our observation of *Anabeana variabilis* in surface ice of Iceberg Lake, Montana, provides the second record of this alga in a cryophilic situation, and the first as a cryophile in North America. Kol (1968) reported that in 1897, Istvanffi detected *A. variabilis* in surface ice from the Baltic Sea. In non-cryophilic situations this species is commonly found on damp soil, brackish mud, in seeps and ditches, or in streams and rivers (Desikachary 1962, Prescott 1962).

The presence of *Romeria elegans* var. *nivicola* interspersed with *Chloromonas nivalis* in snow collected from Mt. Rainier National Park concurs with the findings of Garric (1962). He reported *Romeria* from Glacier National Park in snow which was colored yellow by zygotes of *Chloromonas nivalis* (=*Scotiella nivalis*). *Romeria* has been previously reported from the Three Sisters Wilderness Area, Oregon and from Mt. St. Helens and Mt. Rainier, Washington by Hardy (1966). It was also observed in Yellowstone National Park (Kol 1941).

Observation of *Chlamydomonas nivalis* in many of our snow and ice collections is in agreement with the findings of Kol (1964), Garric (1965), and Hardy and Curl (1972), the latter proposing that *C. nivalis* is probably the most common and widely distributed species of snow

TABLE 1. HABITAT INFORMATION FOR COLLECTION SITES OF SNOW AND ICE ALGAE IN WESTERN NORTH AMERICA. Unless otherwise noted collections by the authors. Collection No. code: "ALT770822.1": ALT = Alberta, 77 = 1977, 08 = August, 22 = 22nd day of the month, .1 = vial number.

Alberta

Jasper Natl. Park, North Glacier of Mt. Athabasca. Surface ice from w. edge of North Glacier, 2743 m, pH 4, pink-dirty ice, (ALT770822.1); cryoconite from submersed ice cups in pond at lower end, w. edge of North Glacier, 2743 m, pH 4, insects on water surface, (ALT770822.3,4); ice from above glacial pond, surface may have been under water at one time, 2743 m, pH 4, dirty ice, (ALT770822.5). All collections from an open exposure.

California

Lassen Volcanic Natl. Park, Reflection Lake, near n. end, 1792 m, pH 5.8, L. Sandrock (coll.), (CA710610.1).

Summit Valley, Six Rivers Natl. Forest, Del Norte Co., T14N R3E Sec 22, 1219 m, rusty colored snow in shade, (CA750618.2).

Grove's Prairie, Six Rivers Natl. Forest, Humboldt Co., T7N R6E Sec 27, 1530 m, dirty snow in shade with abundant conifer litter on surface, (CA760501.1).

Etna Summit, Klamath Natl. Forest, Siskiyou Co., T41N R10W Sec 15, 1700 m, pink snow, (CA760515.3).

Sugar Lake Trail, Klamath Natl. Forest, Siskiyou Co., T41N R9W Sec 20, 1641 m, pink snow, (CA760522.4); Sec 19, dirty snow with conifer litter, (CA760522.5,6).

Snow Camp Mountain, Six Rivers Natl. Forest, Humboldt Co., T4N R4E Sec 7, 1402 m, pink snow from exposed summit snowfield, (CA770417.1).

Mt. Tallac, El Dorado Natl. Forest, El Dorado Co., T13N R17E Sec 4, 2980 m, red snow from exposed snowfield near ne. summit. (CA780810.1,2).

Roundtop Mountain, El Dorado Natl. Forest, El Dorado Co., 120°00′W, 38°40′N, 2895 m, green and orange snow from shaded n.-facing ice chute, (CA780824.3,4).

Mount Shasta, Shasta-Trinity Natl. Forest, Siskiyou Co., e. edge of North Wintun Glacier, T41N R3W Sec 11, 3048 m, very red snow from exposed snowfield, (CA750716.1,2,3). Edge of Hotlum Glacier, T41N R3W Sec 10, 3566 m, pH 6, exposed snow surface pink to dirty brown, covered with insect fallout, (CA760619.7,8). Lower Hotlum Glacier, T41N R3W Sec 3, 3353 m, pH 6, exposed snow pink-dirty brown, (CA760620.9,10); 3200 m, (CA760620.11,12); 3048 m, (CA760620.13,14). Inconstance Cr., T41N R3W Sec 3, 2896 m, pH 6, exposed snow bank surface pink to very dirty, (CA760620.15,16); Sec 34, 2743 m, (CA760620.17,18); 2591 m (CA760620.19,20). Brewer Cr., T41N R3W Sec 11, 2804 m, pH 5, n.-facing snow bank with very red surface, (CA760801.21,22,23); meltwater in snowbank near Brewer Cr., pH 6, (CA760801.24,25); snow from ridge south of Brewer Cr., pH 6, (CA760801.26,27); water sample from Brewer Cr., pH 6, (CA760801.28). Hotlum Ice Slope, T41N R3W Sec 10, 3962 m, pink snow collected under 0.5 m of fresh snow, (CA760820.29). Summit Ridge, T41N R3W Sec 9, 4298 m, fresh snow ca. 15 m n. of summit, (CA760820.30,31). North Wintun Glacier, T41N R3W Sec 10, 3231 m, pH 5, exposed pink snow on moraine n. of glacier, (CA760820.32); 3246 m, pH 8, (CA760820.33); 3262 m, pH 5, (CA760820.34). North Wintun Glacier, T41N R3W Sec 10, 3322 m, pH 5, (CA760820.35,36). Northeast (Clyde ?) Ridge, T41N R3W Sec 10, 3322 m, pH 5, dirty snow, (CA760820.37). Cascade Gulch (Hidden Valley), T41N R3W Sec 17, 2926 m, sample collected under 10 cm of fresh snow (CA760823.42,43); 3292 m, (CA760823.44,45); (P. Rhodes, coll.). Shastina Crater, near Clarence King Lake, T41N R3W Sec 8, 3609 m (P. Rhodes, coll.), (CA760901.46,47). North Wintun Glacier, T41N R3W Sec 11, 3169 m, pH 6, exposed red snow, (CA761030.60,61,62). North Hotlum Glacier, T41N R3W Sec 3, 2743 m, pH 5, dirty snow (CA770910.4,5).

TABLE 1. CONTINUED.

Colorado

Vail Pass, White River Natl. Forest, Eagle Co., 3353 m, exposed red snow, (L. Roloff, coll.), (CO790622.1,2).

Montana

Mollman Pass Col, Mission Mountains, Lake Co., 1829 m, pH 6.3, snow faint rusty-red appearing orange in boot tracks, coloration to 7.5 cm, (MT570629.1).

Glacier Natl. Park, Iceberg Lake, 1857 m, red surface ice on lake, (MT570815.4). Haystack Butte, 1962 m, dirty snow, (M. Mooar, coll.), (MT660805.1). Garden Wall Ridge (e. side) above Granite Park Chalet, 2195 m, dirty snow, (M. Mooar and R. Wunner, colls.), (MT660805.2,3). Sperry Glacier, Glacier Co., 1848 m, (MT760829.1).

Nevada

LaMoille Lake, Ruby Mountains, Elko Co., 3200 m, red snow, (NV760829.33).

Oregon

Crater Lake Natl. Park, West Rim Road, 2438 m, red snow, (OR660624.1).

Washington

Mt. Rainier Natl. Park, Ptarmigan Ridge e. of Spray Park, 2134 m, (WA760630.6). Spray Park, 1829 m, exposed pink snow, (WA760330.7). Trail between Mowich Lake and Spray Park, 1524 m, dirty snow in shade with abundant conifer litter, (WA760630.8). Mowich Lake, 1372 m, exposed snowfields, (WA760630.9,10).

Mt. Adams, Yakima Co., Mazama Glacier, 2682 m, exposed pink snow, (WA760701.1). Sunrise Camp, 2195 m, exposed dirty snow near large moraine, (WA760702.2). Bird Cr. Meadows, T8N R11E Sec 28, 1981 m, dirty snow under trees, (WA760702.3). Bluff Lake, T8N R11E Sec 33, 1676 m, exposed pink snow, (WA760702.4).

North Cascades Natl. Park, Cascade Pass (e. side), 1640 m, exposed pink snow, (WA760920.1). Cascade Pass (ne. side), 1890 m, exposed pink snow, (WA760920.2). Cascade Pass (n. side), 2194 m, exposed red snow, (WA760920.3). Cascade Pass (ne. side), 1981 m, dry reddish-purple material on rocks and soil within 1 m of receding snowfield, (WA760920.4,5).

Pasayten Wilderness Area, ridge above West Pasayten River's sw. source, 2133 m, exposed pink snow, (WA760921.7,8).

Mt. Rainier Natl. Park, Moraine Park, 1676 m, dirty snow, (WA760923.9).

algae. That motile cells were seldom detected is not surprising because they are short-lived, often remaining motile for less than a week. Consequently, unless one is in the field at the correct time of year (and often the proper time of day), motile stages of *Chlamydomonas* will not be observed.

The zygotes of *Chloromonas nivalis* in snows from Alberta, California, Montana, and Washington are similar to those described by Hoham and Mullet (1977, 1978). The zygotes of *Chloromonas brevispina* (formerly *Cryocystis brevispina*) found in snow from California, Montana, and Oregon are similar to those described by Garric (1965). The life history and ecology of this difficult taxon was recently discussed by Hoham et al. (1979). It has been previously reported from Alberta and British Columbia (Kol 1968), Colorado (Stein and

TABLE 2. LIST OF ALGAL TAXA OBSERVED IN SNOW AND ICE COLLECTIONS FROM WESTERN NORTH AMERICA. [1] ALT = Alberta, n. Glacier of Mt. Athabasca, 1 = cryoconite, 2 = glacier ice; CA = California, 1 = Etna Summit, 2 = Groves Prairie, 3 = Mt. Shasta, 4 = Mt. Tallac, 5 = Reflection Lake, 6 = Roundtop Mtn., 7 = Snow Camp Mtn., 8 = Sugar Lake Trail, 9 = Summit Valley; CO = Colorado, Vail Pass; MT = Montana, 1 = Garden Wall Ridge, 2 = Haystack Butte, 3 = Iceberg Lake, 4 = Mollman Pass, 5 = Sperry Glacier; NV = Nevada, Ruby Mtns.; OR = Oregon, Crater Lake; WA = Washington, 1 = Cascade Pass, 2 = Mt. Adams, 3 = Mt. Rainier, 4 = Pasayten Wilderness Area. * = present.

Taxon	ALT[1]	CA	CO	MT	NV	OR	WA
CYANOPHYTA							
Anabaena variabilis Kutz. ex Born. and Flah.				3			
Romeria elegans var. *nivicola* Kol							3
CHLOROPHYTA							
Chlamydomonas nivalis (Bauer) Wille	1, 2	1–4, 7, 8	*	1–5	*	*	1–4
Chloromonas brevispina (Fritsch) Hoh., Roem., and Mull.		9		1		*	
Chloromonas nivalis (Chod.) Hoh. and Mull.	1, 2	3, 5, 7, 9		1–5			1–4
Scotiella polyptera Fritsch		2, 6				*	3
Raphidonema nivale Lagerh.	2	6, 9		4			1, 3
Cryocystis granulosa Kol				1–4			
Actinotaenium cucurbita var. *attenuatum* (G. S. West) Teil.	1, 2						
Ancylonema nordenskioeldii Berg.				1, 3			
Cylindrocystis brebissonii f. *cryophila* Kol	2						2
BACILLARIOPHYTA							
Synedra mazamaensis Sov.	1						
Synedra tabulata var. *acuminata* Grunow. V.H.	1, 2						
Eunotia curvata var. *curvata* (Kütz.) Lagerst.	1, 2						
Achnanthes flexella var. *flexella* (Kütz.) Brun.	1, 2						
Achnanthes lapponica Hustedt	1, 2						
Pinnularia hilseana var. *hilseana* Jan.	1						
Gomphonema acuminatum Ehr.	1						

Amundsen 1967), Montana (Garric 1965), Oregon (Hardy 1966), Utah (Hoham and Blinn 1979), and Washington (Garric 1965, Hoham et al. 1979). Our observation of *C. brevispina* in Summit Valley snow provides the first record of this alga from California.

Cells of *Cryocystis granulosa,* as observed in Montana snow, probably represent zygotes of an undescribed *Chloromonas* sp. (Hoham and Blinn 1979). *Cryocystis granulosa* has previously been reported from Arizona, Colorado, New Mexico, and Utah (Hoham and Blinn 1979); British Columbia and Montana (Kol 1964); and Washington (Garric 1965).

Scotiella polyptera has previously been reported from snow in Arizona, New Mexico and Colorado (Hoham and Blinn 1979). It has also been reported from Alaska (Kol 1942) and Yellowstone National Park, Wyoming (Kol 1941). *Raphidonema nivale* has been previously reported from most of western North America (Garric 1965, Kol 1968, Hoham 1971); however, our observation of it in snow of Summit Valley and Roundtop Mountain provides the first record of this alga in California. The variable form of *Raphidonema nivale* encountered in Alberta, California, Montana, and Washington supports Hoham's (1973) suggestion that this species is a pleiomorphic snow algae. He further contends that these pleiomorphic characteristics may result from variations in environmental factors (e.g., light, nutrient levels).

Ancylonema nordenskioeldii has been reported from Alaska, British Columbia, Montana, and Washington (Prescott et al. 1972). Gerdel and Drouet (1960) observed this species in cryoconite of Greenland. Prescott et al. (1972) suggested that *Cylindrocystis brebissonii* f. *cryophila* is an endemic of Alaska. However, Hoham (1971) reported this desmid from Mt. Pugh, Washington. Gerdel and Drouet (1960) observed *C. cylindrospora* in Greenland cryoconite. Prescott et al. (1972) indicated that *C. cylindrospora* is a synonym of *C. brebissonii*. Our observation of *C. brebissonii* f. *cryophila* from Mt. Athabasca provides the first record of this snow alga in Alberta.

The presence of *Actinotaenium cucurbita* var. *attenuatum* in Mt. Athabasca's ice and cryoconite provides the first record of this organism from a cryophilic situation in Alberta. It has, however, been observed in non-cryophilic freshwater habitats of western North America (Croasdale 1962, Prescott et al. 1981).

Synedra mazamaensis was originally described from Crater Lake, Oregon by Sovereign (1958). Our observations represent the first report of this alga from cryoconite. Sovereign (1958) indicated a pH range of 7.2 to 8.4 for Crater Lake water, but the water from which we obtained it had a pH of 4. *Synedra tabulata* var. *acuminata* which was abundant in ice and cryoconite, has not been reported from these habitats. *Eunotia curvata* var. *curvata,* common in ice and cryoconite, has been reported from shallow ponds in California, Montana, Washington, and Wyoming (Patrick and Reimer 1966). It has not been reported from ice or cryoconite. Patrick and Reimer (1966) indicate that this species prefers acid waters. Our observations support their findings because *Eunotia* was collected in ice and cryoconite with a pH of 4. The presence of *Achnanthes flexella* var. *flexella* in surface ice and cryoconite represents a new habitat and distribution record for this diatom. It has been reported from lakes, ponds, and bogs in

Montana (Patrick and Reimer 1966). *Achnanthes lapponica, Gomphonema acuminatum,* and *Pinnularia hilseana* var. *hilseana* have not been previously reported from ice or cryoconite.

Diatoms have been reported in snow (Lichti-Federovich 1980), sea-ice (Bunt 1964, Richardson and Whitaker 1979, Whitaker and Richardson 1980), and cryoconite holes (Gerdel and Drouet 1960, Wharton et al. 1981). With the exception of a diatom-rich red snow from Isbjorneo, Greenland (Lichti-Federovich 1980) diatoms do not appear to be a persistent part of the snow flora. This probably results from the unstable and often ephemeral nature of snowfields. In fact, the diatom-rich red snow from Isbjorneo was found on the surface of a "permanent snow patch." Alternatively, diatoms are often a persistent component of ice, sea ice, and cryoconite hole habitats. These habitats are relatively stable and persistent compared to snowfields. The sediment (i.e., cryoconite) at the bottom of cryoconite holes provides a relatively stable benthos. Richardson and Whitaker (1979) suggest that sea ice provides a solid but porous substrate which resembles a benthic type of habitat. We suggest that diatoms only become a persistent part of the cryoflora when a stable and perennial habitat is provided, such as perennial snow fields, glacial ice, cryoconite holes, supraglacial ponds, and sea ice. In western North America these habitats will most likely be found on or near glaciers. The cryoflora of temporary snowfields will typically lack diatoms and consist primarily of members of the Chlamydomonadaceae (e.g., *Chlamydomonas nivalis, Chloromonas nivalis*).

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DUDLEYA CALCICOLA (CRASSULACEAE), A NEW SPECIES FROM THE SOUTHERN SIERRA NEVADA

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ABSTRACT

A new species, **Dudleya calcicola,** is described from the southern Sierra Nevada in Kern and Tulare Counties, California. The xeric limestone habitat, associated species, and ecological adaptations of the plant are discussed.

Recent explorations of the xeric limestones of the southern Sierra Nevada yielded a new *Dudleya*. Although Katharine Brandegee reportedly was intent on describing this plant from collections made by C. A. Purpus (Purpus 1897a,b), she failed to do so. Moran (1951) noted that the Purpus collections had narrower leaves than *D. cymosa*; however, he did not recognize these collections as distinct. Nevertheless, we believe a combination of vegetative and floral features separate *D. calcicola* from *D. abramsii* and *D. cymosa*.

Dudleya calcicola Bartel & Shevock, sp. nov.

Caudex ramosus caespitosus rosulas compactas increbre producens. Folia glauca vel pulverulenta lanceolata. Inflorescentia ex ramis patulis plerumque denuo ramificantibus constans. Flores duo usque ad octo per cincinnum, pedicellos 1–6 mm longi terminantes. Petala anguste acutata flava haud rubrotincta apicibus valde extrinsecus curvatis (Fig. 1).

Plants to 1.5 dm wide, of 5–20 or occasionally 50 densely packed rosettes. Caudex short, 1–2 cm thick, simple or frequently cespitosely many-branched. Rosettes 1–9 cm in diameter of 10–20(–30), with erect or ascending leaves. Rosette leaves oblong-lanceolate or tapering from base, acute to acuminate, infrequently apiculate, 1–8(–10) cm long, 3–13(–16) mm wide, 2–5 mm thick, pruinose to pulverulent to glaucous, glaucescent in age; ventral surface slightly convex on smaller rosettes but usually plane or concave and frequently somewhat sulcate; dorsal surface convex, the margins rounded except towards base; base

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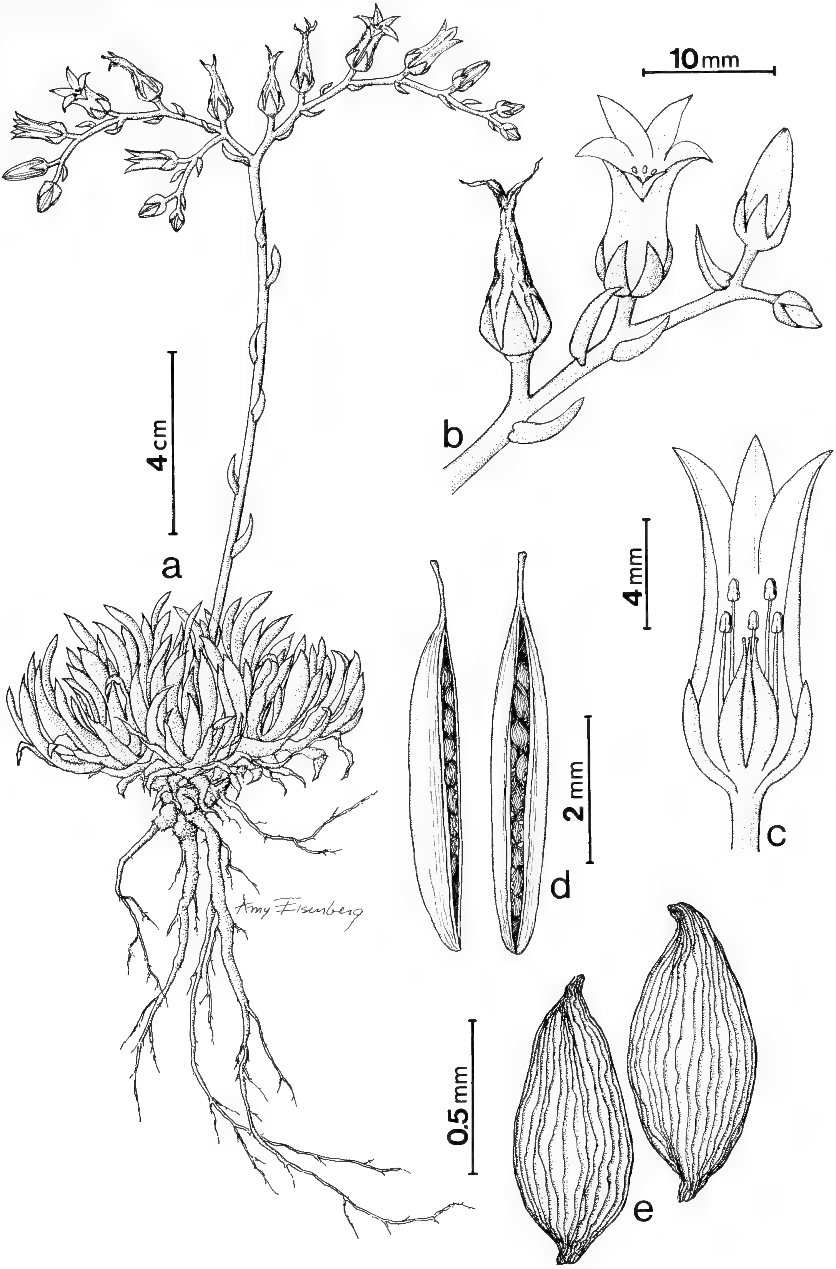

FIG. 1. *Dudleya calcicola*. a. Flowering habit with cespitosely many-branched rosettes. b. Inflorescence. c. Flower with two petals removed. d. Carpel with seeds. e. Seed. All from *Shevock 8728* and *8802*.

5–10(–13) mm wide. Floral stems erect, glaucous, 3–18(–25) cm high, 1.5–4(–4.5) mm thick, naked in the lower 1–7 cm, with 5–20 usually spreading glaucous leaves, triangular lanceolate, acute to acuminate, the lowermost 4–20 mm long, 2–10 mm wide. Inflorescence obpyramidal, of 2–4 ascending to mostly spreading branches that rebranch 0–3 times; cincinni circinate, in age spreading to rarely ascending, 1–6 cm long with 2–8(–10) flowers; pedicels ascending to erect, 1–6(–8) mm long, 1–1.5 mm thick at base, slightly thickened upward. Calyx subtruncate to rounded below, 3–7 mm long, 3–7 mm wide, the sepals appressed, triangular-ovate to -lanceolate, acute, 2.5–6 mm long, 2–4 mm wide, usually glaucescent to glaucous. Corolla straw-colored to mostly pale yellow with darker yellow on petal keel, 9–15(–18) mm long, 3.5–5(–6) mm thick, the petals connate 1–3 mm, erect with tips strongly outcurved especially in age, lanceolate to usually narrowly acute, 2–4(–4.5) mm wide. Filaments straw-colored to pale yellow, the epipetalous 3.5–6 mm long, adnate 1–3 mm, the antesepalous 4.5–7.5 mm long, adnate 1.5–4 mm; anthers yellow, 1–1.5 mm long. Nectaries white to yellowish, 0.5–1.3 mm wide. Gynoecium 3–5(–7) mm high, 2–3 mm thick, the carpels erect, appressed, slender, tapering into styles ca. 1–2 mm long; seeds 7–18 per carpel, 0.7–1 mm long, brown, striate-reticulate. Chromosome number: $n = 17$.

TYPE: USA, CA, Tulare Co., Kern River at Roads End, T23S R32E S13, Sequoia Natl. For., 1220 m, 11 Jul 1981, *Shevock 8802*. (Holotype: CAS; isotypes: FSC, NY, RSA, SBBG, SD, UC.)

PARATYPES: USA, CA, KERN Co., rocks, Walker Pass, Apr–Sep 1897, *Purpus 5402* (UC, US); rocks, Pahute [sic] Peak, Apr–Sep 1897, *Purpus 5192* (UC, US); w. of Cane Cr., T26S, R32E, S25, 13 May 1981, *Bartel 1023* (UC) and 27 Jun 1981, *Bartel 1034* (UC); divide between Erskine and Bodfish Creeks, T27S R33E S8, 17 Apr 1981, *Shevock 8254* (CAS) and 13 May 1981, *Shevock 8468* (CAS); Long Canyon, T27S R34E S4, 26 Apr 1981, *Shevock 8467* (CAS); Sand Canyon, T30S R33E S22, 25 Jul 1981, *Shevock 8848* (CAS); 3 km n. of Twin Oaks along Caliente Creek Road, T30S R33E S12, 25 Jul 1981, *Shevock 8851* (CAS, RSA). TULARE Co., Kern River (near Johnsondale Bridge), 4 Jun 1939, *Lewis s.n.* (LA); Brush Creek Canyon, 13 May 1968, *Howell & True 44347* (CAS); Kern River Canyon e. of Limestone Campground, 14 May 1969, *Howell & True 45761* (CAS); Kern Plateau near Rincon Trail, T22S R33E S30, 15 May 1981, *Shevock 8500* (CAS, RSA); Packsaddle Cave, T23S R33E S7, 7 Jun 1981, *Shevock 8728* (CAS).

Dudleya calcicola is distinguished from other species by a combination of morphological characters. The caudex of *D. calcicola* is typically cespitosely many-branched with as many as 50 densely packed rosettes. Conversely, *D. cymosa* exhibits a simple or few-branched caudex (Moran 1951). The narrow, glaucous to pulverulent leaves and short pedicels of *D. calcicola* are similar to those of *D. abramsii.* However, the foliar bloom is generally much heavier and the pedicels are slightly longer in *D. calcicola* when compared to *D. abramsii.* The inflorescence, like that of *D. cymosa,* is usually somewhat obpyramidal with relatively short spreading cincinni. Although the floral stem of *D. calcicola* is occasionally bifurcate as in *D. abramsii,* the stem is thicker and the cincinni generally are spreading rather than ascending. The petals of *D. calcicola* also lack the red flecks and/or red lineolate keel typical of *D. abramsii.* The narrowly acute petals resemble those of *D. cymosa* subsp. *cymosa,* but they are generally more strongly outcurved and are slightly longer in maturity. Although the narrow leaves and pale yellow flowers of *D. calcicola* are similar to some populations of *D. cymosa* subsp. *setchellii,* these populations, confined to serpentine grassland within the Santa Clara Valley in Santa Clara County, have longer cincinni that support twice the number of flowers in *D. calcicola.* Moreover, these populations have erect cincinni and lack the narrowly acute petal apices typical of *D. calcicola.*

In many respects *D. calcicola* is intermediate between *D. abramsii* and *D. cymosa,* although it seems slightly closer to *D. abramsii.* This could account for the difficulty in determining where to place *D. calcicola* in the past. Nevertheless, the combination of morphologic features of the species and characteristic limestone habitat make *D. calcicola* readily distinguishable.

Dudleya calcicola occurs predominantly on pre-Cretaceous limestones (Smith 1965) within chaparral or pinyon-juniper woodland at 850–1700 m. Extensive field searches on adjacent Mesozoic granitic, Mesozoic basic intrusive, pre-Cretaceous metamorphic, and pre-Cretaceous metasedimentary rocks (Smith 1965), have located only a few populations of *D. calcicola* in the Kern River watershed generally east of Lake Isabella. Thus, the species seems to be restricted primarily to isolated limestone ridges and steep slopes. The habitat of this *Dudleya* is the basis for the specific epithet, which also provides a good vernacular name: limestone live-forever.

Populations of *D. calcicola* are scattered over a relatively large area of the southern Sierra Nevada from the Rincon area south of Durrwood Creek in Tulare County to the southern Piute Mountains near Caliente Creek in Kern County (Fig. 2). The total area of limestone habitat, however, is quite restricted and isolated. Several species are associated with all the surveyed *D. calcicola* populations occurring on limestones. These species include: *Delphinium purpusii, Ephedra viridis, Eriogonum fasciculatum* subsp. *polifolium, Eriogonum saxatile, Eriophyllum confertiflorum, Fremontodendron californicum, Haplopappus linearifolius, Notholaena jonesii, Selaginella asprella, Stephanomeria pauciflora,* and *Yucca whipplei* subsp. *caespitosa.* Associ-

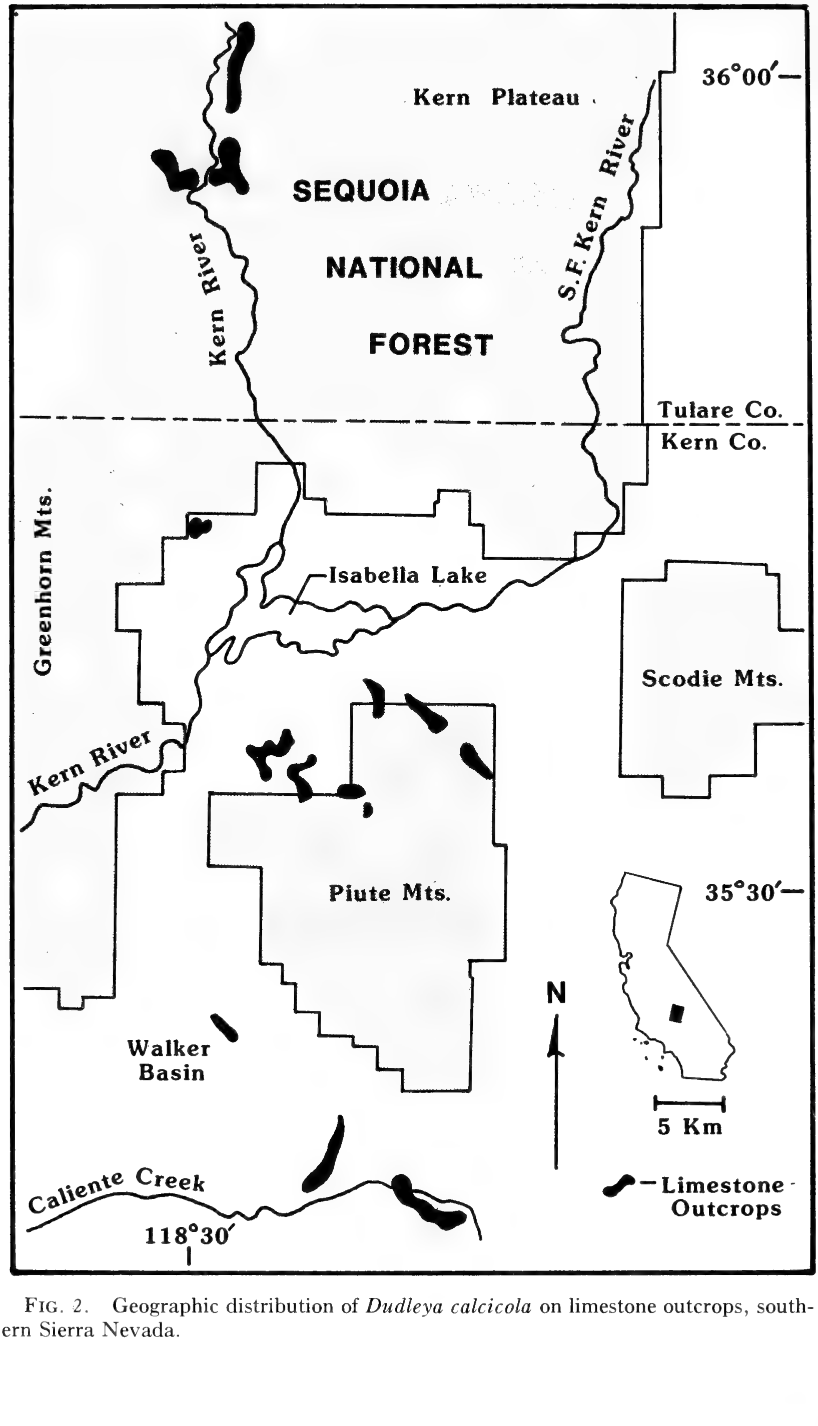

FIG. 2. Geographic distribution of *Dudleya calcicola* on limestone outcrops, southern Sierra Nevada.

ated with *D. calcicola* in the northern Piute Mountains are several plants that are usually found in the desert regions east of the Sierran crest. These species are: *Cheilanthes viscida, Ephedra nevadensis, Forsellesia nevadensis, Purshia glandulosa, Salvia dorrii, Tetradymia axillaris,* and *Tetradymia stenolepis*.

The densely glaucous leaves of *Dudleya calcicola* are typical of dudleyas growing on open rock outcrops (Mulroy 1979). Glaucescence, a genetically controlled feature, enables the leaves to reflect a great percentage of the ultraviolet, visible, and near-infrared radiation and thus reduce ultraviolet damage and desiccation (Mulroy 1979). The heavy glaucous leaves probably enable *D. calcicola* to occupy these xeric limestone habitats; a less glaucescent form of *D. cymosa* (Lemaire) Britton & Rose grows nearby in more mesic sites along the banks of the Kern River. Although glaucescence may have other adaptive properties (Mulroy 1979), the density of the bloom in *D. calcicola* appeared to intensify in summer even under cultivation. This suggests that glaucescence is affected at least partially by the level of light. Although Denton (1982) reported that substrate may effect changes in glaucescence in *Sedum,* this was not observed with cultivated specimens of *D. calcicola*. In addition, the unusual dwarfed cespitose habit of *D. calcicola* recalls "cushion plants" of alpine environments. This growth form, too, may buffer the plant from summer drought and high light levels prevalent on the limestone outcrops. Nevertheless, the dwarfed habit is evidently environmentally controlled to some degree, because many plants growing on deeper soil, in partial shade, or in cultivation are obviously more robust.

Carl A. Purpus was first to collect this *Dudleya* and to distinguish it from the widespread *D. cymosa*. In a letter of 23 May 1897, Purpus wrote Katharine Brandegee (UC) that he had collected an "*Echeveria* [*Dudleya*], which is all together different from *E. purpusii* [*D. cymosa* subsp. *cymosa*]." He further noted its smaller leaves, straw-colored flowers, and limestone or granite habitat. Later, Purpus (1897a,b) wrote that the plant would shortly be described by Mrs. Brandegee in the journal *Erythea*; but neither she nor her husband T. S. Brandegee (who named *Delphinium purpusii* and *Penstemon purpusii* in 1899) ever described it.

Moran (1951) in his revision of the genus placed the Purpus collections with *D. cymosa* subsp. *cymosa*. However, he noted the narrow leaves and suggested that some of the dudleyas from the southern Sierra Nevada might belong better with *D. cymosa* subsp. *setchellii* (Jepson) Moran. Others, however, have anonymously annotated the various collections of *D. calcicola* as *D. abramsii* Rose, *D. saxosa* (M. E. Jones) Britton & Rose, and *D. cymosa*.

Dudleya calcicola, because of its erect petals and pistils, is placed in the subgenus *Dudleya*. Buds fixed in the field on 17 April and 13 May 1981, *Shevock 8254* and *8467,* yielded a meiotic count of $n =$

17. This number is basic for *Dudleya* (Uhl & Moran 1953), and thus the species is a diploid.

ACKNOWLEDGMENTS

We greatly appreciate the meiotic counts made by Tsan-Iang and Fei-Mei Chuang. We also thank Amy Eisenberg for the illustration and Tim Jensen for the distribution map. In addition, we are most grateful to Rimo Bacigalupi, Alice Howard, Tom Howell, Reid Moran, and Kei Nakai for their valuable assistance.

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PERITYLE (ASTERACEAE), NEW SPECIES AND NOTES

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Alpine, TX 79830

ABSTRACT

Three new species of *Perityle* (Asteraceae) are described and their immediate relationships identified. Chromosome numbers for the new species and five other taxa and notes about *Perityle* are included.

Following the monographic studies of *Perityle* (Powell 1969, 1973, 1974), continuing investigations have resulted in additional information about the genus. Most species of *Perityle* occur as perennials in crevices of rock bluffs and have followed a pattern of speciation by geographic isolation. Consequently it is of no surprise that three additional species have been discovered in several under-collected areas. Also included in this report are chromosome numbers and other miscellaneous information about various species of *Perityle*.

Peritvle fosteri A. M. Powell, sp. nov.

Suffrutices 6–15 cm alti dense pubescentes pilis brevibus; laminae foliorum 0.8–1.2 cm longae 0.5–1.2 cm latae lobatae saepe tripartitae; flores radiati nulli; flores disci ca. 10 corollis pallide flavis ca. 4.5 mm longis; achaenia 1.5–1.6 mm longa; pappus setiformis setis ca. 20 tenuibus inaequalibus; chromosomatum numerus $n = 17$. Fig. 1.

Plants suffruticose, 6–15 cm high, in mats or rock faces, profusely branched and leafy, rather densely short-pubescent, the leaves mostly alternate, the blades 0.8–1.2 cm long, 0.5–1.2 cm wide, lobed, basically tripartite, short-pubescent and gland-dotted; petioles 4–8 mm long; heads discoid, borne on short peduncles, clustered among the upper leaves, funnelform-cylindric, 6–7 mm long, ca. 4 mm wide; phyllaries 8, 5–6 mm long, 0.8–1.3 mm wide; disc flowers ca. 10; disc corollas cream-color to pale yellow, ca. 4.5 mm long, the tube ca. 1 mm long, glandular-pubescent, the throat ca. 3 mm long, tubular-funnelform, the lobes acute, 0.5 mm long; anthers ca. 2.3 mm long; styles 1–1.2 mm long, slender, flattened, truncate, minutely pubescent, achenes 1.5–1.6 mm long, nearly oblong, flattened, short pubescent on faces and margins; pappus of ca. 20 slender, unequal bristles, these minutely antrorse-ciliate; chromosome number, $n = 17$.

TYPE: Texas, Culberson Co., Apache Mts., Panther Canyon, lime-

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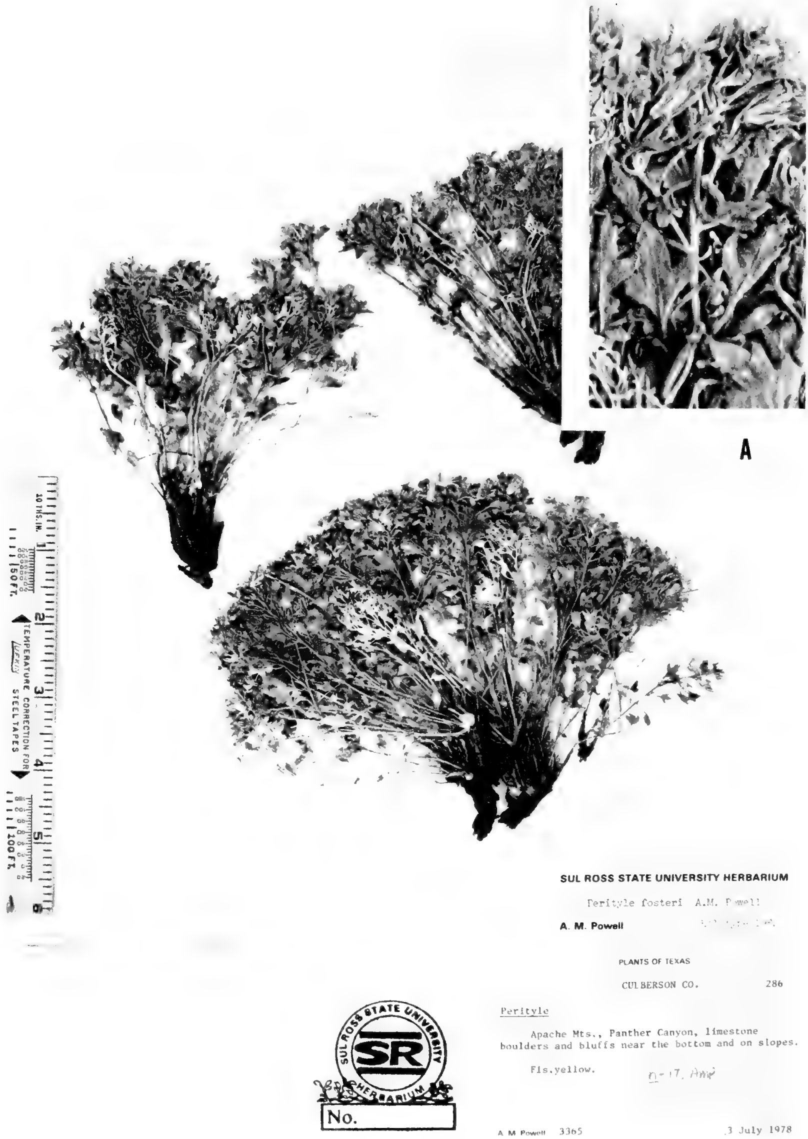

FIG. 1. Holotype of *Perityle fosteri* (*Powell 3365*). A. Inset is close-up of upper branches.

stone boulders and bluffs, 3 Jul 1978, *A. M. Powell 3365* (Holotype: SRSC; isotypes: TEX, to be distributed).

PARATYPE: Apache Mts., bluffs of upper slopes of Panther Canyon, 4 Jul 1978, *Weedin 1188*. Known only from the type locality.

Perityle fosteri is the sixth species of sect. *Pappothrix* (Powell 1969) and is most closely related to *P. rupestris*. *Perityle fosteri* is best distinguished by its tripartite leaves, pale yellow disc corollas, and distribution. The Apache Mountains are a small range isolated from the Guadalupe Mountains and the Sierra Diablo (locality of *P. quinqueflora*) to the north and west, and from the Davis Mountains (locality of *P. rupestris*) is the southeast. Panther Canyon, the type locality, is a rather deep and protected canyon on the east end of the Apache Mountains where *P. fosteri* occurs in small mats on rock faces in the manner of the more widespread *P. rupestris*.

The species name honors J. B. (Jap) Foster, long-time rancher in Culberson County. Mr. Foster, from a pioneer family, began his own operation in 1909 with ranch land that included the Apache Mountains. In Trans-Pecos Texas where private land is predominant, plant habitats are usually best protected by ranches, and landowners, exemplified by Mr. Foster, should be recognized for their conservation.

Perityle huecoensis A. M. Powell, sp. nov.

Suffrutices 10–20 cm alti dense pubescentes pilis brevibus; laminae foliorum 0.7–1.2 cm longae 0.7–1 cm latae ovatae vel ovato-deltoideae vel ovato-rhomboideae; flores radiati 3–5 ligulis flavis 2.5–3 mm longis; flores disci 11–13 corollis flavis ca. 3 mm longis; achaenia 2.8–3.2 mm longa; pappus saepe 3-meris setis longioribus 2, 1–2.5 mm longis, seta breviore solitaria; chromosomatum numerus $n = 17$. Fig. 2.

Plants suffruticose, 10–20 cm high, densely short-pubescent; leaves opposite or alternate, the blades 0.7–1.2 cm long, 0.7–1 cm wide, short-pubescent, gland-dotted, subcoriaceous, ovate to ovate-deltoid or ovate-rhombic, the margins entire to serrate lobed; heads loosely aggregated on peduncles ca. 1 cm long; involucres somewhat funnelform, heads 5–6.5 mm long, florets ca. 14; phyllaries 4–5 mm long, 0.6–1 mm wide; ray flowers 3–5, ligules yellow, 2.5–3 mm long, ca. 1.5 mm wide; disc flowers 11–13, corollas yellow, ca. 3 mm long, the tube ca. 1.3 mm long, the throat ca. 1 cm long, markedly expanded to campanulate-funnelform, the lobes ca. 0.7 mm long; style branches 1.2–1.5 mm long, subulate and pubescent; anthers ca. 1.5 mm long; achenes 2.8–3.2 mm long, linear-lanceolate, flattened, minutely pubescent on faces and margins; pappus typically of 2 longer bristles and 1 shorter, the longest 1.0–2.5 mm long, or with 2–3 longer bristles and 2–4 shorter bristles, the bristles slender and antrorse-ciliate, often caducous; chromosome number, $n = 17$.

SUL ROSS STATE UNIVERSITY HERBARIUM

A M Powell

PLANTS OF TEXAS

EL PASO CC.

Peritylı

Hueco Mts., Hueco Tanks an [illegible]
Ranch, ca. 31°54', 106° 07'.

N.F. McCarten and Van Devender
No. 2508 Date 24 September 1977

FIG. 2. Holotype of *Perityle huecoensis* (*McCarten and Van Devender 2508*). A. Inset is close-up of capitulescence (see arrow).

TYPE: Texas, El Paso Co., North Hueco Mts., Hueco Tanks area, Navar Ranch, ca. 31°54′N, 106°07′W, 24 Sep 1977, *McCarten and Van Devender 2508* (Holotype: SRSC; isotype: TEX). Known only from the type locality.

Perityle huecoensis belongs in sect. *Laphamia* (Powell 1973), where it apparently is most closely related to *P. staurophylla,* which has subcruciform leaves. The new taxon is distinguished by its ovate to ovate-deltoid leaves, small heads with ca. 12 disc florets, disc corollas ca. 3 mm long with markedly expanded throats, and short pappus bristles. *Perityle huecoensis* exhibits some resemblance to *P. lindheimeri* of central Texas, a relationship that is further discussed elsewhere (Powell 1973).

Perityle batopilensis A. M. Powell, sp. nov.

Suffrutices 10–20 cm alti dense pilosi vel villosi; laminae foliorum 0.9–2 cm longae 1–2 cm latae deltoideae vel deltoideo-cordatae; radiati nulli; flores disci 45–50 corollis flavis demum rubris 4.5–5.5 mm longis; achaenia 2.5–3 mm longa; pappus nullus; chromosomatum numerus $n = 17$. Fig. 3.

Plants suffruticose, 10–20 cm high, densely pilose to villous, viscid; leaves opposite or alternate, the blades 0.9–2 cm long, 1.2 cm wide, pilose to villous with shorter glandular hairs, deltoid to deltoid-cordate, the margins serrate-lobed; heads discoid, on short peduncles, 1–3 cm long, clustered among or slightly above upper leaves; involucres cylindric, ca. 9 mm long, 4–4.5 mm wide; phyllaries ca. 21, 5–5.5 mm long, 1–1.5 mm wide; disc flowers 45–50, corollas yellow, upper parts reddish at maturity, 4.5–5.5 mm long, the tube 1–1.2 mm long, glandular-pubescent, the throat 2.5–3 mm long, tubular-funnelform, the lobes acute, ca. 1 mm long; anthers ca. 2 mm long; styles ca. 2 mm long, slender, subulate; achenes 2.5–3 mm long, linear-oblong, flattened, sparsely short-pubescent on faces and callous margins; pappus absent; chromosome number, $n = 17$.

TYPE: Mexico, Chihuahua, Mpio. Batopilas, n. side of Barranca de Batopilas between La Bufa and Quirare, 1590 m, 26 Mar 1979, *Bye et al. 9276* (Holotype: COLO; isotype: SRSC).

PARATYPES: Mexico, Chihuahua, Mpio. Batopilas, along arroyo Wimivo (=Arroyo Samachige) between Wimivo and Rio Batopilas on n. side of Barranca de Batopilas, 990–890 m, 28 Feb 1973, *Bye 3432B* (COLO, SRSC); also possibly *Bye 3210* (COLO), which looks similar (R. A. Bye, pers. comm.).

Collections of *P. batopilensis* were obtained by R. A. Bye and associates during the course of floristic studies of the Sierra Madre Occidental in northwestern Mexico. In my view *P. batopilensis* is but one of the taxa that originated from a formerly widespread entity in

FIG. 3. Isotype of *Perityle batopilensis* (*Bye et al. 9276*). A. Inset is close-up of capitulescence (see arrow).

northern Mexico and adjacent southwestern United States. Other described members of this complex are *P. lemmoni, P. dissecta, P. castillonii* (Powell 1973), and *P. carmenensis* (Powell 1976). Geographically *P. batopilensis* is closest to *P. lemmoni* from which it is distinguished by its deltoid to deltoid-cordate leaves that are serrate-lobed but not dissected, more densely pilose herbage, 18–20 phyllaries, achenes that are epappose, slightly narrower, and nearly glabrous, and longer disc corollas with lanceolate lobes.

Chromosome numbers. The chromosome counts reported here were obtained through standard acetocarmine squashes of microsporocytes. All are consistent with previously established base numbers. Vouchers are deposited in SRSC and elsewhere. Other significant chromosome number reports for *Perityle* are found in Powell and Powell (1978).

Perityle batopilensis, $2n = 17_{II}$. Mexico, Chihuahua, n. side of Barranca de Batopilas, *Bye et al. 9276,* greenhouse progeny. One bivalent was notably smaller than the other 16 bivalents. Counts for other members of this species alliance (see above) are also diploid, but in addition $2n = 34_{II}$ has been reported for *P. dissecta* (Powell 1973).

Perityle fosteri, $2n = 17_{II}$. Texas, Culberson Co., Apache Mts., *Powell 3365, Weedin 1188.* Polyploidy is widespread in the related species, *P. rupestris* (Powell 1969).

Perityle huecoensis, $2n = 17_{II}$. Texas, El Paso Co., North Hueco Mts., *McCarten and Van Devender 2508,* greenhouse progeny. The bivalents are heteromorphic with $2–3_{II}$ larger and $2–3_{II}$ smaller than the others.

Perityle leptoglossa, Harv. & Gray in A. Gray. $2n = 17_{II}$. Mexico, Sonora, Palm Canyon, 17 mi se. of Magdalena, *Van Devender s.n.,* greenhouse progeny.

Perityle lineariloba Rydb., $2n = 17_{II}$. Mexico, Sonora, near Guiricoba, *Miller and Leuck 819.* In a few cells 2–3 round fragments or univalents are present with the 17 bivalents. This is the first count for *P. lineariloba,* previously known only from the type locality at San Ramon, Durango, and $2n = 17_{II}$ is consistent with other numbers known for the white-rayed complex (Powell 1974).

Perityle megalocephala var. *intricata* (Brandeg.) Powell, $2n = 17_{II}$. Nevada, Nye Co., 0.5 mi nw. of Checkpoint Pass, Red Mountain, Nevada Test Site, *Cochrane 744,* greenhouse progeny. Of the three varieties recognized for this species (Powell 1973), chromosome numbers were previously known for two of them, var. *megalocephala* ($2n = 17_{II}$) and var. *oligophylla* ($2n = 34_{II}$), but this is a first report for var. *intricata.* The variety *intricata* was poorly known taxonomically (Powell 1973) and poorly represented in herbaria until recently when several collections were obtained by Susan Cochrane on the Nevada test site. Also, a recent collection (*Castagnoli, Nevers, and Stone 419*) from the Kingston Range, San Bernadino and Inyo Counties, California, appears to be nearly intermediate between var. *intricata* and var. *oligophylla.* The latter collection supports the recognition of var. *intricata* as a variety of *P. megalocephala* and tends to negate the reference by Powell (1973) that future studies may show var. *intricata* to warrant specific status.

Perityle microglossa var. *saxosa* (Brandeg.) Powell, $2n$ = ca. 17_{II}. Mexico, Chihuahua, Mpio. Batopilas, Rio Batopilas e. of La Bufa, *Bye et al. 9216* greenhouse progeny; possibly $2n = 16_{II}$ plus 2_{I}. The label of *Bye et al. 9216* describes the specimen as "annual" although another collection of this taxon, *Bye et al. 9190,* from Mpio. Batopilas, is labeled "small woody-based plant." The seed progeny of *Bye et al. 9216* in the greenhouse developed into a self-incompatible woody-based perennial, tending to support the hypothesis (Powell 1974) that var. *saxosa* is a perennial, diploid, self-incompatible ancestor of the annual polyploid, self-compatible weed, *P. microglossa* Benth. var. *microglossa.*

Perityle socorrensis Rose, $2n$ = ca. 19_{II}. Mexico. Socorro Island, Cabo Middleton, *Moran 25535,* greenhouse progeny. The count was most consistently $2n = 19_{II}$, but possibly $2n = 17\text{–}20_{II}$ in that the heteromorphic chromosomes, particularly several smaller bivalents, were difficult to interpret. The related species *P. crassifolia* also is $2n = 19_{II}$ (Powell 1974).

Notes. Several collections of *P. aurea* Rose (Mexico, Sonora, Tiburon Island, *Fegler 12205, 15727, 15733*) increase the known distribution of this restricted species (Powell 1974). Both *P. vitreomontana* Warnock and *P. cinerea* (A. Gray) Powell were early considered for rare and endangered species status, but my recent observations indicate that the species are rather common in their restricted areas of distribution (Powell 1969) and are at present not threatened or endangered. *Perityle cernua* (Greene) Shinners was reported only from Dripping Springs Canyon, Organ Mountains, New Mexico (Powell 1969), but more recent collections primarily by T. K. Todsen and R. Spellenberg have shown the plant to occur in other localities in the Organ Mountains (Fillmore Canyon, Long Canyon, just e. of Peña Blanca, sw. of Organ Needle; 1800–3000 m; specimens at NMC).

ACKNOWLEDGMENTS

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A NEW CHIHUAHUAN DESERT ROSE (ROSACEAE)

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ABSTRACT

Rosa woodsii var. **maderensis** is described from the Sierra de la Madera in central Coahuila, Mexico. It is distinguished by its smaller, glabrous leaves, reduced ovary and stamen number and smaller hips with few fruits.

Continued studies in connection with M. C. Johnston's Chihuahuan Desert Flora have uncovered distinct populations of a native rose from the Sierra de la Madera near Cuatro Ciénegas in central Coahuila. The new taxon, which represents the southernmost known stand of *R. woodsii,* is characterized by reduced leaf size and reduced number of ovaries and stamens per flower.

Rosa woodsii Lindl. var. **maderensis** Henrickson var. nov.

A var. woodsii foliis parvioribus glabris 3.5–5.5 cm longis foliolis 5–7 serratis dentibus ad apicem glandulis stipitatis rubris, pistillis paucioribus 4–6(–8), (non 15–30), fructis parvioribus achaeniis 1–4 differt (Fig. 1).

Slender, gracefully arching shrubs 1–2(–3) m high; young stems greenish, turning maroon, waxy, smooth; bark gray; enations few, infrastipular, divergent, straight, slender, stramineous, 7–14 mm long, abruptly expanded vertically to an obovate base 2.5–5.5 mm long; internodes glabrous. Leaves oblong-ovate in outline, 3.5–5.5 cm long, 2–3 cm broad; petioles 1–2 cm long; stipules 4.5–10 mm long, the pair 1.5–3(–5) mm wide, adnate to petiole except for free, oblong-lanceolate, 1–2 mm long tips, stipitate-glandular along margins, otherwise glabrous, glaucous, green to reddish; leaflets 5–7, obovate to oblong-obovate, (5–)8–14(–19) mm long, 4–9(–13) mm wide, rounded to retuse at tip, broadly cuneate to rounded at base, at margins closely serrate, often partially doubly serrate along sides, with acute to acuminate teeth each tipped with a stipitate or sessile gland, glabrous, green above, whitish-glaucous beneath; terminal leaflets largest, on petiolules 4–8 mm long, lower lateral leaflets reduced in size, with petiolules 0.5–1.5 mm long; rachis glabrous to sparsely stipitate-glandular; glands sometimes continuing to midvein on lower leaf surface. Flowers mostly solitary at new stem tips on glabrous pedicels 2.5–5 mm long; bracts

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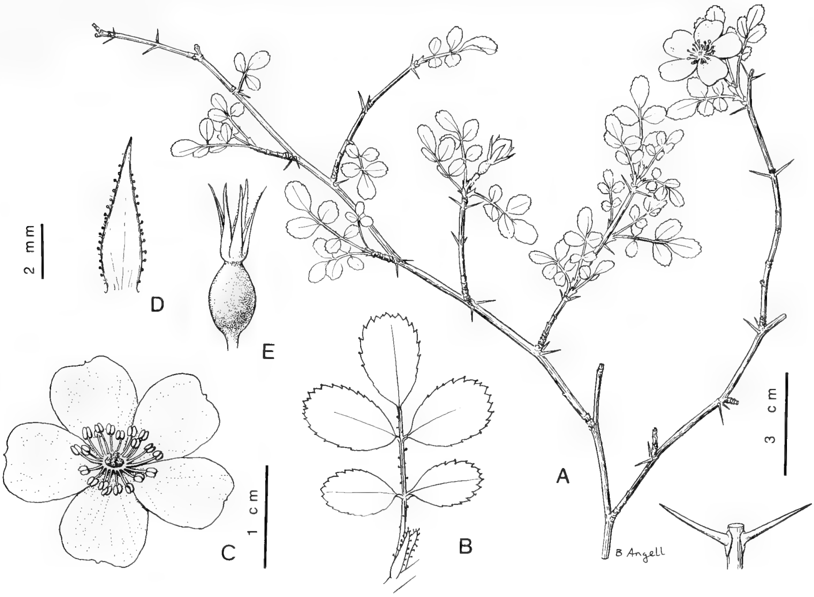

FIG. 1. *Rosa woodsii* var. *maderensis* Henrickson. A. Branch showing infrastipular enations (enlarged on lower right), and new shoots of season (*Henrickson & Prigge 15296,* TEX). B. Leaf showing stipitate glands on stipule margins, rachis (*Henrickson & Prigge 15296,* TEX). C. Flower with only 20 stamens (*Wendt & Lott 1371A,* LL). D. Abaxial surface of sepal. E. Immature hip showing characteristic ellipsoidal shape, persistent sepals (both *Wendt et al. 1826,* TEX). Magnifications as indicated: 3 cm scale for A; 1 cm scale for B–C, E; 2 mm scale for D.

oblong-ovate, stipule-like but broader; hypanthium narrowly ovoid, 4–5 mm long, 2–3 mm wide, glabrous; sepals lanceolate, 6–11 mm long, to 1.5–2.5 mm wide, attenuate to caudate, entire, glabrous outside, the outer margins often stipitate-glandular, villous inside and along margins when eglandular, persistent, erect on fruit; petals obovate, emarginate at tip, 12–14 mm long, 9–12.5 mm wide, pink to white at base or throughout; stamens 20–40, filaments 3–4 mm long, white, glabrous; anthers 0.9–1.3 mm long, yellow; ovaries 4–6(–8), setose above; styles stramineous, villous, barely exserted, expanded at truncated stigmatic tips. Hips orange- to bright-red, 8–10 mm long, 6–7 mm wide; achenes 1–3(–4), broadly ellipsoidal, stramineous, setose at tip, 4.5–6 mm long, ca. 3 mm wide.

TYPE: México, Coahuila; ca. 42 (air) km wnw. of Cuatro Ciénegas on n. slope of Sierra de la Madera, 14 km w. by road from Rancho Cerro de la Madera up n.-facing Cañón Desiderio in oak-pine forest; low shrubs 0.6–1 m high; petals pink-white; 2000–2300 m, 12 Aug 1976, near 27°08′N, 102°31′W. *J. Henrickson and B. Prigge 15296.* (Holotype: TEX; isotypes: GH, MEXU, NY, RSA).

The new taxon occurs on rocky, moist, shaded slopes and margins in wooded higher canyons of the limestone Sierra de la Madera from about 2200 to 2900 m elevation with *Pinus strobiformis, P. arizonica, Pseudotsuga menziesii, Cupressus arizonica, Juniperus flaccida, Quercus gravesii, Quercus pringlei, Rhammus betulaefolia, Arctostaphylos pungens,* etc. It flowers from August to September.

PARATYPES: Mexico, Coahuila, Sierra de la Madera, Cañón de la Hacienda, 5 Aug 1973, *Henrickson & Wendt 11879* (TEX, MO); 10 May 1972, *M. C. Johnston et al. 10958* (LL); Cañón de la Barrica, on se. side of Picacho El Pajaríto, 29 Aug 1975, *Wendt & Lott 1371A* (LL) *1371* (LL); Cañón Desiderio, 28 Sep 1976, *Wendt et al. 1812* (TEX, 2 sheets); Cañón del Agua, 9 Sep 1939, *C. H. Muller 3237* (GH, LL); 2 km e. of Picacho de Zozáya, 13 Sep 1941, *I. M. Johnston 9026* (GH, 2 sheets).

The new taxon clearly lies within the highly variable and widespread *Rosa woodsii* complex (Erlanson 1934) of central and western North America, having mostly 5–7, oblong-obovate, rather thin leaflets with serrate margins, attached stipules, terete infrastipular enations, glabrous hypanthia, and narrow, externally glabrous, internally villous, persistent sepals. Within this complex, it has some characters typical of *Rosa fendleri* Crepin and *R. hypoleuca* Wooten and Standley, namely conspicuous stipitate glands on leaflet and stipule margins and a tendency for doubly serrate leaflet margins.

This complex of taxa has been treated as a series of distinct species by Rydberg (1918) and as a highly variable species by Erlanson (1934), whose field observations and experimental evidence showed that many of the characteristics Rydberg used in his treatment tended to exhibit Mendelian assortment and tended to be variable within many populations. Her experimental evidence showed up to five nominal species identifiable from offspring grown from seeds of single plants within this complex (Erlanson 1934). She relegated 14 of Rydberg's species to synonomy under *R. woodsii.* More recently, Hitchcock et al. (1961) have recognized two varieties within *R. woodsii* for the Pacific Northwest; and Martin and Hutchins (1980) have recognized most of Rydberg's taxa, making a series of illegitimate varietal combinations under *R. woodsii* in their New Mexico flora.

This new variety differs from the other taxa in this complex by its highly reduced ovary number of 4–6(–8) per flower (not 15–30), and its commensurately smaller, more ellipsoidal hips containing often only 1–3(–4) achenes. Some of the other characteristics of this new taxon, such as glabrous, small leaves, reduced stamen number, and largely glabrous internodes, occur frequently in in the *R. woodsii* complex, but not in this combination.

The collections of the new taxon are also quite uniform in most characteristics including leaf glabrosity, leaf size, presence of stipitate or sessile reddish glands on tips of leaflet serrations, straight, slender infrastipular enations, glabrous, narrow hypanthium and short sepal length and small flower size. Differences occur mainly in the extent of the red-tipped, stipitate glands, which may continue onto the midvein of the lower leaflet surface in some collections, but may be present or absent on the abaxial surface on some stipules. Stamen number also varies from around 20 to 40 in available collections.

Because this new taxon is certainly recognizable in its features, relatively uniform in its characteristics, and isolated in its occurrence, its recognition at least at the infraspecific level is supported. Much work, of course, needs to be done on the variability inherent in the *R. woodsii* complex sensu lato.

ACKNOWLEDGMENTS

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NEW *STREPTANTHUS* TAXA (CRUCIFERAE) FROM CALIFORNIA

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ABSTRACT

Two California serpentine endemics, **Streptanthus drepanoides** Kruckeberg & Morrison, from the North Coast Ranges (Tehama to Trinity Counties) and **S. insignis** Jeps. subsp. **lyonii** Kruckeberg & Morrison from western Merced County, are described. Five new sections in *Streptanthus,* subgenus *Euclisia,* are also described.

We offer two new taxa in *Streptanthus* (Cruciferae) native to California. They are *Streptanthus drepanoides* Kruckeberg & Morrison, sp. nov. and *S. insignis* Jeps. subsp. *lyonii* Kruckeberg & Morrison, subsp. nov. Both are members of the subgenus *Euclisia,* noted for its high incidence of plants narrowly endemic to serpentine outcrops. We also give nomenclatural changes in the subgenus.

These two serpentine endemics were recognized as new by Morrison (1941) but were not published at that time. Recent study of the two enlarges our understanding of them. Several additional collections of *S. drepanoides* and periodic revisiting of the very local sites for *S. insignis* subsp. *lyonii,* combined with observations of the taxa under cultivation, their crossability with related taxa, and their chemotaxonomic profiles are the noteworthy recent contributions. These studies are part of a larger biosystematic investigation of the genus by Drs. T. Crovello, A. R. Kruckeberg, and J. Rodman. Recognition of these rare entities contributes to the inventory of rare and endemic plants of the California flora (Smith 1980).

Streptanthus drepanoides Kruckeberg & Morrison, sp. nov.

Herba annua erecta glaberrima et glauca, 0.5–1.5 dm alta, simplex vel ramosa divaricata; folia orbiculata imbricata, disticha, folia radicalia petiolis brevibus, folia caulina sessilia amplexicaulia auriculata; racemi breves (4.0–8.0 cm); flores conferti; alabastra turbinata carinata saepe setis brevibus; sepala ochroleuca, apicibus erosis refractis; petala exserta, apicibus recurvatis, 0.6–0.8 cm longa, hyalina, venis unguis amplis, pari superiori curtiori quam pari inferiori; stamina paribus tres inaequalibus, pari superiori longissima (1.3 cm), exserta et

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recurvata, connata usque ad antheras reductas, pari inferiori ex parte connato; stamina lateralia discreta; siliquae torulosae, arcuatae vel falcatae vel rectae, 6.0–9.0 cm longae; semina exalata vel alata vestigiale ad apicem (extremum). (Figs. 1, 2).

Annual, 0.5–1.5(–3.5) dm tall, the stem erect, simple to divaricately branched from near the base; leaves mostly basal, strongly overlapping and distichous, glabrous and glaucous, mottled gray-green, often anthocyanous beneath, succulent, entire to shallowly dentate, 2–5 cm long, 1–4 cm broad; lowermost leaves with a short broad laminate petiole, the lower cauline leaves sessile, broadly orbicular and cordate-auriculate, the upper cauline leaves broadly cordate, oblong; flowers erect in short (4.0–8.0 cm) dense, straight racemes, 0.7–0.9 cm long, the buds turbinate, carinate, and often short bristly when young; sepals ochroleucous to greenish white (or purplish), 0.5–0.65 cm long, keeled, the erose-hyaline tips reflexed, glabrous to sparingly hispidulose, the trichomes slender, simple, hyaline; petals exserted, recurved at tips, 0.6–0.85 cm long, hyaline with crisped margins and with a broad median brownish purple vein, the upper petals somewhat shorter than the lower ones, the claw 0.4 cm long and narrowly oblanceolate, the channelled blade 0.2 cm long, narrower than the claw, and undulate; stamens in three unequal pairs; upper pair of stamens markedly longer (0.75–1.3 cm long) than the other two pairs, filaments of the upper pair connate to apex and broadly veined, exserted and recurved, their sagittate anthers reduced, barely polliniferous or vestigial; filaments of the lower pair of stamens connate two-thirds of their length (0.9 cm), just exceeding the petals, the sagittate anthers polliniferous; lateral stamens free, polliniferous, approximately 0.6 cm long; siliques 5.5–9 cm long, divaricate, straight, or slightly falcate to arcuate, dense and numerous, torulose; stigma sessile; seeds wingless or with vestigial wing at one tip; cotyledons accumbent, after germination. $n = 14$ (*Kruckeberg 5901, 6627*).

TYPE: California, Tehama County, serpentine outcrops on the Paskenta-Covelo road, 12.8 km from Paskenta, 21 May 1940, *Morrison and Belshaw 3215* (Holotype: UC! UC no. 644783).

PARATYPES: California, Tehama Co., between Mud Flat and Bennett Spring, on the Newville-Covelo Rd., *Heller 11549* (WTU, UC, G, P, F, M); 8 km w. of Paskenta on the Covelo Rd. (serpentine?), *Bailey s.n.,* 16 Apr 1938 (UC); serpentine, 19.2 km w. of Paskenta on the Paskenta-Covelo Rd., 1 Sep 1966, *Kruckeberg 5903* (WTU); serpentine chaparral and Jeffrey pine woodland, along road to Wells Cr. campground ca. 1.6 km se. of Tedoc Gap, 22 Jun 1980, *Nelson and Nelson 5802* (WTU, HSC); serpentine chaparral, along Colyear Springs Rd. (25N01) 2.6 km w. of jct. with Raglin Ridge Rd. (25N01 and 25N05), 23 Jun 1970, *Nelson and Nelson 5870* (WTU, HSC). Trinity Co.: serpentine of Jeffrey pine woodland, just above Salt Cr.,

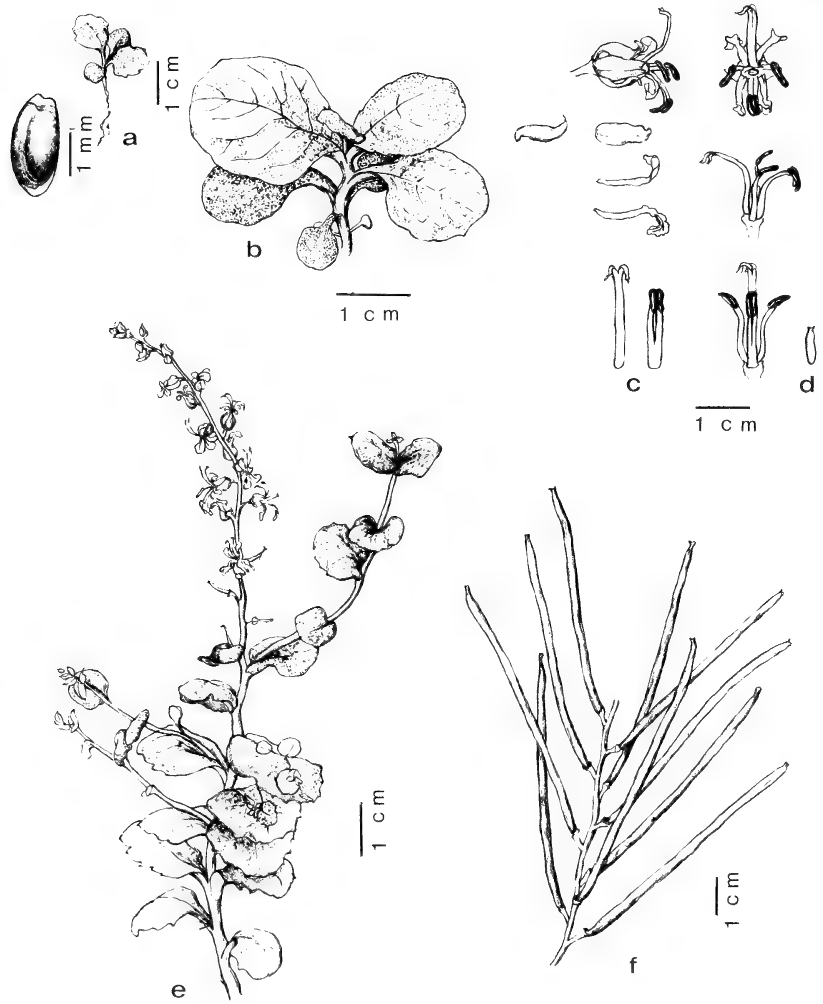

FIG. 1. *Streptanthus drepanoides:* a. Seed and seedling; b. Rosette; c. Flower (side view), sepals, upper and lower petals, sterile and fertile stamens; d. Flower (face view), androecium (2 views), pistil; e. Habit; f. Raceme with mature siliques. Drawing by Hazel Thelen from *Kruckeberg 5903*.

FIG. 2. Members of sect. *Hesperides:* a. *Streptanthus barbiger* Greene (*Kruckeberg 6595*); b. *S. drepanoides* (*Kruckeberg 5901*); c. *S. breweri* Gray (*Kruckeberg 5914*).

ca. 3.2 km sw. of Peanut on Highway 3, 3 Sep 1978, *Kruckeberg 6625, 6627* (WTU); serpentine barren, along road 29N28, 11.2 km s. of jct. with State Route 36 and 1.6 km from Goat Camp, 1350 m, 22 Jun 1980, *Nelson and Nelson 5744* (WTU, HSC); Jeffrey pine woodland, along Panther Camp trail 180 m n. of jct. with road 29N73, 4.8 km from Hayfork Cr., 1620 m, 22 Jun 1980, *Nelson and Nelson 5765* (WTU, HSC): serpentine, Jeffrey pine woodland, along State Route 36 on ridge between Salt Cr. and Muldoon Gulch, 4 km w. of jct. with road 30, 1290 m, 22 Jun 1980, *Nelson and Nelson 5729* (WTU, HSC); serpentine chaparral and Jeffrey pine woodland, along State Route 3, 0.5–0.8 km s. of Salt Cr. Bridge, 750 m, 19 Jun 1980, *Nelson and Nelson 5630* (WTU, HSC): serpentine chaparral and Jeffrey pine woodland, along State Route 3, 0.8 km s. of Salt Cr. Bridge, 750 m, 18 Jun 1980, *Nelson and Nelson 5547* (WTU, HSC): serpentine barrens, along Salt Cr. Rd. at junction with road 30N24, 930 m, 17 Jun 1980, *Nelson and Nelson 5502* (WTU, HSC). Shasta Co.: openings on serpentine chaparral, jct. of roads 41 and 28N08, 1200 m, 22 Jun 1980, *Nelson and Nelson 5827* (WTU, HSC); serpentine scrub and Jeffrey pine woodland, along For. Ser. Rd. ca. 1.6 km w. of Regan Meadow, 1500 m, 22 Jun 1980, *Nelson and Nelson 5839* (WTU, HSC).

Distribution. Serpentine outcrops in the inner North Coast Ranges of northwestern California; confined to western Tehama, northeastern

Mendocino, southwestern Shasta and southern Trinity Counties. *Streptanthus drepanoides* grows in open serpentine chaparral, and open Jeffrey pine and digger pine woodlands, especially in intervening barren serpentine rubble. It is also locally common on serpentine roadcuts: 610 to 1635 m.

The strongly two-ranked (distichous) lower leaves, broadly orbicular in outline, the erect, short congested inflorescence and the falciform siliques set *S. drepanoides* apart from its nearest relatives. It clearly shows close affinity to members of the *Hesperides* section of subgenus *Euclisia,* particularly to *S. breweri* Gray and *S. hesperidis* Jepson. Specimens of *S. drepanoides* have been filed in herbaria as *S. hesperidis*. It can be distinguished readily from these congeners by vegetative, floral, and fruit characters (Table 1).

Streptanthus drepanoides, endemic to serpentine, has been collected with increasing frequency in recent years. Besides our own collections, those of Thomas and Jane Nelson (Humboldt State University, Arcata, CA), extend the range from the type locality north and west into eastern Mendocino, Shasta, and Trinity Counties. The Nelsons' collections from the Mt. Lassic massif of southwestern Trinity County and both theirs and ours from near Peanut, Trinity County, definitely show the species to be more centrally located north of the type locality. At the latter station, *S. drepanoides* is associated with serpentine chaparral: low statured *Quercus durata* with *Arctostaphylos* and *Garrya,* and widely scattered *Pinus sabiniana*. In Trinity County, plants of *S. drepanoides* frequently occur on serpentine slopes and openings in Jeffrey pine parkland, with *Rhamnus californica* var. *crassifolia* and *Arctostaphylos stanfordiana*. It coexists here on serpentine with *S. tortuosus* Kell. and the Trinity County serpentine endemic, *S. barbatus* Wats.

Streptanthus drepanoides is the northernmost member of the section *Hesperides* (subgenus *Euclisia*). The inner Coast Range taxa of this group appear to replace one another from south to north. Although *S. breweri* and *S. hesperidis* can be locally sympatric in Lake County, we have found no case in which *S. drepanoides* coexists with other members of the section. Instead, it can be found growing with members of two other groups, as mentioned above.

Streptanthus drepanoides is diploid ($n = 14$), as are all members of the section *Hesperides*. Artificial crosses with *S. breweri* and *S. hesperidis* have reduced fertility (0–50% pollen stainability).

The specific epithet refers to the sickle-shaped siliques.

Streptanthus insignis Jepson subsp. **lyonii** Kruckeberg & Morrison, subsp. nov.

Herba annua hispidissima, erecta, simplex vel pauciramosa vel multiramosa, 1.0–3.5 dm alta; folia a var. *insignis* optime congruentia,

TABLE 1. COMPARISON OF *S. drepanoides* TO OTHER TAXA OF SECT. *Hesperides*.

	S. drepanoides	*S. breweri*	*S. hesperidis*
Habit	low (0.5–1.5 dm), simple to branched	tall (1.5–5.0 dm), usually much branched	intermediate (1.0–1.5 dm), simple
Plant color	gray-green	bluish green	yellow-green
Leaf arrangement	congested, distichous	openly spaced; spiral	openly spaced; spiral
Basal and cauline leaves	orbicular, obscurely toothed or entire, margin revolute	ovate, shallowly toothed; margin plane	obovate-lanceolate, deeply toothed; margin plane
Inflorescence	straight, erect, congested, mostly unbranched	erect to divaricate; open, elongate, amply branched	zig-zag in outline, short, erect, mostly unbranched
Flower color	ochroleucous	rose-purple or white	ochroleucous
Flower	small; constricted at throat	larger; open at throat (anthesis)	small; constricted at throat
Siliques	erect or divaricate, falcate	strongly recurved	erect to divaricate, straight
Habitat	serpentine chaparral, Jeffrey pine woodlands	serpentine chaparral or barrens	serpentine chaparral or barrens
Range	Tehama, Shasta and Trinity Counties	San Benito to Colusa Counties	Napa, Lake Counties

sed hispidiora; flores fertiles lutescentes, sed flores in fasciculibus terminalibus conferti, melanopurpurei vel lutescentes; stamina et siliquae a var. *insignis* optime congruentia.

Annual, with the habit and vegetative features of subsp. *insignis,* densely hispid throughout, erect, simple or usually much branched, compact, 10–35 cm tall; basal and lower cauline leaves linear-lanceolate, pinnatifid, the teeth tipped with callosities, calyx greenish-yellow, the petals lemon-yellow or yellowish-white, much exserted, crisped, obtuse; flowers often secund, abundant; terminal cluster of sterile flowers ("color spot") purplish black or pale yellow; stamens in three unequal sets, the upper set with filaments connate to the reduced anthers, exserted, the lower set shorter and less connate, the lateral set with filaments free, approximate, and short; silique narrow, often sharply deflexed, copiously hispid with flavescent setae; seeds winged; cotyledons accumbent. $n = 14$.

TYPE: California, Merced County, serpentine outcrop, 2 mi n. of Ortigalita Peak, inner South Coast ranges, 3 Apr 1938, *Lyon 1223* (Holotype, UC!).

PARATYPES: California, Merced Co., 4 May 1940, *Morrison 3127* (UC!); on steep, w.-facing serpentine slope, just e. of road above and ne. of Wiseman Flats, 535 m, 24 Aug 1978, *Kruckeberg 6578* (WTU, type locality); on steep, w.-facing chert-shale slopes just n. of ridge between Wiseman Flats and Piedra Azul Springs, ca. 0.5 km n. of type locality, 540 m, 24 Aug 1978, *Kruckeberg 6581* (WTU), the "bicolor" form.

Distribution. Restricted to western Merced County, subsp. *lyonii* is locally frequent, mostly on serpentine of low hills at east base of inner South Coast Ranges between Wiseman Flats and Piedra Azul Spring, Arburua Ranch, T13S R9ES1, (Mt. Diablo Base Meridian), ca. 600 m. The habitat is mostly annual grassland with a rich forb cover. Widely spaced blue oaks (*Quercus douglasii*) are in the vicinity; occasional plants of *Juniperus californica* and *Artemisia californica* occur adjacent to the serpentine outcrop of the wholly yellow-flowered form. The variant with yellow flowers and a purple terminal "color spot" grows on a chert-shale slope (*Kruckeberg 6578*). It is probable that other localities exist along the lower stretches of Piedra Azul Creek and nearby lower slopes of the range, just to the north of Ortigalita Peak. Associated species on serpentine (*Kruckeberg 6578*) include *Eriogonum inflatum, Eschscholtzia lemmonii, Bromus rubens, Camissonia refracta, Emmenanthe penduliflora, Phacelia fremontii, P. distans, Cryptantha* sp., *Malacothrix obtusa, Chaenactis glabriuscula* (or *C. fremontii*), *Salvia columbariae,* and *Silene multinervia.* On the non-serpentine site just south of Piedra Azul Spring associes were *Eriogonum fasciculatum, Calochortus venustus* (?), *Trifolium* (large annual species), *Chorizanthe membranacea, Lupinus* (annual species), *Avena fatua, Bromus rubens* and *B. mollis*.

Apart from the collections by Gregory Lyon and John Morrison in the 1930s, this rare and local variant remained little known until the 1970s, when it was revisited by Lyon and Morrison, and then in 1978 by Lyon and Kruckeberg (*Kruckeberg 6578, 6581*). Subspecies *lyonii* is just to the east of the main range of *Streptanthus insignis* subsp. *insignis*; the typical form occurs on serpentine along the western flank of the Inner South Coast Ranges from New Idria north to Panoche Pass, and is thus more widespread than subsp. *lyonii*. The members of section *Insignes* are all confined to the Diablo Range and thus form a geographically coherent group. *Streptanthus hispidus* Gray, endemic to non-serpentine sites on Mt. Diablo (Contra Costa Co.), is the northernmost species. Proceeding southward, the extremely rare *S. callistus* Morrison is known from only one non-serpentine chaparral hillside just east of Mt. Hamilton. *Streptanthus insignis* subsp. *insignis* and subsp. *lyonii* are the southernmost taxa of the group, confined to southwestern Merced, southeastern San Benito, and eastern Monterey Counties (and possibly southwestern Fresno County).

Although subsp. *insignis* is rather uniform in character, with purplish white flowers and a purple-black "color spot" terminating the inflorescence, subsp. *lyonii* in flower has two distinct variants. The serpentine locality at Wiseman Flats has plants with wholly lemon yellow inflorescences (*Kruckeberg 6578*), whereas the non-serpentine plants near Piedra Azul Spring (*Kruckeberg 6581*) have yellow flowers below the terminal purple-black cluster (the "color spot"). Morrison (1941) in his unpublished thesis gave this latter variant the name "bicolor." Subsequent greenhouse observations and crosses between the two suggest the recognition of the two variants as one subspecies. Another taxonomic solution would be to recognize two varieties under subsp. *lyonii*. The serpentine plants would be "var. lyonii" and the non-serpentine "bicolor" plants "var. bicolor." We refrain from taking this step at this time.

Besides flower color, other features serve to distinguish subsp. *insignis* from subsp. *lyonii*. The latter is much more hispid throughout the entire plant than is subsp. *insignis*; particularly notable are the short, stiff setae copiously clothing the ovary and the mature silique.

Gregory Lyon, then of Firebaugh, California, discovered this unique variant of *S. insignis* in 1938 in the course of his many seasons of botanizing this little known sector of the South Coast Ranges. Often with the authors, Lyon then revisited the localities over the years, providing a faithful record of its occurrences, in good years and bad. In manuscript, Morrison (1941) proposed the name of *S. lyonii,* which we now happily formalize in print as subsp. *lyonii*.

All members of sect. *Insignes* are diploid (n = 14), and all but *S.*

TABLE 2. CROSSES AMONG SOME MEMBERS OF *Streptanthus* SECTION *Insignes*.

Cross	Features	Pollen stainability	Seed set
lyonii × *lyonii* (*Kruckeberg 6578* × *6581*)	Intermediate to variable; calyces yellow green, green, or green suffused with purple; petals dull white; terminal "color spot" with tips of calyces barely colored to colored ¼ way from tip. Copious pollen; normal siliques.	>95% (4)	high
lyonii × *insignis* (*Kruckeberg 6581* × *6574*)	Intermediate; calyces pale green to ochroleucous; "color spot" variable	>95% (2)	high
lyonii × *callistus* (*Kruckeberg 6581* × *6590*)	Hybrids like ♂ parent but with paler flowers	0, 25, 50–75% (4)	high
insignis × *lyonii* (*Kruckeberg 6574* × *6578*)	Intermediate; greenish-yellow calyces; white-tipped petals with purple veins	>95%	high
insignis × *callistus* (*Kruckeberg 6574, 6031a* × 6590)	Flowers and habit intermediate	>50% (few grains)	high
[*insignis* (*6031a*) × *hispidus* (*6025*)—no hybrid plants]			

hispidus can be intercrossed to yield hybrid plants. The crosses between *S. insignis* subsp. *insignis* and subsp. *lyonii* have good pollen (>95% stainable), set viable seed on selfing, and show a range of parental characters in the F_1 plants. Intentional hybrids between both subspecies of *S. insignis* and *S. callistus* have reduced fertility (0–50% stainable pollen), are either good intermediates or favor *S. callistus* in character, and have set some seed on backcrossing and selfing. Meiotic behavior of the hybrids is normal (Table 2). These crossing results then support the subspecific status of *lyonii* within *S. insignis* and further highlight the species level discontinuity between *S. insignis* and *S. callistus*. Even though no viable hybrids have been obtained using *S. hispidus* as a male or female parent, the features of this species clearly align it with the other *Insignes* taxa. (See Fig. 3.)

Rodman et al. (1981) have compiled 27 seed glucosinolate characters from most of the taxa (39) in *Streptanthus*. Their summary diagram (fig. 2, Rodman et al. 1981, listed as "drepanoides" and "lyoni") includes the two new taxa described here. *Streptanthus drepanoides* is well separated (distance coefficient of 0.3) from the other taxa of sect. *Hesperides* that were tested (*S. barbiger* Greene and *S. breweri*). The two subspecies of *S. insignis* proved to have close chemical affinities

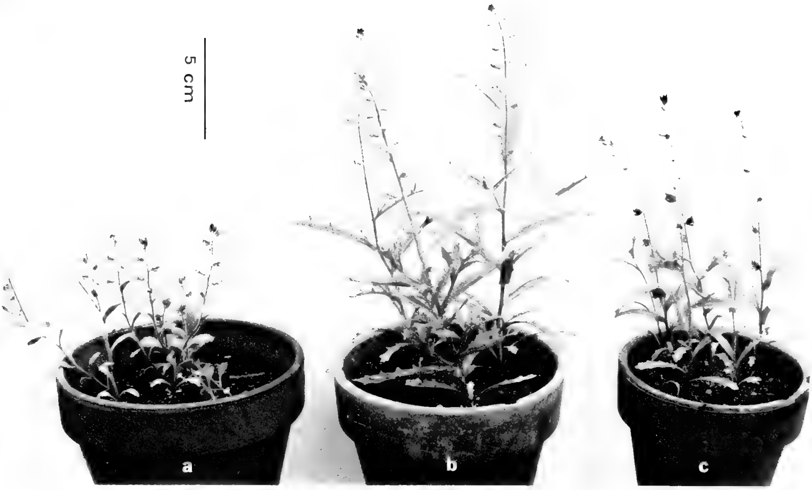

FIG. 3. Members of sect. *Insignes:* a. *Streptanthus hispidus* Gray (*Kruckeberg 6025*); b. *S. insignis* subsp. *lyonii* (*Kruckeberg 6581*); c. *S. insignis* subsp. *insignis* (*Kruckeberg 6574*).

(distance coefficient of 0.1). The distance coefficient between the subspecies of *S. insignis* and *S. hispidus* is 0.2; in fact, *S. insignis* has closer chemical affinity with other taxa outside of its section than it does with *S. hispidus,* here placed in sect. *Insignes.*

Both *S. drepanoides* and *S. insignis* should be considered rare and perhaps endangered. We suggest that they be given formal status in the Inventory of Rare and Endangered Vascular Plants of California (Smith et al. 1980). *Streptanthus drepanoides* and *S. insignis* subsp. *insignis* could be assigned to List 3—Plants Rare but not Endangered; *S. insignis* subsp. *lyonii* seems appropriate for List 2—Plants Rare and Endangered. *Streptanthus callistus* and *S. hispidus* are already on List 2 of this inventory.

SECTIONAL TAXONOMY

Five new sections for subgenus *Euclisia.* The subgenus *Euclisia* Nutt. ex T. & G. of *Streptanthus,* to which these new taxa belong, has five clearly definable subgroups. We wish to recognize them formally as sections here. Biosystematic studies to support these sections are in progress; a monograph of subgenus *Euclisia* will be one facet of the work. The junior author, Morrison (1941), recognized in manuscript four sections of subgenus *Euclisia.* An additional section is proposed here, on the basis of the discovery of distinctive biennials with euclisian affinities by Hoffman (1952). The five sections are: *Euclisia, Insignes, Hesperides, Biennes,* and *Polygaloides*. Earlier treatments of the the subgenus *Euclisia* Nutt. are found in Jepson (1925, 1936), Morrison (1941) and Hoffman (1952). The earliest application of *Euclisia* was by Torrey and Gray (1838); they used the epithet as one of two subdivisions of *Streptanthus* Nutt. The name *Euclisia* (spelled *Euklisia* by Torrey and Gray) embraced six of the 12 taxa in *Streptanthus* known at that time. Plants of their concept of euclisian affinity were characterized by Torrey and Gray as having "petals narrow; calyx closed." They give the epithet as "*Euklisia,* Nutt., mss." All subsequent authors have cited the taxon as *Euclisia* (or *Euklisia*) Nutt., but in fact it should be rendered *Euclisia* Nutt. ex Torrey and Gray. As construed by Nuttall and Torrey and Gray, *Euclisia* included a heterogeneous set of species.

E. L. Greene (1904) first redefined the limits of *Euclisia* as a genus and specified the taxa referred to it. Then Jepson (1925, 1936) treated the group as subgenus *Euclisia* of the genus *Streptanthus*. Morrison (1941), Hoffman (1952), and the present authors have followed Jepson's circumscription of the subgenus. The salient features of subgenus *Euclisia* include zygomorphic flowers, non-bracteate inflorescences, filaments of one or two pairs of stamens partially to completely connate, and the upper pair of stamens usually with reduced to vestigial (and sterile) anthers. While no one of these features is unique to *Euclisia,* the consistent co-occurrence of them distinguishes the group from other subgenera of *Streptanthus*. Furthermore the great majority of euclisian taxa are partially to obligately serpentinicolous, often narrowly endemic to serpentinites.

Subgenus *Euclisia* Nutt. ex. Torr. & Gray, Fl. N. A. 1:77. 1838.

STREPTANTHUS Section EUCLISIA.

Annuals, usually with hispid stems and leaves, base of setae on leaves pustulate; basal leaves 5–10 cm long, hispid (except *S. niger* and *S. albidus* subsp. *albidus*), narrowly lanceolate, coarsely and sinuately toothed to shallowly pinnatifid, the teeth callus-tipped; cauline leaves sessile, auriculate-clasping, narrowly lanceolate, remotely toothed, gradually reduced upwards, there becoming entire, auriculate, lanceolate, and acuminate. Flowers in open simple or branched ebracteate racemes; calyx zygomorphic, inflated and umbilicate, red, purple, lilac or ochroleucous to yellow or white, sepals carinate; petals unequal, usually strongly recurved, red, purple or white; stamens in 3 unequal pairs, the upper with connate filaments; stigma flat, round; siliques flattened, glabrous or hispid; seeds winged; cotyledons accumbent.

TYPE SPECIES. *S. glandulosus* Hook., Ic. Pl. 1, pl. 40. 1836.

Distribution. Cismontane California, west of the Great Valley from San Luis Obispo County to northwestern California (and southwestern Oregon); usually on serpentine.

This section is typified by *S. glandulosus* Hook., the most variable and the widest ranging species in subgenus *Euclisia.* It includes, besides *S. glandulosus, S. niger* Greene and *S. albidus* Greene. These species and their infraspecific taxa have been treated elsewhere (Kruckeberg 1958).

Streptanthus Section **Insignes** Kruckeberg & Morrison, sect. nov.

Herbae annuae hispidissimae; inflorescentia fasciculibus terminalibus confertibus florum sterilium laete colorum; siliquae hispidae, planae vel teretae; semina alata vel exalata, plana vel rotunda.

Densely hispid, mostly low, compact annuals; inflorescence usually simple, compact, with a terminal "color spot" composed of sterile calyces much elongated, highly colored, mostly purplish black (or yellow); sepals purple or greenish yellow; petals purplish white to red, or flavescent, narrow, channeled, the blade margin crisped, the claw broad, yellowish; stamens in three unequal sets, the filaments of the upper and lower sets connate; siliques flattened or terete, erect or spreading or deflexed, hispid; stigma two-lobed; seeds winged or wingless, flattened or rounded; cotyledons accumbent.

TYPE SPECIES. *Streptanthus insignis* Jepson, Man. Fl. Pl. Calif. 420. 1925.

Section *Insignes* consists of three disjunct species, *S. hispidus* Gray, *S. callistus* Morrison and *S. insignis* (with two subspecies *insignis* and *lyonii*). They are confined to the inner South Coast Ranges of California (the Diablo Range), from Mt. Diablo in Contra Costa County to the New Idria country of San Benito County. Habitat, distribution, interfertility, and other attributes have been given in an earlier section of this paper. Figure 3 shows three *Insignes* taxa.

Streptanthus Section **Hesperides** Kruckeberg & Morrison, sect. nov.

Herbae annuae glabrae et glaucae; folia radicalia petiolata, ovata vel lanceolata, dentata; flores irregulares (zygomorphi), purpurei, viridio-albidi vel lutei; sepala carinata, glabra vel parce setosa; petala paribus inaequalibus, recurvata, purpurascentia vel albida; stamina paribus tres inaequalibus, pari superiori connata, antheris sterilibus, pari inferiori saepe ex parte connata; siliquae graciles, planae, reflexae, arcuatae vel divaricatae vel erectae; semina plerumque exalata.

Annuals, entire plant glabrous, glaucous, semi-succulent; basal leaves petiolate, ovate, deltoid to lanceolate, broad to narrow, usually coarsely toothed, the cauline leaves sessile, auriculate-clasping, toothed to entire; calyx flask-shaped in bud, purple, greenish-white or yellow, glabrous or rarely slightly setose-pubescent, slightly irregular, prominently keeled; petals purple or yellowish white, in two unequal sets, narrow, channeled, recurved, the blade scarcely broader than the claw, slightly crisped; stamens in three unequal pairs, the filaments of the upper pair wholly connate with sterile anthers, the filaments of the lower pair often partly connate; silique slender, flat, slightly torulose, erect to curved, spreading or deflexed; seeds slightly winged or wingless; cotyledons accumbent. Figure 2 shows three *Hesperides* taxa.

TYPE SPECIES: *Streptanthus breweri* Gray, Proc. Amer. Acad. 6: 184. 1864.

Section *Hesperides* contains five species, all restricted to serpentine soil; they are *S. breweri* Gray, *S. barbiger* Greene, *S. hesperidis* Jepson, *S. batrachopus* Morrison and *S. drepanoides* Kruckeberg & Morrison. The range, habitat and other attributes of the species are to be found within the discussion of the new species, *S. drepanoides,* given in this paper.

Streptanthus section **Biennes** Kruckeberg & Morrison, sect. nov.

Herbae biennes glabrae et glaucae, humiles (2.0 dm) vel altae (7.5–12.5 dm); folia radicalia juvenilia petiolata, spathulata dentata; flores irregulares, in racemis vel paniculis amplis ramosis; calyces ampulliformes, glabri vel setosi, lutei vel purpurei, tres paribus inaequalibus, pari superiori connata recurvata, sterili, inferiori ex parte connata, reflexa; siliquae torulosae, erectae vel deflexae; semina fere exalata.

Glaucous and glabrous biennials, low (20 cm) to tall (75–125 cm), the first year rosettes of petiolate, broadly spatulate and coarsely dentate leaves; flowers in openly branched racemes or panicles, zygomorphic; calyx flask-shaped; sepals glabrous or setose, yellow to purple, carinate; petals white to salmon-colored, crisped, unequal, recurved; stamens in 3 unequal pairs, the upper with connate filaments, strongly recurved upward, the lower set partially connate and recurved downwards; siliques erect, divaricate or reflexed, usually torulose; seeds only weakly winged at tip; cotyledons accumbent.

TYPE SPECIES. *Streptanthus morrisonii* F. Hoffman, Madroño 11: 225. 1952.

Section *Biennes,* with at least two species [*S. morrisonii* Hoffman and *S. brachiatus* Hoffman (Hoffman 1952)] is wholly serpentinicolous and restricted to Sonoma and Lake Counties of central California. Recent studies (Dr. J. A. Neilson, unpubl.) made in connection with environmental impact surveys of geothermal power sites in the vicinity of these endemics, suggest the presence of considerable interpopulational variation in *S. brachiatus.* Hoffman's (1952) taxonomy of this remarkable and polymorphic group may have to be modified.

Streptanthus Section **Polygaloides** Kruckeberg & Morrison, sect. nov.

Herbae annuae graciles et glaucae, folia flavo-virescentia, linearia, inferioria grosse pinnata, caulinia integra, filiforma; florae valde zygomorphae et applanatae, luteae vel purpureae; sepala superiora ampla, scutiforma exteriora, sepala lateralia et abaxialia interiora; petala breve exserta, fere aequalia; stamina inaequalia tres paribus, pari superiori late connata, antheribus sterilibus; semina exalata.

Slender, erect, branched annuals, glabrous throughout; leaves yellow-green, linear-filiform, the lower coarsely pinnate, the upper entire; inflorescence of open to erect and branched racemes; flowers very zygomorphic, strongly dorsiventrally flattened, yellow or purple, the upper sepal broad, banner-like, cuneate-truncate, overlapping the two smaller lateral and one abaxial sepals; petals shortly exserted, pale yellow to white, crisped, nearly equal in shape; stamens in 3 pairs, the upper with broad, bright green, connate filaments, tipped with tiny aborted anthers, the other pairs not connate; siliques short, flat, arcuately reflexed; seeds not winged; cotyledons accumbent.

TYPE SPECIES. *Streptanthus polygaloides* Gray, Proc. Amer. Acad. 6:519. 1865.

Section *Polygaloides* is monotypic, with a species whose *Polygala*-like flowers are strikingly deviant from any other California crucifer. With perhaps good cause, E. L. Greene (1904) proposed the genus *Microsemia* [*M. polygaloides* (Gray) Greene] for this remarkable plant. The idea that the species may be generically monotypic has been revived recently by the finding (Reeves et al. 1981) that it is a "hyperaccumulator" (>1000 ppm) of nickel, a heavy metal often associated with serpentine soils. Other serpentine species of *Streptanthus* did not show the high levels of nickel (3300–14,800 ppm) that point to *S. polygaloides* as the first hyperaccumulator found in North America.

However, features of foliage and details of flower and fruit mark its affinity with other euclisian species, though *S. polygaloides* does share some attributes with *S. tortuosus* Kell. and *S. diversifolius* Wats. of subgenus *Pleiocardia*. This monotypic section is wholly confined to the serpentines of the Sierra Nevada foothills from Mariposa to Butte Counties, California.

ACKNOWLEDGMENTS

This paper is part of a biosystematic and monographic study of *Caulanthus* and *Streptanthus*. Funding for the work has come to the senior author from the NSF (Grant #GB 4579) and from the University of Washington Graduate School Research Fund. We pay homage to two *Streptanthus* enthusiasts who have contributed to our understanding of the taxonomy of *Euclisia*: Freed W. Hoffman (†) of Guerneville, CA, and Gregory Lyon of San Raphael, CA. We record our appreciation of the hospitality and services rendered by the staffs of the UC and JEPS Herbaria, at Berkeley, CA, over the years.

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Note added in proof: The range of *S. drepanoides* must now include Butte County, in the western Sierra Nevada. R. E. Preston, of Chico State University, collected it on a s.-facing serpentine slope, along the w. branch Feather River fork of Lake Oroville, ca. 1.1 km ese. of Kunkle Reservoir, ca. 7.2 km se. of Paradise, Butte County, California (T21NR4E, ne. ¼ ne. ¼ S6, Cherokee 7½′ quad), at 278 m. Plants grown from seed of this collection (*Preston 293*) are confirmed by the senior author to be *S. drepanoides*. Until this recent find, all members of Sect. *Hesperides* (subgenus *Euclisia*) were known only from the Coast Ranges.

A NEW WOOLLY-HEADED, MONOCEPHALOUS *ERIGERON* (ASTERACEAE) FROM MONTANA

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Abstract

Erigeron lackschewitzii Nesom and Weber (Asteraceae) is described from the Rocky Mountains of northwestern Montana. Its closest relatives appear to be *E. simplex* Greene and *E. grandiflorus* Hooker.

Two recent collections from Montana have proved to represent a previously undescribed species of *Erigeron*.

Erigeron lackschewitzii Nesom & Weber, sp. nov.

Ab affinibus *E. simplex* et *E. grandiflorus* distinctus radice palari longa crassa foliis basalibus lineari-oblanceolatis radiis parvioribus et caulis pubescentia lanata non manifeste glandulosa (Fig. 1).

Perennial herbs from a long, woody taproot with few or no branch or adventitious roots; caudex simple or with a few short (up to 2.5 cm long), thick branches to which old petiole bases may remain attached, each branch producing 1–5 stems. Stems 3.5–8 cm high, more or less ascending, unbranched, lanate-villous with loosely ascending to appressed, white-vitreous, flattened and twisted trichomes mostly 0.8–1.8 mm long, more sparsely pubescent near the base. Basal leaves linear-oblanceolate to narrowly oblanceolate, 20–60 mm long, 1.2–3 mm wide, gradually narrowed to a petiolar region, usually widened and purplish at the very base, the apices acute or rarely obtuse to rounded, the margins entire, often with a thin, stramineous rim, cauline leaves 5–10 in number, similar to the basal, slightly reduced upwards or not, extending fully halfway up the stem; leaves densely to sparsely pubescent with a mixture of spreading and appressed or ascending trichomes up to 3 mm long, long-ciliate near the petiole base. Heads solitary; involucres shallowly hemispheric, 12–17 mm wide (pressed), 6–8 mm high; phyllaries in ca. 3 equal series, herbaceous, sometimes with thinner margins, green, often with a golden midvein, narrowly lanceolate with acuminate, loose or reflexed tips, 0.5–1 mm wide, 5–8 mm long, densely white-villous. the trichomes usually with

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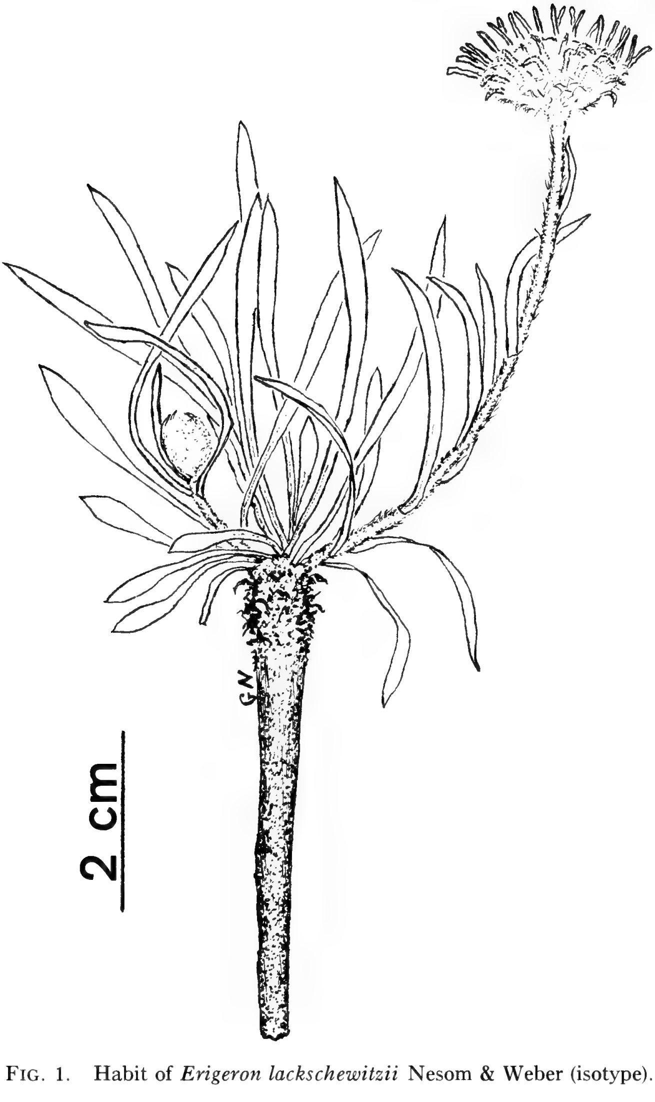

FIG. 1. Habit of *Erigeron lackschewitzii* Nesom & Weber (isotype).

blackish-purple crosswalls, at least near the base, the granular glandularity obscured by the lanate indument; receptacles not observed. Ray flowers fertile, 30–68 in 1(–2) series, apparently somewhat erect, 7.8–11.3 mm long, the tubular portion 1.8–2.5 mm long, conspicuously pubescent with both seriate and long uniseriate trichomes, ligules narrowly obovate, 1.6–3 mm wide, not reflexing or curling, drying light lilac to purple, 4–7 veined, the margins slightly introlling, apex with 2–3 shallow to deep notches; style branches 0.8–1.1 mm long, partially included within the tube. Disc corollas yellow, tubular, slightly indurated above the lower ¼ but without an inflated or constricted portion, pubescent with biseriate and uniseriate trichomes, 3.5–4.3 mm long, 0.5–0.7 mm wide, lobes 0.6–0.9 mm long, erect; anther thecae 0.7–1 mm long, with lanceolate apical appendages 0.6–0.9 mm long; style branches 0.7–1 mm long, including the deltate to shallowly triangular collecting appendages 0.2–0.3 mm long. Achenes oblong-obovate, radially compressed, tan, with 2 thin ribs, ca. 2.3–2.8 mm long and 0.7–0.8 mm wide, fully mature achenes not observed, strigose with long, untwisted, duplex trichomes; carpopodium of 5–7 rows of cuboidal cells with a lower, inner row of subsidiary cells; pappus of ray and disc flowers similar, of 15–24 relatively thick but extremely brittle bristles 2.9–3.5 mm long, ca. ¾ as high as the disc corollas but somewhat uneven in length, with an outer series of numerous, conspicuous bristles and flattened squamellae 0.4–0.9 mm long.

TYPE: USA, Montana, Flathead Co., Bob Marshall Wilderness Area, Flathead Range, "N Wall" of continental divide, summit of mtn. above Sock Lake, 2500 m, common in *Arctostaphylos* polygons, also in dry meadow, associated with *Erigeron radicatus* and *Townsendia parryi,* 26 Jul 1979, *K. H. Lackschewitz 9101* (Holotype: MONTU!; isotype: COLO!).

PARATYPE: USA, Montana, Teton Co., Bob Marshall Wilderness Area, Flathead Range, summit of Headquarters Pass, 2365 m, large colony in small, dry meadow on the narrow saddle, 29 Jul 1978, *Lackschewitz 8487* (COLO, MONTU, NY).

The new species is named for its collector, Klaus Lackschewitz, University of Montana, Missoula, who has made great contributions through his perceptive field work to our knowledge of the vegetation of western Montana. As now known, *E. lackschewitzii* is a narrowly endemic population system along the continental divide in northwestern Montana. The description has been drawn from a total of 18 individual plants from the two collections.

Erigeron lackschewitzii apparently is most closely related to *E. simplex* Greene and the "southern alpine race" of *E. grandiflorus* Hooker (sensu Spongberg 1971). According to Spongberg's distributional data (1971), the new species could be expected to occur sympatrically with *E. simplex* but not with *E. grandiflorus*; all three taxa are alpine in habitat. All three are monocephalous with lanate-villous pubescence on the involucre, usually blue-rayed, entire-leaved, and have a conspicuous, squamellate, outer pappus. The trichomes of the involucres often have colored cross-walls, particulary near the base, but the pubescence is never blackish or dark-colored in overall appearance.

Erigeron lackschewitzii differs from both *E. simplex* and *E. grandiflorus* in several features: 1) basal leaves linear-oblanceolate to narrowly oblanceolate, without a well-demarcated blade (vs. spatulate);

2) ray flowers 30–68 (vs. 50–125 in *E. simplex* and 56–123 in *E. grandiflorus*); and 3) stem pubescence woolly-villous with glandularity lacking or not at all evident (vs. stem pubescence spreading but not villous or woolly, with erect, stipitate-glandular trichomes usually conspicuous). There are two types of glandular trichomes on the upper stems of *E. grandiflorus*: the biseriate, large and conspicuous, often stipitate-glandular Type C, and the uniseriate, much smaller, usually appressed Type B that impart a somewhat viscid appearance (see Nesom 1976). The Type C trichomes of *E. simplex* are much smaller, the whole pubescence is more variable in density, and the glandular trichomes in particular may be less abundant than on *E. grandiflorus*. In neither species are the Type A trichomes so long and dense as to obscure completely the other types of pubescence, as is the case of *E. lackschewitzii*. Probably the most conspicuous unique feature of plants of the new species is their production of a long, thick taproot lacking any conspicuous secondary branches. Plants of *E. grandiflorus* sometimes produce a short length of thick, unbranched root immediately below the caudex, but this develops into a fibrous system further below; plants of *E. simplex* always produce fibrous roots, very often from a slender, branching caudex.

Achenes of *Erigeron lackschewitzii* produce a greater number of pappus bristles (15–24) compared to the southern alpine race of *E. grandiflorus* (9–14); achenes of *E. simplex* and the northern races of *E. grandiflorus* produce bristles paralleling those of *E. lackschewitzii* in number (Spongberg 1971).

Judging from the very few and highly abortive pollen grains produced by plants of *Erigeron lackschewitzii,* the species is apomictic (and probably polyploid). Of its two putatively close relatives, Spongberg (1971) found that *E. simplex* is a sexual diploid and *E. grandiflorus* a triploid apomict, and he hypothesized that the former was involved in the synthesis of the latter. It might be tempting to ally the new species with *E. grandiflorus* because of its apomictic condition, but the plants of *E. lackschewitzii,* uniform in their diagnostic characteristics, differ more strongly from *E. simplex* and *E. grandiflorus* than the latter do between themselves. If *E. lackschewitzii* were thought to be an allopolyploid, it would be unlikely that its ancestry were the same as that of *E. grandiflorus*.

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NEW SPECIES OF *CALOCHORTUS* (LILIACEAE) AND *LINUM* (LINACEAE) FROM NORTHERN MEXICO

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Abstract

Two new species are described from a localized gypseous area in southwestern Nuevo Leon; plants of both apparently grow only on the outcrops. **Calochortus marcellae** is most closely related to *C. barbatus, C. pringlei,* and *C. fuscus*. **Linum gypsogenium** is most closely related to *L. scabrellum*.

Collections of vascular plants from an area of gypsum outcrops in southeastern Nuevo Leon near the Tamaulipas border have included several previously unrecognized species. Two of these are described below; descriptions of others are being prepared by Dr. B. L. Turner and other specialists of various groups.

Calochortus marcellae Nesom, sp. nov.

Species nova *C. barbato, C. pringlei,* et *C. fusco* proxima, axillae foliorum superiorum bulbillis flores crateriformi-campanulati sepala purpurea petala carmina obscura obovati-elliptica apicibus acutis vel aliquantum obtusis non barbatis infra glandem pili glandis basaliter connati (Fig. 1).

Similar in habit to *C. barbatus*. Bulb ovoid with thick, fibrous-reticulate coats. Stems slender. erect, 25–48 cm tall, sometimes branched. Basal leaf up to 6 mm wide, equalling the stem-inflorescence height, the upper leaves not amplexicaul, the axils of upper leaves and bracts bulbiliferous. Inflorescence 1–3 flowered; pedicels 28–85 mm long. Flowers crateriform-campanulate, nodding; petals dark carmine, drying brownish and sometimes with a yellowish tinge inside, elliptic to obovate-elliptic with acute to slightly obtuse apices 4.5–8 mm wide, 11.5–16 mm long, sparsely to densely bearded above the glandular spot with thick, bright yellow hairs, the glandular spot slightly depressed, bordered above by hairs basally fused to form a short membrane; sepals purplish-red, glaucous outside, drying purple to blue and sometimes with a yellowish tinge inside, narrowly oblanceolate-elliptic with acuminate to acute apices, 3.5–6 mm wide, 10–15 mm long, the hairs of beard very sparse and limited to a cluster in the sepal center, rarely extending upward; anthers oblong, 2.5–3.1 mm long, apiculate, the filaments basally dilated, 3.5–4.1 mm long;

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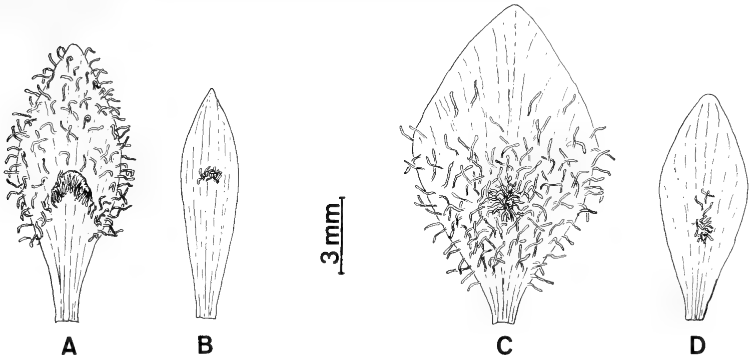

FIG. 1. Perianth morphology of *Calochortus* species. A–B. *C. marcellae* (type). A. Petal. B. Sepal. C–D. *C. barbatus* (*Rose and Painter 6457*-US). C. Petal. D. Sepal.

ovary linear, glaucous. Young fruit very narrowly elliptic, not winged, mature fruit and seeds not observed.

TYPE: México, Nuevo León, ca. 30 km ene. of Doctor Arroyo, 2.5 km ene. of San Antonio de Peña Nevada, w. base of Cerro Peña Nevada, large area of gypsum outcrops, ca. 1980 m, 3–5 Aug 1981, *Nesom 4280* (Holotype: US; isotypes: CAS, ENCB, MEXU, NY, TEX, to be distributed).

PARATYPE: México, San Luis Potosí, ne. slopes of hills near Aguaje de García in the Sierra de Guadalcazar, 1980 m, 1 Oct 1954, *Sohns 1497* (US).

With its monochasial inflorescence, fibrous-reticulate bulb coat, nodding flowers, and conspicuously bearded petals, *Calochortus marcellae* belongs to *Calochortus* sect. *Cyclobothra* subsect. *Barbata* as delimited by Ownbey (1940). Related species differ from *C. marcellae* as follows: *C. fuscus* Schultes f. has subclasping leaves, narrower petals, and brownish-purplish corollas; *C. barbatus* (HBK) Painter produces no, or rarely very few and small, bulbils in the leaf axils, its petals are bearded to below the gland, and the beard hairs of the gland are not basally fused; *C. pringlei* B. L. Robins. has much more shallowly and widely campanulate flowers, its petals are broadly truncate apically, and the beard hairs of the gland are not basally fused. Fresh corollas of *C. marcellae* are deep red, apparently similar to *C. pringlei,* but they sometimes dry with a yellowish tinge inside, suggestive of *C. barbatus* coloration. Flowers of *C. barbatus* rarely may have purplish-red, more or less glaucous (abaxially) sepals and reddish petals (e.g., *Palmer 415*-US and *Pennell 18833*-US) as in *C. marcellae,* but there is always a conspicuous yellow color inside the corolla. Corollas of *C. barbatus* typically are distinctively yellow inside and out. Color forms (dried) of *C. marcellae* resembling *C. barbatus* can easily be separated by the abundant production of bulbils and the bearding pattern of both the petals and sepals (Fig. 1). In the new species, the beard hairs are not produced below the petal gland and usually do not extend upward above the cluster of hairs on the sepal. The conspicuous basal fusion of the beard hairs is similar to that found in *C. fuscus*. According to Ownbey (1940), the structure known as the "gland" does not seem to be always glandular . . . ." On the petals of *C. marcellae* it is simply a very small region of slightly thickened and translucent tissue strictly confined to the area immediately below the fused bases of the central arc of hairs and usually hidden from view by the hairs. On the sepals, there does not appear to be any similarly differentiated tissue.

The new species, like *Calochortus pringlei,* has a very restricted distribution compared to *C. barbatus*. The *Sohns* collection was made 150 km southwest of the type, but according to Ownbey's distributional data (1940), both known localities of *C. marcellae* are considerably northeast of the range of any of its relatives; it is geographically as well as morphologically distinct.

At the type locality, plants of *Calochortus marcellae* apparently are restricted to the gypsum outcrops in shallow soil accumulations. They are abundant and almost always sheltered under large shrubs or mixed in relatively large clumps of other herbaceous or suffruticose species.

The new species is named for my wife, also a redhead, who assisted in making the 1981 collections of gypsophytes.

Linum gypsogenium Nesom, sp. nov.

A *L. scabrello* caulium et foliorum pubescentia stipitati-glandulosa praecipue differt (Fig. 2).

Perennial herbs with a woody taproot, 24–30 cm tall, similar in habit to *L. scabrellum* and *L. rupestre,* branched at or near the base and in the inflorescence, spreading pubescent throughout with simple hairs 0.1–0.3 mm long, ca. ½–¾ of the hairs stipitate with large, orange glands. Leaves opposite and overlapping near the plant base, alternate and separated above, linear lanceolate, 4–8 mm long, 0.5–1 mm wide, largest near base, sessile, entire or the upper and floral bracts with marginal glands, acute, indurate-apiculate, often gland-tipped; stipular glands large, usually dark. Sepals ovate-acuminate, apiculate, 4–5 mm long, 1–1.2 mm wide, the margins with stipitate-glandular teeth. Petals yellow, slightly orange-tinged, oblanceolate-obovate, 7.5–8.5 mm long, pilose at base. Stamens 5, glabrous. Styles separate, 5.5–7 mm long. Fruit broadly ovate, 2.2 mm high, slightly puberulent, the false septa nearly complete, ciliate. Seeds reddish-brown, shiny, 1.3–1.5 mm long.

TYPE: México, Nuevo León, ca. 30 km ene. of Doctor Arroyo, 2.5 km ene. of San Antonio de Peña Nevada, w. base of Cerro Peña

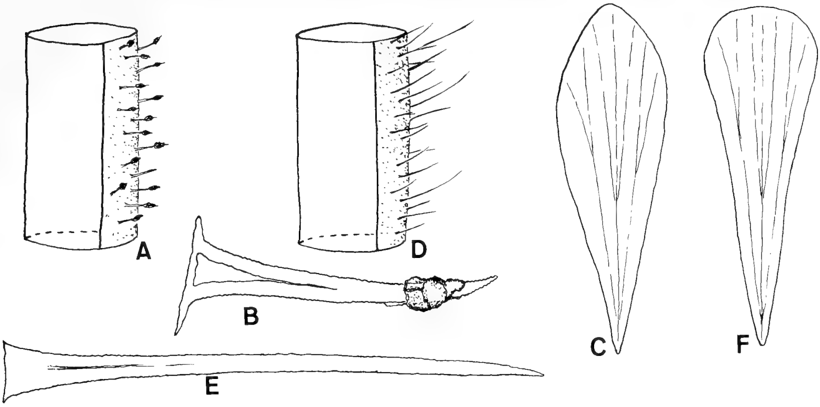

FIG. 2. Details of *Linum gypsogenium* and *L. scabrellum*. A–C. *L. gypsogenium* (type). A. Portion of stem. B. Stem trichome. C. Petal. D–F. *L. scabrellum* (*Stanford et al. 2382*-US). D. Portion of stem. E. Stem trichome. F. Petal.

Nevada, large area of gypsum outcrops, ca. 1980 m, 3–5 Aug 1981, *Nesom 4285b* (Holotype: US; isotype: MEXU).

The completely separate styles and fruits splitting into ten 1-seeded segments clearly place *Linum gypsogenium* in the "*Linum schiedeanum* group" as delimited by Rogers (1968). Further, the small leaves, stipular glands, and glandular toothed outer sepals are similar to features of *L. rupestre* (A. Gray) Engelm. ex Gray, *L. scabrellum* Planch., and *L. flagellare* (Small) Winkl.; among these, the new species would key to *L. scabrellum* in Rogers' treatment because of the hairiness of the stems and leaves, but the hairs are conspicuously gland-tipped (Fig. 2, A–B, D–E). This feature was not mentioned by Rogers and does not appear in any of the specimens of *L. scabrellum* I have examined from over its entire range (Oax., Pue., Hid., Que., S.L.P., Tam., and N.L.). Also in contrast to *L. scabrellum, L. gypsogenium* usually has markedly less dense pubescence of shorter hairs, smaller, more widely spaced (non-overlapping) upper leaves, marginal "teeth" of the sepals without large, dark, subterminal glands, and differently shaped petals (Fig. 2, C, F), those of *L. scabrellum* being strongly obtriangular.

Besides *Linum gypsogenium* and *L. scabrellum,* only two other species of American yellow-flowered *Linum* are consistently pubescent, *L. tenellum* Schlecht. & Cham. and *L. puberulum* (Engelm.) Heller, the latter of which is also in the "*schiedeanum* group" (Rogers 1968), and both of these have eglandular trichomes. The lower stems of *L. rupestre* rarely may be sparsely hairy, but the trichomes are also eglandular.

Linum gypsogenium apparently is allopatric or parapatric with *L.*

scabrellum, occurring at the northern tip of its range. The type of *L. macradenium* Brandg. (a synonym of *L. scabrellum*) was collected at Minas de San Rafael in San Luis Potosí, a gypseous area with many endemics about 200 km to the south of the Peña Nevada gypsum area, but these plants lack gland-tipped trichomes. The conversion into "glands" of the leaf and sepal apices noted by Rogers (1968) on the holotype of *L. macradenium* also occurs in other plants of *L. gypsogenium.* Other collections of *L. scabrellum* I have studied from gypseous substrate in the area of Minas de San Rafael do not show any of the features unique to the new species; I have concluded that *L. gypsogenium* is more than simply an ecotypically differentiated population of *L. scabrellum,* and as such, warrants recognition as a species. The occurrence of such edaphic endemism within *Linum* is not an isolated phenomenon, because Rogers (1968) has recognized another gypsophilous endemic from Nuevo León, *L. modestum* Rogers; it is also a member of the "*L. schiedeanum* group," but among those species it is not closely related to *L. gypsogenium.*

At the type locality of *Linum gypsogenium, L. rupestre* also grows on the exposed gypsum and is more abundant than the new species; no intermediates between the two have been observed. *Linum schiedeanum* is common in the gypseous soil of flat pastures in the immediate vicinity of the rock outcrops, but it was not collected on the outcrops proper.

Acknowledgments

I thank the curators of TEX and US for loans of pertinent specimens.

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(Received 17 Sep 82; accepted 21 Dec 1982.)

Note added in proof: Further collections in 1983 have shown *Calochortus marcellae* to be relatively common on limestone outcrops up to about 3500 m elevation on Cerro Peña, Nevada.

NOTES AND NEWS

Lemanea (RHODOPHYTA) IN MOUNTAIN STREAMS OF SOUTHERN CALIFORNIA.—This note calls attention to a population of *Lemanea* (Rhodophyta) in San Diego County and reviews the few other records, mostly very old, of this freshwater red alga in southern California.

In May 1978 clumps of stringy dark-colored plants were found on rocks in a stream flowing out of Japaca Springs on Cuyamaca Mountain (116°38′W, 32°58′N), between 1300–1500 m elevation. The coarse cylindrical strands, mostly about 5–10 cm, rarely up to 18 cm long, were tapered at both ends, unbranched and rough in surface texture. The collection was referred to *Lemanea,* subgenus *Paralemanea* (Silva, Taxon 8:60–64, 1959) in which axial filaments are surrounded by entwined longitudinal filaments, and spermatangia are in continuous bands encircling the thallus, dividing groups of carpospores. Smith (The Freshwater Algae of the United States, 1950) provides a general description of the morphology and development of *Lemanea* species. I know of only one published report mentioning the presence of *Lemanea* in California (Atkinson, Annals of Bot. 4:177–229, 1890; posthumous Notes, Bot. Gaz. 92:225–242, 1931).

The following *Lemanea* collections from southern California have been located (herbaria outside this State have not been surveyed):

San Bernardino County. Specimens collected by S. B. Parish, March to August, 1884–1897, from near Bloomington; some were distributed as part of the Phycotheca Boreali-Americana (UC, AHFH, RSA). Robert Thorne, at RSA, comments that the site described on the specimen label appears to be well away from both the San Gabriel and San Bernardino ranges.

Riverside County. Specimens collected by Parish, April 1896 (UC).

Kern County. Specimens collected by Van der Eike, November 1916, from Kern River, with Gardner accession number (UC).

San Diego County. Specimens collected by Parish, June 1897, from Doane Creek, Smith Mt. (UC); specimens collected by Fosberg, May 1929 from Palm Canyon, Borrego Valley (UC). The small herbarium of marine algae at Scripps Institution includes a single *Lemanea* sheet, collected by Marko Zalokar from "near campsite" Cuyamaca Mt. in June 1965.

Atkinson's study (Annals of Bot. 4:177–229, 1890) cites no specimens from southern California. The specimens from this region received between 1889 and his death in 1918 and discussed subsequently (Bot. Gaz. 92:225–242, 1931) were mostly deposited in the herbarium of Cornell University, although some of the Parish collections are now in California herbaria as noted above.

Attribution of the recently found Cuyamaca mountain plants to *L. annulata* is provisional. Atkinson, in 1890, referred specimens of '*L. catenata*' from Nevada in addition to all the then available specimens from northern California to *L. annulata.* In 1931, however, he recognized both species in the specimens collected by Parish in the southern localities mentioned above. C. M. Palmer, studying *Lemanea* at Butler University in Indianapolis in the early 1940s, annotated several of the older sheets presently in California herbaria. In some instances he confirmed Atkinson's earlier identifications, but in others the epithets *catenata* and *annulata* were reversed. The only specimen in the herbaria surveyed (other than Zalokar's) that definitely was not studied by Atkinson is the 1929 collection by Fosberg that Palmer determined as *L. catenata.* Type material for both species (Kützing, Phycologia germanica, 1845) from Europe must be studied with respect to California specimens before these can be attributed properly to one or both species. Clear distinctions between forms, varieties, or species apparently are lacking among other groups of taxa within the genus. Israelson (Symbolae Botanicae Upsalienses VI:1. A.–B. Lundequistska Bokhandeln, Uppsala, 1942) considered many described species in Europe to be variants of earlier-known species, with forms related to habitat or the season.

Lemanea thalli were again conspicuous in the same creek, but this time on rocks somewhat upstream from the site of the May collection, in July 1981. Water temperature (July) was 15°C and the pH was ~5. Vegetation along the edges of the flowing water included *Quercus agrifolia* Neé, *Rhus toxicodendron* L., *Rosa californica* Cham. & Schlecht., *Mimulus cardinalis* Dougl. ex Benth., *M. guttatus* Fisch. ex DC., *Urtica holosericea* Nutt., *Thalictrum* sp., *Aquilegia formosa* Fisch. in DC., and *Libocedrus decurrens* Torr., and *Apium graveolens* L. A bluegreen alga, *Nostoc* sp., grew in the creek, but not on the same rock with *Lemanea*.

This note establishes the recent presence of *Lemanea* in southern California and documents the scarcity of earlier collections. *Batrachospermum,* another freshwater red alga, according to holdings in the above-listed herbaria, grows in central and northern California but apparently has not been found in the southern counties. I was unable to find plants of either genus in numerous small lake-fed streams between 3300 and 4000 m in the southern Sierra Nevada in the summer of 1981. World wide, the Rhodophyta includes approximately 36 non-marine genera with 175 species (Dixon, Biology of the Rhodophyta, 1973). Smith (The Fresh-Water Algae of the United States, 1950) included about 32 species in 10 genera in the United States. This represents 5.2–5.7% of the known red algal taxa (Skuja, Bot. Rev. 4:665–676, 1938; Dixon, Biology of the Rhodophyta, 1973). Several of the freshwater taxa have rather restricted distributions geographically or by habitat but others are widely dispersed and have been intensively studied in Europe. Israelson (Symbolae Botanicae Upsalienses VI: 1. A.–B. Lundequistska Bokhandeln, Uppsala, 1942) writing about freshwater Swedish red algae, introduced a chapter on their ecology and distribution by stating that most "show a decided predilection for running water," a comment perhaps quite applicable to *Lemanea.*

Lemanea is a panboreal genus, found between 10° and 70°N (Abyssinia to Arctic Scandinavia) with a center of distribution in North America, according to Skuja (Bot. Rev. 4:665–676, 1938). Smith (1950) lists "rapids, falls, mill dams, and the like" as typical habitats, following Atkinson who stressed the requirement for forceful currents. Israelson suggested that "within wide limits, the conditions of temperature seem not to be very important for the occurrence" of this genus. Atkinson similarly believed that cold water (but what did 'cold' mean to him?) may not be necessary.

Lemanea plants can be considered perennial because a filamentous prostrate stage persists throughout the year from which the clumps of erect macroscopic gametophytic thalli develop seasonally. Studies of populations in these dry, warm mountains of California should considerably amplify the understanding of the conditions that determine the distribution of this alga.

The macroscopic plant commonly observed is the monoecious haploid gametophyte. Magne (C.R. Acad. Sci. Paris, t. 265, p. 670–673, 1967) showed that meiosis occurs in the apical cells of very small *Lemanea* plants that grow from the diploid prostrate filamentous "Chantransia" stage.

Genera that reproduce in fresh water, as *Lemanea* does, are believed to have invaded these habitats from marine areas much earlier than other genera that propagate only vegetatively in fresh water. The more ancient freshwater species, including *Lemanea,* predictably may have evolved physiological, morphological, or life history characteristics that adapt them to non-marine conditions. In this respect, *Lemanea* already has proved useful for comparing photosynthesis in freshwater, marine, and terrestrial environments (Raven and Beardall, Br. Phyco. J. 16:165–175, 1981). Very recently, Pueschel and Cole (Am. J. Bot. 69:703–720, 1982) used ultrastructural data from plants of this genus in their suggested rearrangement of families into orders within Rhodophyta.

This genus has been overlooked for many years in southern California or else it has an extremely restricted distribution, either spatially or seasonally. Perhaps this note will challenge botanists in the field to seek additional contemporary localities where freshwater red algae grow and to deposit up-to-date records in herbaria where they can be used by other biologists.—JOAN G. STEWART, A-002, Scripps Institution of Oceanography, University of California, La Jolla 92093. (Received 25 Aug 1981; accepted 4 Nov 1982.)

NOTES ON *Ivesia rhypara*.—*Ivesia rhypara* Ertter & Reveal, a candidate for federal endangered status, was first discovered in 1973 by Patricia L. Packard and several of her students from the College of Idaho (CIC). The species was found in Leslie Gulch in Malheur County, Oregon, where several other interesting endemics have been discovered by the same group of people. At the time of publication (Ertter and Reveal, Madroño 24:224–227, 1977), only one population scattered in an area less than one km^2 was known, and this was bisected by the access road to a boat-launching site on Owyhee Reservoir. Later a much smaller population was discovered in a side canyon.

During the summer of 1981 another very small population of *Ivesia rhypara* was discovered almost 200 km southeast of Leslie Gulch in Elko County, Nevada (ca. 1 km sw of Il Ranch, 25 Jun 1981, *Grimes, Parkard, and Ertter 2127,* NY, CIC, to be distributed). Plants of this population have leaves and pubescence like those of the Orgeon plants but differ slightly in their more compact cushion-form, narrower yellow-tinged petals, and occasional flowers with two ovaries and achenes rather than only one.

In several respects the Nevada plants approach the recently described *Ivesia paniculata* Nelson & Nelson (Brittonia 33:165–167, 1981). This species from Lassen County, California, differs from *I. rhypara* primarily in its 1–3 ovaries, more tightly imbricated leaflets, and sparser pubescence, which is densely canescent in *I. rhypara* but loose enough in *I. paniculata* to make the leaves appear greener and the stems redder. The inflorescence is also more open in *I. paniculata.* Nelson and Nelson further distinguished *I. paniculata* as having linear, yellow (vs. narrowly oblanceolate, white) petals and ascending to erect (vs. prostrate) stems. In the NY material the petals of *I. paniculata* have faded to white and are not markedly narrower than those of *I. rhypara.* In addition, although the stems of *I. rhypara* were described as prostrate, subsequent field observations have shown that at the beginning of the summer its flowering stems are also ascending to erect and only become prostrate as they lengthen. The known substrates of the two species differ somewhat; *I. paniculata* grows on loose volcanic ash, and *I. rhypara* on welded tuff in Oregon and unsorted riverbed deposits mixed with volcanic ash in Nevada (J. Grimes, pers. comm.).

When *Artemisia packardiae* Grimes & Ertter (Brittonia 31:454–458, 1979) was described as a derivative of the montane *A. michauxiana* Besser, it was also suggested that *Ivesia rhypara* was similarly derived from the montane *I. gordonii* (Hook.) T. & G., a comparison attributable to my inadequate knowledge of the genus. Superficially *I. gordonii* does indeed look more like *I. rhypara* than does *I. baileyi* S. Wats., and these are the only species of *Ivesia* that were known from the northern Intermountain region. However, the shallow hypanthium of *I. rhypara* is very different from the deeply turbinate one of *I. gordonii,* and I now believe that both *I. rhypara* and *I. paniculata* belong in a group of closely related species that includes *I. baileyi, I. shockleyi* S. Wats., and *I. jaegeri* Munz & Johnst. All are characterized by a shallow hypanthium, low growth habit, and preference for rocky substrates. The three last-named species are montane, whereas *I. rhypara* and *I. paniculata* grow at lower elevations in the northern Intermountain Desert. A logical hypothesis to explain the origin of these two species is that an ancestral stock, perhaps similar to *I. shockleyi,* which presently is known from the Sierra Nevada of California and some central Nevada mountain ranges, was widespread in the valleys of the northern Intermountain region during the pluvial periods of the Pleistocene. When this area became hotter and drier most of the descendents retreated to the mountains, but remnants persisted on certain edaphically restrictive sites where competition was less intense and water relations were more favorable. These remnants evolved into *I. rhypara* and *I. paniculata.* A similar hypothesis has been used to explain the evolution of other narrow endemics whose nearest relatives are montane (e.g., *Artemisia packardiae*).

The fairly recent discovery of both *Ivesia rhypara* and *I. paniculata* reflects the modern increase in the number and activities of botanists in the previously undercollected portions of the northern Intermountain region. It is highly probable that additional highly localized populations are waiting to be discovered on isolated edaphically interesting sites, especially in the sparsely roaded area dissected by steep-walled canyons between the Oregon and Nevada populations of *I. rhypara*. If such additional populations are discovered they may very well reduce the apparent differences between the populations of *I. rhypara,* and between this species and *I. paniculata* as well. I therefore believe that even though the Nevada population of *I. rhypara* could conceivably be treated as a distinct taxon, such a move should be discouraged pending a search for intermediate populations.—BARBARA ERTTER, Department of Botany, University of Texas at Austin 78712. (Received 18 Nov 1982; accepted 27 Mar 1983.)

NOTEWORTHY COLLECTIONS

CALIFORNIA

OPUNTIA BIGELOVII Engelm. (CACTACEAE).—USA, CA, San Bernardino Co., s. end of Kelso Mts. (T11N R12E S18 nw. ¼ w. ½), locally abundant within area of ca. 1 ha on moderately steep to gentle, southerly facing desert pavement slopes with developed varnish, 884 m, 2 Jun 1980, *Baldwin and Reseigh 255.* Extensive vegetative propagation evident.

Significance. First record for the California Mojave Desert outside of the Colorado River vicinity and a range of extension of 80 km wnw. from the Sacramento Mts., CA.

MENTZELIA PUBERULA Darl. (LOASACEAE).—USA, CA, San Bernardino Co., near summit of Old Dad Mt. (T12N R11E S30 nw. ¼ nw. ¼), frequent in calcareous bedrock crevices, 1280 m, 31 May 1980, *Baldwin and Martens 249.* Det. by H. J. Thompson.

Significance. A range extension of 100 km n. from Sheephole Pass, CA, the only other known occurrence outside of the Colorado River vicinity.

NEMACAULIS DENUDATA Nutt. var. GRACILIS Goodman & Benson. (POLYGONACEAE).—USA, CA, San Bernardino Co., ne. edge of Devils Playground (T13N R10E S34 n. ½ n. ½), frequent on gently sloping, partially stabilized sand dunes, 560 m, 26 Apr 1980, *Baldwin 65.*

Significance. First record for San Bernardino Co. and the Mojave Desert. A range extension of 100 km from Whitewater, CA. Highest elevational occurrence known.

PENSTEMON PSEUDOSPECTABILIS Jones (SCROPHULARIACEAE).—USA, CA, San Bernardino Co., mouth of steep canyon at w. base of Old Dad Mt. (T12N R10E S25 nw. ¼ nw. ¼), infrequent in sandy wash, 580 m, 6 May 1980, *Baldwin 169.*

Significance. The northernmost occurrence known in California and a range extension of 35 km n. from the Granite Mts., CA.—BRUCE G. BALDWIN and SCOTT N. MARTENS, Dept. of Botany, Univ. California, Davis 95616.

COLORADO

CRYPTANTHA MENSANA (Jones) Payson (BORAGINACEAE)—Garfield Co., se.-facing slopes, 17 km s. of Douglas Pass, Trail Canyon (T6S R102W S34, 39°30′N, 108°45′W), 1830 m, 8 Jun 1981, *Kelley 81-72* (Mesa College Herb., CS), 26 May 1982, *Kelley 82-33* (Mesa College Herb., CS).

Significance. This is the first record of the species in CO. Nearest known locality 16 km e. in Grand Co., UT.—WALT KELLEY, Dept. of Biology, Mesa College, Grand Junction, CO 81502.

IDAHO

SALIX CANDIDA Fluegge (SALICACEAE).—Boundary Co., Kootenai River drainage, Bonner Lake, 15 km ene. of Bonners Ferry (T62N R3E S18 ne. ¼), 760 m, *Carex lasiocarpa*-dominated fen above lake inlet, 31 Jul 1982, *Johnson and Brunsfield 1967* (ID, IDF); Herman Lake Road, 5 km nw. of Herman Lake, 16 km ene. of Bonners Ferry (T62N R3E S8 s. ½), 760 m, shrub and sedge dominated bottomland, 28 Oct 1982, *Brunsfeld 2005* (ID,IDF).

Significance. Boreal species; previously known in Idaho from single locations in Lemhi and Fremont Cos., at least 525 km se.

CAREX FLAVA L. (CYPERACEAE).—Boundary Co., Kootenai River drainage: Bonner Lake, 15 km ene. of Bonners Ferry (T62N R3E S18 ne. ¼), 760 m, *Carex lasiocarpa*-dominated fen above lake inlet, 31 Jul 1982, *Johnson and Brunsfeld 1968* (ID, IDF, NY); n. shore of Herman Lake, 18 km e. of Bonners Ferry (T62N R3E S27 nw. ¼), 757 m, *Carex lasiocarpa*-dominated fen, 28 Oct 1982, *Brunsfeld 2002a* (ID, IDF); Herman Lake Road, 5 km nw. of Herman Lake, 16 km ene. of Bonners Ferry (T62N R3E S8 s. ½), 760 m, shrub and sedge dominated bottomland, 28 Oct 1982, *Brunsfeld 2006* (ID, IDF). (NY collection verfied by A. Cronquist.)

Significance. Previously known in Idaho from one site in Boise Co. (ca. 530 km s.) and thus appearing on the State Watch List (Henderson, D. M. 1981. *In* Vasc. Plt. Spp. of Concern in Idaho. Univ. Idaho, For. Wldlf. and Range Expt. Sta. Bull. 34). The species is well represented in the 3 reported localities.—FREDERIC D. JOHNSON and STEVEN J. BRUNSFELD, College of Forestry, Wildlife and Range Sciences, Univ. Idaho, Moscow 83843.

WASHINGTON

LOMATIUM TUBEROSUM Hoover (APIACEAE).—USA, Washington, GRANT CO., Saddle Mtns., steep n.-facing loose basaltic talus, ca. 250–500 m (T15N, R24E, S. 2), 4 May 1980, *R. & D. Naas 3993* (WS); KITTITAS CO., Saddle Mtns., steep ne.-facing loose basaltic talus, ca. 230 m (T15N, R23E, S. 4), 23 May 1982, *Gill & Hoff 2047* (WS), ca. 270 m (T16N, R23E, S. 33), 17 April 1982, *Gill 2022* (WS), *Mastrogiuseppe & Marsden 3251* (WS); YAKIMA CO., rocky slopes above Priest Rapids [probably Umtanum Ridge], 7 Apr 1922, *St. John 3334* (WS) [previously mis-identified as *L. columbianum* Math. & Const.]; Umatanum Ridge, ne.-facing basaltic talus, ca. 210–270 m (T13N, R23E, S. 4), 14 Apr 1978, *Gill s.n.* (WS), 28 Apr 1978, *Smookler & Sauer s.n.* (Battelle NW Herb., Richland, WA); steep ne.-facing loose basaltic talus, ca. 250–300 m (T13N, R23E, S. 4), 19 Apr 1981, *Mastrogiuseppe & Gill 2801* (WS); BENTON CO., Umtanum Ridge, steep ne.-facing active basaltic talus, ca. 150 m (T13N, R24E, S. 15), 9 Apr 1982, *Mastrogiuseppe 3237* (3 photos) (WS).

Significance. Previously known only from near White Swan and Ft. Simcoe, Yakima Co., WA. The collections from Grant and Kittitas Cos. and the photographic record from Benton Co. are the first from these counties and the first records outside of Yakima Co. Although *St. John 3334* is the oldest collection, it was previously mis-identified as *L. columbianum*. These collections extend the known range 90 km ne. of previously reported localities (Hitchcock and Cronquist, 1976. Flora of the Pacific Northwest, corrected printing. Seattle). A rare endemic of south-central Washington, it is on the state list of threatened species, and a candidate for federal status (Washington Natural Heritage Program, 1982. Endangered, threatened and sensitive vascular plants of Washington. Olympia.).—STEVEN J. GILL and JOY D. MASTROGIUSEPPE, Marion Ownbey Herbarium, Washington State Univ., Pullman 99164-4309.

SALIX CANDIDA Fluegge (SALICACEAE).—Pend Oreille Co., Selkirk Mts., Slate Cr. drainage of the Pend Oreille River, Halliday Fen, 9 km ne. of Metaline Falls (T40N R44E S31 sw. ¼), 900 m, fen/swamp mosaic dominated by *Betula glandulosa, Carex* *lasiocarpa* and *Scirpus acutus,* 27 Jul 1982, *Johnson and Brunsfeld 1898* (ID, IDF, V). (Verified by T. C. Brayshaw, V.)

Significance. First record for WA, a range extension from directly adjacent BC (Brayshaw 1976).

SALIX MACCALLIANA Rowlee (SALICACEAE).—Pend Oreille Co., Selkirk Mts., Slate Cr. drainage of the Pend Oreille River, Halliday Fen, 9 km ne. of Metaline Falls (T40N R44E S31 sw. ¼), 900 m, fen/swamp mosaic dominated by *Betula glandulosa, Carex lasiocarpa* and *Scirpus acutus,* 27 Jul 1982, *Johnson and Brunsfeld 1899* (ID, IDF, V). (Verified by Brayshaw, V.)

Significance. First record for WA and contiguous U.S., a range extension from s. BC.

ERIOPHORUM VIRIDICARINATUM (Engelm.) Fern. (CYPERACEAE).—Pend Oreille Co., Selkirk Mts., Slate Cr. drainage of the Pend Oreille River, Halliday Fen, 9 km ne. of Metaline Falls (T40N R44E S31 sw. ¼), 900 m, fen/swamp mosaic dominated by *Betula glandulosa, Carex lasiocarpa* and *Scirpus acutus,* 27 Jul 1982, *Johnson and Brunsfeld 1901* (ID, IDF, NY). (Verified by A. Cronquist, NY.)

Significance. First record for WA, a range extension from s. BC.—STEVEN J. BRUNSFELD and FREDERIC D. JOHNSON, College of Forestry, Wildlife and Range Sciences, Univ. Idaho, Moscow 83843.

REVIEW

William Robinson 1838–1935. Father of the English Flower Garden. By MEA ALLAN. 255 p., 37 plates, 10 line drawings. Faber and Faber Ltd., London. 1982. $19.95.

William Robinson certainly was the "father" of today's English flower garden, just as his friend Gertrude Jekyll was its "mother." Any Californian familiar with the genre will not be surprised to find that Robinson visited the state early in his career (1870) and was profoundly affected by what he saw. After visiting Asa Gray in Cambridge, Massachusetts, Robinson and his brother James set out on the newly completed transcontinental railroad for San Francisco. Here he visited Henry Bolander and went on a collecting trip with Dr. Albert Kellogg to the Sierra Nevada and the White Mountains looking for North American alpines. Thus, the gardens of San Francisco and Santa Barbara may be considered as predecessors of (or at least influential on) those of Sussex and Kent, and not vice versa. He was also impressed with how Americans planted their cemeteries. This is reflected in *God's Acre Beautiful: Or the Cemeteries of the Future* (1880), revised as *Cremation and Urn Burial* (1889). On the boat back to England, he took not only ideas that were to change profoundly gardening in Britain, but also a box of apples for Joseph Hooker, Director of the Royal Botanic Gardens, Kew as a gift from Gray.

Robinson was born on 15 July 1838 in County Down, Northern Ireland. At the age of 23, having worked as a gardener since age 10, he went to London to join the newly created Royal Botanic Society's Garden in Regent's Park, now the home of the London Zoo. In less than three years, he was Foreman in Charge of the Educational and Herbaceous Department. During this time he began to write for *The Gardener's Chronicle,* establishing his reputation as a knowledgeable plantsman and soon becoming a regular contributor. Robinson resigned from the RBSG in 1866, determined to make his way as a writer on horticultural subjects.

The International Exhibition of 1867 in Paris provided Robinson with a look at Continental gardens and gardening methods, and also with his first two published books: *Gleanings from French Gardens* (1868; ed. 2, 1869) and *The Parks and Gardens of Paris* (1869; ed. 2, 1878). He spent nearly a year in France, visited alpine Switzerland and Italy, and returned to England inspired to write his first book (*Alpine Flowers for English Gardens*), which, however, was not published until 1870 (ed. 3, 1903). It anticipated Reginald Farrer, usually thought of as the inspiration for alpine flower gardening, by 37 years.

Robinson's revolutionary ideas on gardening and garden design were expounded in a number of books and periodicals. He founded, among others, *The Garden* (1871), *Gardening Illustrated* (1879), *The Garden Annual, Almanack and Address Book* (1881), *Farm and Home* (1882), *Woods and Forests* (1883), *Cottage Gardening* (1892), and *Forest and Sylva* (1903). Most were quite popular, and several are still published, although under other names. His *The Wild Garden* (1870; ed. 5, 1895, reprinted 1977) still bears reading by those who wish to garden in a less formal manner, or who, like me, have a piece of woods they wish to make more attractive. *The English Flower Garden* (1883; ed. 15, 1933; ed. 16 revised by Roy Hay, 1956) is "the most widely read flower gardening book ever written."

As a result of the income from his popular books and periodicals, William Robinson became a wealthy man. In 1885 he bought Gravetye Manor, 360 acres in Sussex. By 1892 he had acquired additional property, bringing his total to 1100 acres. He was now able to put theory to the test and begin to garden on a grand scale himself. The results were spectacular. Planting, cutting, testing, and discarding turned him into a first-rate landscape gardener. Thus, the later editions of his books are full of advice gleaned from his own growing experiences, not merely descriptions of how the Americans or the French grow this or that.

Charles Sprague Sargent, Director of Harvard's Arnold Arboretum, in 1898 invited the now-famous Robinson to make a second visit to the United States, but this never came about. From 1910 until his death, Robinson was confined to bed and wheelchair because of a spinal injury complicated by what appears to have been syphilis. In spite of the latter, he lived and wrote for another quarter of a century. Gravetye Manor was left to the British nation upon Robinson's death. Despite neglect and change during the Second World War, it is once again as Robinson planned it, the quintessential English flower garden.

One might quibble with an occasional nomenclatural error, or the publisher's choice of some of the illustrations, but these are minor criticisms. As she did with *Darwin and His Flowers* (1977), the late Mea Allen in her last book has made a man, his era, and its flowers come alive for us avid readers.—DUNCAN M. PORTER, Department of Biology, Virginia Polytechnic Institute & State University, Blacksburg 24061.

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REVIEWERS OF MANUSCRIPTS

It is only partially true that a journal's quality depends on the quality of the papers submitted to it. Almost all papers submitted to scientific journals are susceptible to some form of improvement, and Madroño is no exception to this process. The task of helping authors with communication and organization falls mainly on the community of reviewers, and Madroño wishes to thank the people listed below for their thoughtful and constructive criticisms offered for papers included in volume 30.

D. I. Axelrod
G. D. Barbe
Michael G. Barbour
Mary Barkworth
Spencer Barrett
Jim Bartel
George Batchelder
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John Strother
Dean W. Taylor
R. J. Taylor
R. F. Thorne
T. K. Todsen
Frank Vasek
David Young
Joy Zedler

EDITOR'S REPORT FOR VOLUME 30

Between 1 Jul 1982 and 30 Jun 1983, 44 manuscripts were received. This represents a 42% decrease from the submissions of 1981–1982. This possibly represents the effects of the economic condition of the United States over the past couple of years; there has also been a lengthy wait from time of first submission to final appearance of an article, governed to some extent by promptness in returning revisions. Sources who wish to remain anonymous have suggested also that sunspots are involved with the reduced manuscript submissions without specifying just how. Of the papers received, 33 were articles, 8 were noteworthy collections, and 3 were notes and news. Also received were 7 reviews.

Published in volume 30 are 29 articles (vs. 26 in vol. 29), 7 news and notes (8), and 17 noteworthy collections (16). Total reviews are 9. The supplement to volume 30 contains 7 floras, making a total of 36 articles published in 1983. Total pages came to 266, plus the 105-page supplement.

The current status of manuscripts is as follows: in review 9 (vs. 17 in 1981–82); in revision 23 (22); accepted and awaiting publication 17 (23). The smaller backlog compared with that in 1981–82 means that there will be a shorter wait now from time of acceptance to publication.

The supplement contains floras published at author's expense, for which the authors should be commended. Increased press charges have made scientific publication very expensive, and the cost of increasing Madroño's page number (and therefore its usefulness and diversity) have risen accordingly. Madroño will continue to entertain the idea of publishing significant symposium papers and groups of papers on closely allied topics in single supplementary issues to be funded from sources other than the California Botanical Society. Otherwise articles will appear spread through the regular issues.

The editorial office appreciates the advice and information contributed by interested readers and contributors during the past year and continues to welcome criticisms.

C.D. 18 Aug 1983

INDEX TO VOLUME 30

Classified entries: major subjects, key words, and results; botanical names and plant families (new names are in **boldface**); geographical areas; reviews. Incidental references to taxa (including lists and tables) are not indexed separately. Species appearing in Noteworthy Collections appear under plant family, state, or country. Authors and articles are listed alphabetically in the Table of Contents. "S" indicates supplement.

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals ($18 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships ($20) include one eight-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available ($25). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Manuscripts prepared on dot matrix printers will not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren and Keuken, Index Herbariorum, 6th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted eight pages in MADROÑO over a two year period. Joint authors are each assessed the full page number. Beyond that number of pages a required editorial fee of $40.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

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MADROÑO

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Contents

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CALIFORNIA BOTANICAL SOCIETY, INC.

Officers for 1983

THE VASCULAR PLANT FLORA OF TABLE MOUNTAIN, BUTTE COUNTY, CALIFORNIA

JAMES D. JOKERST
Route 4, Box 507B, Chico, CA 95926

ABSTRACT

Table Mountain, a basalt-capped mesa north of Oroville, supports an island of grassland and vernal pool vegetation in the northern Sierra Nevada foothills. This mesa is considered a valuable botanical resource because its flora represents a diverse remnant of the once extensive Sacramento Valley grasslands. No bunchgrass stands are present, but 224 of its taxa are natives, including several endangered, rare, or uncommon species. Table Mountain's herbaceous flora is diverse compared with other areas supporting a grassland-vernal pool mosaic in the valley. Three factors strongly influence this high diversity: 1) Habitat destruction is minimal; seasonal grazing is the only significant impact; 2) Species typically confined to the valley floor and others characteristic of higher elevations mix here with taxa expected in the grassy openings and understory of the oak woodland and chaparral vegetation normally present at this elevation (270–481 m); 3) The mesa's diversity of habitats include intermittent streams, vernal pools, hog wallows, and 11 soil-related types. The later represent various stages in the mechanical decomposition of the bedrock and subsequent accumulation and development of soil. In the present study 287 species (66.6% annuals, 21.9% non-natives) from 175 genera and 58 families are reported.

Table Mountain supports a well-preserved, strikingly diverse, remnant of the Sacramento Valley's native grassland vegetation. Although grazing livestock probably eliminated any extensive stands of native bunchgrass species, this change in composition has not drastically altered the characteristic of the vascular plant flora. Only 63 (21.9%) of Table Mountain's 287 taxa are non-natives; and many are strictly confined to "weedy" habitats. Its widespread fame and attraction to botanists probably results from the partitioning of this diverse flora into an interdigitating network of plant associations that results in a beautiful mosaic of springtime color. The large number of native Californian species that occur here, and the well-preserved nature of the Sacramento Valley's increasingly threatened grassland vegetation attest to Table Mountain's value as a botanical resource.

LOCATION AND PHYSICAL GEOGRAPHY

Irregularly shaped and highly dissected, North Table Mountain roughly comes to a point at its north tip and is widest at its southern edge. The mountain is approximately 4.8 km long and is 6.5 km north of Oroville, very near the center of Butte County, California. Although adjacent to the Sacramento Valley, it is geographically situated in the Sierra Nevada foothills. The slopes of Table Mountain, and the sur-

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rounding foothills, support Oak Woodland and Chaparral vegetation that grades into Valley Grassland at its base to the west.

Table Mountain is classified as a mesa because of its low relief and flat top. The mesa's geology has been described by Turner (1896), Durrell (1959), and Creely (1965). The basalt that caps the mesa is part of the Lovejoy Formation, a basalt flow vented forth somewhere east in the Sierra Nevada during the late Eocene or early Oligocene (Durrell 1959). Most of Durrell's Lovejoy Formation is overlain by more recently deposited stratigraphic units; however, at Table Mountain and elsewhere the formation is exposed.

Table Mountain dips slightly (1–2°) to the west-southwest. Consequently, elevations range from 481 m at the north tip of 270 m along the west-central edge. Although originally smooth-topped, Table Mountain is presently dissected by a series of fracture systems that probably have given rise to the numerous east–west oriented intermittent drainages. Beatson Hollow, the largest intermittent drainage, has cut over 65 m into the mesa top. Here, during the spring, one of Table Mountain's many impressive waterfalls cascades over the vertical western edge.

In addition to the drainage ravines, a series of fracture systems have produced numerous longitudinal depressions over the mesa's surface. These give rise to steep-sided, notch-like gullies at the west edge. Although much of Table Mountain's surface is exposed solid or fractured basalt, soil is present and is the thickest along the sides of the intermittent drainages and fracture depressions, and on occasional slopes and benches. Creely (1959, p. 59) describes the older basalt of Table Mountain as ". . . typically black, hard, microcrystalline to extremely fine grained, more or less equigranular olivine basalt." Creely adds that little deformation or change in the mesa's surface (neglecting drainages and fractures) has occurred, probably due to the basalt's highly resistant nature. A majority of Table Mountain's erosion is via mass-wasting along its edges where less resistant underlying strata erode and undermine the basalt cap causing blocks to break off along weakly bonded vertical fractures. As a result the edge of Table Mountain is a basalt wall varying from 65 m cliffs on the west edge to the lower, more gentle basalt slopes on the east.

VEGETATION

Table Mountain is a nearly treeless plain that supports a diverse assemblage of herbaceous vascular plant species. These inhabitants partition the different soil- and moisture-related habitats into discrete plant associations that collectively form the annual grassland and vernal pool plant communities of Barbour and Major (1977) or the valley grassland of Munz (1968). In addition, two pine, five oak, and twelve shrub species are present but restricted to the mesa's drainage ravines and edges.

At present 287 taxa (21.9% non-natives, 66.6% annuals) from 175 genera and 58 families are known from Table Mountain. This number is large, and even if the 21 woody perennials and 28 rarely observed species are subtracted from this total, 238 taxa remain. These can be considered Table Mountain's characteristic annual grassland/vernal pool species. When compared with the same vegetation type(s) elsewhere in the Sacramento and San Joaquin Valleys, the flora here appears quite diverse. There is little information detailing the composition of similar California grasslands, but observations of the author and colleagues in the northern Sacramento Valley, and the few studies available support this contention.

Schlising and Sanders (1983) list 134 taxa at the 80 acre Richvale Vernal Pool Site, Butte County, 12 miles southwest of Table Mountain. In Tehama County Hayes and Jokerst (unpubl. checklist) record 126 species from the Leininger Road Vernal Pool Site and Broyles (1983) lists 235 taxa from the 1500-acre Nature Conservancy Vina Plains Preserve's Grasslands and Vernal Pools. At the Jepson Prairie Nature Conservancy Preserve, Solano County, Holland (1981a) reported 195 species. Near Roseville, Placer County, 99 species were observed at Maidu Park (Holland 1982), and at Burns Reservoir east of Haystack Mt. and Merced, Merced County, 91 species were recorded (Holland 1981b). McClintock (1970) reports 145 species from 40 acres at the Pixley Pools, Tulare County.

Three important aspects contribute to the high diversity encountered on Table Mountain. First is the lack of habitat disturbance. With the exception of seasonal grazing, and the few dirt roads, the mesa is still in a very natural state; soil tilling, fertilization, or seeding with introduced forage species is unknown. Secondly, Table Mountain's diversity may be enhanced by its geology. The mesa's thin soils and extensive amounts of exposed basalt create habitats that allow species normally restricted to the valley floor (e.g., *Achyrachaena mollis* and *Navarretia leucocephala*), and higher elevation species typical of poor rocky soils (e.g., *Cheilanthes gracillima* and *Navarretia divaricata*), to co-occur with herbaceous species expected at this elevation. The last and most important factor is the many different water and soil habitats present on the mesa. Aquatic habitats include vernal pools, hogwallows, seepages, and intermittent creeks; terrestrial habitats represent the various stages of soil development and accumulation, and form a habitat-continuum ranging from exposed fractured bedrock to deeper, well-developed grassland soils. Between-site differences in the degree and nature of bedrock fracturing, and in the amounts of accumulated soil result in noticeable changes in species composition. This suggests a succession is occurring where species groups replace each other as habitat characteristics are modified.

The following habitats have not been quantitatively analyzed for differences in moisture content or soil characteristics. The fourteen habitats listed below can, however, be intuitively identified and each supports a characteristic association of species that repeatedly occur across the mesa.

Grassland and Vernal Pool Habitats

Bedrock Outcrops. These are areas of exposed, flat-surfaced basalt bedrock that often resemble miniature mesas. Small amounts of soil particles and organic matter accumulate in the fractures, depressions, and margins.

Thin Soils. This type is formed by thin accumulations of soil and organic matter that overlie the Bedrock Outcrops. Floristically both habitats share many species.

Outcrop Edges. These are represented by a narrow band (less than 0.75 m) of small (0.1–1.0 cm in diameter) fractured basalt cobbles, mostly overlain by soil, that encircles the Bedrock Outcrops. The large amount of surface water runoff appears to influence which species occur here.

Dry Cobbles. These are areas with moderate amounts of accumulated soil and large (greater than 15 cm diameter), partially exposed, basalt cobbles.

Wet Cobbles. These are the same as Dry Cobbles habitats but occur in areas where water seeps over the surface after moving horizontally along impervious subsurface strata.

Cliff Faces. The vertical basalt cliffs that merge characteristics of the previous five habitat types. During the spring, water often seeps over these.

Fractured Basalt. Such areas are represented by piles of large, dry, fractured basalt cobbles with no visible soil present, often found at the base of sloping or vertical outcrops.

Low Mounds. This habitat is defined by thin, well-drained, somewhat rocky soils with no exposed cobbles. These areas resemble mima mounds on portions of the mesa.

Thick Soils. The thickest, most highly developed grassland soils typify this type of habitat and represent the final stage of grassland succession on the mesa.

Shaded Soils. Thick, well-developed soils of shaded or protected localities, such as under oaks or in steep-sided draws, characterize this habitat.

Wet Margins. These are adjacent to intermittent creeks and also encircle vernal pools at or above their high water mark with damp, somewhat clayey soils.

Vernal Pools. This habitat occurs in vernal pools and hogwallows below their high water mark after drying has occurred.

Standing Water. This habitat is formed by the standing water of intermittent creeks and vernal pools.

Ruderal. Ruderal habitats are represented by disturbed sites, dirt roads, and areas adjacent to the only public road across the mesa: Cherokee Road.

DISCUSSION OF HABITATS

Although different habitats exist, often no well-defined boundary separates them and, in effect, they are continuous in nature. Most species occur in more than one habitat, and often these sites represent consecutive successional stages that replace each other as bedrock decomposition and soil development proceed. A notable exception is the sharing of species, e.g., *Blennosperma nanum, Lasthenia californica,* between the Wet Margins and Outcrop Edges. Each species reaches peak abundance in one habitat, but some species (e.g., *Dichelostemma pulchellum, Senecio vulgaris*) are highly competitive and occur in many habitats. Conversely, each habitat has one or more species entirely restricted to it.

The distribution of introduced species is also of interest. The 63 non-natives occur in all habitats except the Bedrock Outcrops, the areas with the poorest, least developed soils. As expected, introduced species dominated the Ruderal habitat and were most abundant in others with the deepest soils; 61.9% of the introduced species were observed *only* on the Thick Soils and Ruderal Habitats. Twenty-five of the non-natives are European grasses that now dominate California's annual grassland. However, native grasses are abundant on sites with thin, rocky soils (e.g., *Vulpia* spp., *Poa scabrella*) and in Vernal Pools (e.g., *Alopecurus saccatus, Deschampsia danthonioides*).

A final comment concerns several species whose presence on Table Mountain is of phytogeographical interest. *Allium cratericola, Arabis breweri* var. *austinae, Lewisia rediviva, Navarretia divaricata, Streptanthus diversifolius,* and *S. tortuosus* var. *suffrutescens* are extremely uncommon in the Sacramento Valley's low- to mid-elevations, but all occur on the Bedrock Outcrops here. Possibly these uncommon species, characteristic of poor rocky soils, can occur here because of reduced interspecific competition on the mesa's thin soils and exposed bedrock.

FLORA

The author has surveyed most of the mesa and noted the continuity of its habitats and vegetation. This list of species is therefore considered representative of the entire mesa's flora, but is limited to taxa known to occur on its top. This study does not record the flora of the wooded canyons that cut into the mesa (e.g., Beatson Hollow, Coal Canyon). Field work consisted of numerous trips during all seasons from 1976–1982. A voucher specimen of each species reported is on file at California State University, Chico (CSUC). Taxonomy follows Munz (1968) with nomenclatural updates included from Mary S. Taylor's unpublished, mimeographed "Flora Buttensis." Each species is annotated with the habitat(s) in which it was observed. Non-native species are preceded by an asterisk, and occasional comments on abundance and distribution of selected species have been inserted. The checklist is followed by an additional list of taxa reported from Table Mountain but not observed by the author.

LYCOPHYTA

Selaginellaceae

Selaginella hanseni. Bedrock Outcrops, Thin Soils, Wet Cobbles, Cliff Faces. Common.

Isoetaceae

Isoetes howellii. Vernal Pools. Occasional.
Isoetes nuttallii. Low Mounds, Vernal Pools. Overlooked, common.

PTEROPHYTA

Marsileaceae

Pilularia americana. Vernal Pools.

Polypodiaceae

Cheilanthes gracillima. Bedrock Outcrops, Thin Soils, Cliff Faces. Common on basalt in protected localities.
Pellaea andromedaefolia. Dry Cobbles, Cliff Faces, Fractured Basalt.
Pellaea mucronata. Dry Cobbles, Cliff Faces, Fractured Basalt.
Pityrogramma triangularis. Wet Cobbles, Cliff Faces, Shaded Soils. Common in mesic, protected areas.
Pityrogramma triangularis var. *semipallida*. Fractured Basalt. Rare, known from single location at mesa's north tip.
Polypodium californicum. Wet Cobbles, Cliff Faces, Shaded Soils.

CONIFEROPHYTA

Pinaceae

Pinus ponderosa. Shaded Soils. Uncommon in draws at the mesa's edge.
Pinus sabiniana. Shaded Soils. Common along the mesa's edge.

ANTHOPHYTA—DICOTYLEDONEAE

Amaranthaceae

**Amaranthus albus*. Ruderal. Along Cherokee Road.

Anacardiaceae

Toxicodendron diversilobum. Shaded Soils. Protected ravines.

Apiaceae

Eryngium vaseyi var. *vallicola*. Vernal Pools, Common.
Lomatium marginatum. Fractured Basalt, Low Mounds.
Lomatium utriculatum. Thin Soils, Outcrop Edges, Dry Cobbles, Cliff Faces. Common.
Perideridia oregana. Fractured Basalt. Occasional.
Sanicula bipinnata. Thick Soils. Common.
Sanicula bipinnatifida. Thick Soils. Common.
**Scandix pecten-veneris*. Shaded Soils, Ruderal. Common weed.

Aristolochiaceae

Aristolochia californica. Dry Cobbles, Fractured Basalt. Common.

Asteraceae

Achyrachaena mollis. Outcrop Edges, Dry Cobbles.
Agoseris heterophylla. Thin Soils, Low Mounds, Thick Soils.
Blennosperma nanum. Thin Soils, Low Mounds, Wet Margins. Common.
**Bidens frondosa*. Vernal Pools. Uncommon.
Calycadenia oppositifolia. Thin Soils. Uncommon. Rare but not endangered in California (Smith et al. 1980).
Calycadenia truncata subsp. *scabrella*. Dry Cobbles, Fractured Basalt, Low Mounds. Common.
**Centaurea solstitialis*. Thick Soils, Ruderal.
**Conyza floribunda*. Shaded Soils. Rare.
**Filago gallica*. Vernal Pools, Ruderal.
Gnaphalium microcephalum var. *thermale*. Dry Cobbles. Uncommon at north edge.
Gnaphalium palustre. Vernal Pools.
Grindelia camporum. Ruderal.
Hemizonia fitchii. Low Mounds, Thick Soils encircling Wet Margins.
**Hypochoeris glabra*. Dry Cobbles, Low Mounds, Thick Soils.
**Lactuca serriola* var. *integrata*. Thick Soils.
Lagophylla glandulosa. Thick Soils encircling Wet Margins.
Lasthenia californica DC. ex Lindl. [=*L. chrysostoma* (F. & M.) Greene]. Outcrop Edges, Low Mounds, Wet Margins. Common.
Lasthenia fremontii. Wet Margins, Vernal Pools. Common.
Layia fremontii. Wet Margins, Vernal Pools. Uncommon.
**Matricaria matricarioides*. Dry Cobbles, Low Mounds, Thick Soils, Ruderal. Common, a well-integrated, introduced species.
Micropus californicus. Low Mounds, Vernal Pools.
Microseris acuminata. Wet Margins.
Microseris lindleyi. Dry Cobbles, Cliff Faces.
Psilocarphus brevissimus. Vernal Pools. Abundant in nearly all vernal pools.

Psilocarphus oregonus. Vernal Pools, Ruderal. Uncommon.

Psilocarphus tenellus. Vernal Pools. Mixed with *P. brevissimus*.

**Senecio sylvaticus*. Low Mounds.

**Senecio vulgaris*. Thin Soils, Outcrop Edges, Low Mounds, Thick Soils. Ruderal. Common, well-integrated species in the annual grassland.

**Silybum marianum*. Thick Soils, Shaded Soils. Common under oaks.

**Xanthium strumarium* var. *canadense*. Vernal Pools.

Boraginaceae

Amsinckia intermedia. Thick Soils, Ruderal. Common on grassy slopes.

Amsinckia menziesii. Thick Soils, Ruderal. Common.

Cryptantha flaccida. Low Mounds. Uncommon.

Plagiobothrys austinae. Vernal Pools.

Plagiobothrys bracteatus. Vernal Pools. Common.

Plagiobothrys fulvus var. *campestris*. Thick Soils.

Plagiobothrys glyptocarpus. Vernal Pools. Common.

Plagiobothrys nothofulvus. Thick Soils. Common.

Plagiobothrys stipitatus. Vernal Pools. Uncommon.

Plagiobothrys stipitatus var. *micranthus*. Vernal Pools.

Brassicaceae

Arabis breweri var. *austinae*. Cliff Faces. Common on the mesa's west edge. Rare but not endangered in California (Smith et al. 1980).

Athysanus pusillus. Shaded Soils. Uncommon.

**Capsella bursa-pastoris*. Thick Soils, Ruderal.

Cardamine oligosperma. Shaded Soils, Wet Margins.

**Draba verna*. Thin Soils. Uncommon.

Lepidium nitidum. Low Mounds. Common.

**Raphanus raphanistrum*. Thick Soils, Shaded Soils.

**Sisymbrium officinale*. Shaded Soils. Common along mesa's edge.

Streptanthus diversifolius. Bedrock Outcrops, Thin Soils. Possibly the northernmost Sierra Nevada population.

Streptanthus tortuosus var. *suffrutescens*. Bedrock Outcrops, Thin Soils, Cliff Faces. This rare variety is common here.

Thysanocarpus curvipes. Low Mounds, Thick Soils. Infrequent.

Thysanocarpus elegans. Dry Cobbles, Low Mounds, Thick Soils. Common.

Callitrichaceae

Callitriche heterophylla subsp. *bolanderi*. Standing Water.

Callitriche marginata. Low Mounds, Wet Margins. Common but overlooked.

Campanulaceae

Downingia cuspidata. Vernal Pools. Common in dried pools.

Githopsis specularioides. Thin Soils, Outcrop Edges, Low Mounds.
Heterocodon rariflorum. Vernal Pools. Uncommon.

Caprifoliaceae

Sambucus mexicana. Shaded Soils. Uncommon.

Caryophyllaceae

Arenaria californica. Thin Soils, Low Mounds. Uncommon.
**Cerastium glomeratum.* Dry Cobbles, Low Mounds, Thick Soils. Common.
Minuartia douglasii (Fenzl. ex T. & G.) Mattf. [=*Arenaria douglasii* Fenzl ex T. & G.]. Bedrock Outcrops, Outcrop Edges. Common.
**Petrorhagia velutina* (Guss.) Ball & Heywood [=*Tunica prolifera* (L.) Scop.]. Low Mounds, Thick Soils.
Sagina decumbens (Ell.) T. & G. subsp. *occidentalis* (Wats.) Crow [=*S. occidentalis* Wats.]. Wet Margins, Vernal Pools.
**Silene gallica.* Shaded Soils, Ruderal.
**Spergularia rubra.* Low Mounds, Thick Soils, Ruderal.
**Stellaria media.* Wet Cobbles, Low Mounds, Thick Soils, Shaded Soils. Common.

Crassulaceae

Crassula aquatica (L.) Schonl. [=*Tillaea aquatica* L.]. Wet Margins, Vernal Pools.
Crassula erecta (H. & A.) Berger [=*Tillaea erecta* H. & A.]. Thin Soils, Outcrop Edges, Dry Cobbles, Wet Cobbles, Low Mounds, Ruderal. Common.
**Crassula muscosa* (L.) Roth. [=*Tillaea muscosa* L.]. Thin Soils, Outcrop Edges, Dry Cobbles, Wet Cobbles, Low Mounds.
Dudleya cymosa. Cliff Faces.
Parvisedum pumilum. Bedrock Outcrops, Thin Soils, Outcrop Edges, Wet Cobbles.

Cucurbitaceae

Marah fabaceus var. *agrestis.* Fractured Basalt. Common, creeping on cobble piles.
Marah watsonii. Fractured Basalt. Creeping on cobble piles.

Ericaceae

Arctostaphylos manzanita. Low Mounds, Shaded Soils. Occasional.
Arctostaphylos viscida. Low Mounds, Shaded Soils. Occasional.

Euphorbiaceae

Eremocarpus setigerus. Thick Soils, Wet Margins, Ruderal.
Euphorbia ocellata. Low Mounds, Thick Soils.

Fabaceae

Astragalus pauperculus. Thin Soils, Low Mounds. Uncommon, Smith et al. (1980) consider this rare but not endangered in California.

Lotus humistratus. Low Mounds, Thick Soils. Common.

Lotus micranthus. Thin Soils, Outcrop Edges, Low Mounds, Thick Soils.

Lotus subpinnatus. Outcrop Edges, Low Mounds. Common.

Lupinus albifrons subsp. *eminens.* Cliff Faces, Fractured Basalt. Common at the mesa's west edge.

Lupinus bicolor subsp. *pipersmithii.* Shaded Soils.

Lupinus bicolor subsp. *tridentatus.* Thin Soils, Outcrop Edges, Dry Cobbles, Low Mounds. Common.

Lupinus nanus Dougl. ex. Benth. subsp. *apricus* (Greene) Elliot, Harding and Mankinen [=*L. vallicola* subsp. *apricus* (Greene) D. Dunn]. Outcrop Edges, Dry Cobbles, Low Mounds, Thick Soils, Ruderal. Most common lupine on the mesa.

Lupinus pachylobus. Thick Soils, Shaded Soils. Common under oaks.

Lupinus polycarpus. Outcrop Edges, Dry Cobbles, Low Mounds, Thick Soils, Ruderal. Common.

**Medicago polymorpha* L. [=*M. hispida* Gaertn.]. Thick Soils, Shaded Soils, Wet Margins, Vernal Pools.

Trifolium albopurpureum. Thin Soils, Low Mounds.

Trifolium depauperatum. Dry Cobbles, Wet Cobbles, Low Mounds. Common.

Trifolium microcephalum. Dry Cobbles, Thick Soils.

Trifolium subterraneum. Outcrop Edges, Dry Cobbles, Low Mounds, Thick Soils.

**Trifolium tridentatum.* Thick Soils. Common.

Trifolium variegatum. Wet Margins. Common along all waterways. Two forms occur together, a large-headed, large-flowered form and a small-headed, small-flowered one. These mix together, and no intermediates have been observed.

**Vicia villosa.* Ruderal. Only on disturbed soil.

Fagaceae

Quercus chrysolepis. Thick Soils, Shaded Soils. Uncommon.

Quercus douglasii. Thick Soils, Shaded Soils. Common along ravines and at the mesa's edge.

Quercus kelloggii. Shaded Soils. Uncommon.

Quercus lobata. Shaded Soils.

Quercus wislizenii. Thick Soils, Shaded Soils. Common.

Gentianaceae

Centaurium venustum. Wet Margins.

Cicendia quadrangularis (Lam.) Griseb. [=*Microcala quadrangularis* (Lam.) Griseb.]. Wet Margins. Uncommon.

Geraniaceae

**Erodium botrys*. Dry Cobbles, Wet Cobbles, Low Mounds, Thick Soils. A common, well-integrated, non-native species.
**Erodium brachycarpum* (Godr.) Thell. [=*E. obtusiplicatum* (Maire, Weiller, & Wilcz.) J. T. Howell]. Thin Soil, Low Mounds.
**Erodium cicutarium*. Thick Soils. Uncommon.
**Geranium dissectum*. Wet Margins. Rare in seepage areas.
**Geranium molle*. Shaded Soils. Common in ravines and under oaks.

Hippocastanaceae

Aesculus californica. Shaded Soils. Uncommon in ravines.

Hydrophyllaceae

Nemophila heterophylla. Shaded Soils. Common.
Phacelia cicutaria. Fractured Basalt. Common.
Phacelia egena. Dry Cobbles, Cliff Faces, Fractured Basalt.

Hypericaceae

Hypericum anagalloides. Wet Margins, Vernal Pools.
**Hypericum perforatum*. Vernal Pools, Ruderal. Occasional near water.

Lamiaceae

Lycopus americanus. Wet Margins, Vernal Pools.

Lauraceae

Umbellularia californica. Shaded Soils. Common.

Limnanthaceae

Limnanthes douglasii var. *rosea*. Wet Margins. Common.

Lythraceae

Lythrum hyssopifolia. Wet Margins, Vernal Pools. Occasional.

Malvaceae

Sidalcea calycosa. Wet Margins, Vernal Pools. Common along creeks.
Sidalcea hartwegii. Thin Soils. Uncommon.

Onagraceae

Boisduvalia densiflora. Wet Margins, Vernal Pools.
Boisduvalia stricta. Wet Margins, Vernal Pools.

Clarkia arcuata. Thin Soils, Low Mounds.

Clarkia purpurea subsp. *quadrivulnera.* Dry Cobbles, Low Mounds, Thick Soils.

Orobanchaceae

Orobanche uniflora subsp. *occidentalis.* Wet Cobbles. Scarce in shaded areas.

Oxalidaceae

**Oxalis corniculata.* Shaded Soils, Wet Margins. Uncommon.

Papaveraceae

Eschscholzia caespitosa. Thin Soils, Dry Cobbles, Low Mounds.

Eschscholzia lobbii. Thin Soils, Outcrop Edges, Dry Cobbles, Fractured Basalt, Low Mounds, Thick Soils. Common element of the flora.

Plantaginaceae

Plantago bigelovii. Wet Margins, Vernal Pools. Uncommon.

Plantago erecta Morris [=*P. hookeriana* F. & M. var. *californica* (Greene) Poe]. Thin Soils, Outcrop Edges, Low Mounds. Common.

Polemoniaceae

Gilia capitata subsp. *pedemontana.* Dry Cobbles, Fractured Basalt. Occasional.

Gilia tricolor. Low Mounds. Common.

Linanthus androsaceus subsp. *laetus.* Low Mounds. Uncommon.

Linanthus bicolor. Low Mounds, Thick Soils. Common.

Linanthus ciliatus. Vernal Pools. Uncommon.

Linanthus filipes. Outcrop Edges. Common.

Microsteris gracilis. Dry Cobbles, Wet Cobbles.

Navarretia divaricata. Thin Soils, Low Mounds. Common on the mesa but not frequent at low elevations in the Sacramento Valley.

Navarretia intertexta. Wet Margins, Vernal Pools. Uncommon.

Navarretia leucocephala. Vernal Pools. Common in most vernal pools.

Navarretia tagetina. Thin Soils, Low Mounds. Common.

Polygonaceae

Eriogonum nudum. Thin Soils, Dry Cobbles, Low Mounds.

Polygonum californicum. Outcrop Edges, Low Mounds. Uncommon.

Polygonum hydropiperoides var. *asperifolium.* Vernal Pools, Standing Water. Common in wet areas.

Pterostegia drymarioides. Wet Cobbles. Uncommon.

**Rumex acetosella.* Cliff Faces, Thick Soils. Uncommon.

**Rumex crispus*. Thick Soils, Ruderal. Common.
**Rumex pulcher*. Thick Soils, Shaded Soils, Ruderal.

Portulacaceae

Calandrinia ciliata var. *menziesii*. Thin Soils, Outcrop Edges, Low Mounds, Thick Soils. Common.
Claytonia perfoliata Donn. ex Willd. [=*Montia perfoliata* (Donn) Howell var. *perfoliata*]. Shaded Soils.
Lewisia rediviva. Bedrock Outcrops, Thin Soils. Occasional.
Montia fontana L. subsp. *amporitana* Senner [=*M. hallii* (Gray) Greene]. Standing Water. Common on rocks in shallow water.
Montia fontana L. subsp. *chondrosperma* (Fenzl.) Walt. [=*M. minor* Gmel.]. Wet Margins.

Primulaceae

**Anagalis arvensis*. Thick Soils, Shaded Soils, Wet Margins. Common.
Dodecatheon clevelandii subsp. *patulum*. Thin Soils, Low Mounds. Common on well-drained soils.

Ranunculaceae

Delphinium nudicaule. Wet Cobbles, Cliff Faces, Fractured Basalt.
Delphinium patens. Cliff Faces, Fractured Basalt. Common.
Delphinium variegatum forma *superbum*. Low Mounds, Thick Soils.
Myosurus minimus subsp. *apus* var. *sessiliflorus*. Wet Margins, Vernal Pools. Uncommon.
Ranunculus aquatilis var. *hispidulus*. Standing Water.
Ranunculus bonariensis Poir. var. *trisepalus* (Gill.). Lourteig [=*R. alveolatus* Carter]. Vernal Pools. Rare on mesa.
Ranunculus canus. Wet Margins. Common on damp soil.
**Ranunculus muricatus*. Wet Margins. Common.

Rhamnaceae

Rhamnus californica subsp. *tomentella*. Dry Cobbles, Fractured Basalt. Uncommon.

Rosaceae

Alchemilla occidentalis. Low Mounds. Common but overlooked.

Rubiaceae

**Galium aparine*. Dry Cobbles, Wet Cobbles, Fractured Basalt, Shaded Soil.
**Galium parisiense*. Ruderal. Common roadside weed.
Galium porrigens Dempster [=*G. nuttallii* Gray]. Fractured Basalt, Shaded Soils. Rare.
**Sherardia arvensis*. Low Mounds, Thick Soils, Ruderal. Common.

Salicaceae

Populus fremontii. Shaded Soils. Occasional along creeks.
Salix laevigata var. *araquipa.* Shaded Soils. Along creeks.
Salix lasiolepis. Shaded Soils. Along creeks.

Saxifragaceae

Lithophragma bolanderi. Dry Cobbles, Wet Cobbles, Fractured Basalt, Thin Soils.
Lithophragma parviflorum. Wet Cobbles, Fractured Basalt, Occasional.
Saxifraga californica. Wet Cobbles. Common.
Saxifraga fragosa. Wet Cobbles. Common.

Scrophulariaceae

Antirrhinum cornutum. Ruderal. Uncommon.
Collinsia sparsiflora var. *brucae.* Dry Cobbles, Wet Cobbles, Low Mounds. Common.
Collinsia tinctoria. Dry Cobbles, Fractured Basalt. Common.
Gratiola ebracteata. Wet Margins, Vernal Pools.
Keckiella breviflora (Lindl.) Straw [=*Penstemon breviflorus* Lindl.]. Cliff Faces.
Mimulus douglasii. Outcrop Edges, Dry Cobbles.
Mimulus guttatus. Wet Margins, Vernal Pools. Common.
Mimulus floribundus. Wet Cobbles, Cliff Faces, Shaded Soils. Common.
Mimulus kelloggii. Outcrop Edges, Dry Cobbles. Common.
Mimulus nasutus. Wet Margins, Vernal Pools. Common.
Mimulus tricolor. Vernal Pools. Occasional.
Orthocarpus attenuatus. Outcrop Edges, Dry Cobbles, Low Mounds.
Orthocarpus erianthus. Thin Soils, Low Mounds. Common.
Orthocarpus purpurascens. Thin Soils, Outcrop Edges, Dry Cobbles. Common.
Veronica peregrina subsp. *xalapensis.* Wet Margins, Vernal Pools. Common.

Valerianaceae

Plectritis macrocera. Dry Cobbles, Wet Cobbles. Common.

Violaceae

Viola douglasii. Thin Soils, Dry Cobbles, Low Mounds. Common.
Viola pedunculata. Dry Cobbles, Wet Cobbles.

Viscaceae

Arceuthobium americanum. Rare, parasitic on *Pinus sabiniana.*
Phoradendron villosum. Occasional, parasitic on *Quercus douglasii.*

ANTHOPHYTA—MONOCOTYLEDONEAE

Amaryllidaceae

Allium amplectens. Dry Cobbles, Low Mounds, Ruderal. Common.

Allium membranaceum. Dry Cobbles, Fractured Basalt. Scarce at north tip.

Allium cratericola. Bedrock Outcrops, Thin Soils. Abundant on exposed bedrock.

Brodiaea elegans. Low Mounds. Widely scattered, occasional.

Brodiaea minor. Thin Soils, Low Mounds. Uncommon.

Dichelostemma multiflorum (Benth.) Heller [=*Brodiaea multiflora* Benth.]. Dry Cobbles, Low Mounds, Thick Soils, Ruderal. Common.

Dichelostemma pulchellum (Salisb.) Heller [=*Brodiaea pulchella* (Salisb.) Greene]. Thin Soils, Outcrop Edges, Dry Cobbles, Cliff Faces, Low Mounds, Thick Soils. Very Common on the mesa.

Triteleia hyacinthina Greene [=*Brodiaea hyacinthina* (Lindl.) Baker]. Wet Margins. Rare, only found at one locality.

Triteleia ixioides (Ait. f.) Greene subsp. *unifolia* Lenz [=*Brodiaea lutea* (Lindl.) Mort. var. *scabra* (Greene) Munz in part]. Low Mounds, Thick Soils. Common.

Triteleia laxa Benth. [=*Brodiaea laxa* (Benth.) Wats.]. Low Mounds. Occasional.

Triteleia lilacina Greene [=*Brodiaea hyacinthina* (Lindl.) Baker var. *greenei* (Hoov.) Munz]. Thin Soils, Outcrop Edges, Low Mounds. Common.

Cyperaceae

Bulbostylis capillaris (L.) Clark in Hook. [=*Fimbristylis capillaris* (L.) Gray]. Vernal Pools.

Carex subfusca. Wet Margins, Vernal Pools. Occasional.

Cyperus aristatus. Vernal Pools. Uncommon.

Cyperus eragrostis. Wet Margins, Vernal Pools. Common.

Cyperus strigosus. Wet Margins, Vernal Pools. Common.

Eleocharis acicularis. Wet Margins. Common.

Eleocharis macrostachya. Vernal Pools. Common.

Juncaceae

Juncus bufonius. Low Mounds, Wet Margins, Vernal Pools. Common.

Juncus capitatus. Wet Margins, Vernal Pools. Uncommon.

Juncus leiospermus. Wet Margins, Vernal Pools. This species was presumed extinct until recently and is commonly encountered on the mesa. Six extant populations are currently known from S. Butte County to Red Bluff. The California Native Plant Society considers the rush rare and endangered (Smith et al. 1980).

Juncus uncialis. Vernal Pools. Uncommon.

Lilaeaceae

Lilaea scilloides. Vernal Pools. Occasional.

Liliaceae

Calochortus albus. Dry Cobbles. Uncommon in shaded areas at the mesa's north tip.

Calochortus luteus. Thin Soils, Low Mounds, Ruderal.

Chlorogalum pomeridianum. Outcrop Edges, Dry Cobbles, Fractured Basalt, Low Mounds. Common.

Odontostomum hartwegii. Thin Soils, Outcrop Edges, Fractured Basalt.

Lemnaceae

Lemna minor. Standing Water. Uncommon.

Poaceae

Agrostis microphylla. Thin Soils, Outcrop Edges, Low Mounds.

**Aira caryophyllea.* Thin Soils, Outcrop Edges, Low Mounds, Thick Soils.

Alopecurus saccatus. Vernal Pools, Standing Water. Common.

Aristida hamulosa. Thin Soils, Outcrop Edges, Thick Soils. Rare, northernmost known population in Sacramento Valley.

Aristida oligantha. Wet Margins.

**Avena barbata.* Low Mounds, Thick Soils, Ruderal. Common.

**Briza minor.* Low Mounds, Thick Soils, Wet Margins. Common.

**Bromus diandrus* Roth [=*B. rigidus* Roth]. Thick Soils, Ruderal.

**Bromus madritensis.* Dry Cobbles. Uncommon.

**Bromus mollis.* Outcrop Edges, Dry Cobbles, Low Mounds, Thick Soils, Ruderal.

**Bromus molliformis.* Dry Cobbles, Thick Soils. Common.

**Bromus rubens.* Thick Soils, Shaded Soils, Ruderal.

**Cynodon dactylon.* Shaded Soils, Vernal Pools.

**Cynosurus echinatus.* Shaded Soils. Common under shade of oaks.

Deschampsia danthonioides. Wet Margins, Vernal Pools.

**Echinochloa crusgalli.* Vernal Pools. Common.

Elymus glaucus. Dry Cobbles. Uncommon at mesa's west edge.

× *Elysitanion hanseni* (Scribn.) Bowden [=*Sitanion hanseni* (Scribn.) J. G. Sm.]. Dry Cobbles, Cliff Faces. Rare.

**Gastridium ventricosum.* Thin Soils, Outcrop Edges. Common.

Hordeum brachyantherum. Wet Margins. Rare.

**Hordeum geniculatum.* Outcrop Edges, Ruderal. Common.

**Hordeum leporinum.* Shaded Soils, Ruderal. Common.

**Koeleria phleoides.* Thin Soils, Low Mounds, Thick Soils. Common.

**Lamarckia aurea.* Dry Cobbles, Fractured Basalt. Occasional.

**Lolium multiflorum.* Thick Soils, Shaded Soils. Uncommon.

Melica californica. Thin Soils, Dry Cobbles, Cliff Faces, Fractured Basalt. Common.

**Paspalum dilatatum.* Vernal Pools.

**Phalaris caroliniana.* Vernal Pools. Uncommon.

Phalaris paradoxa. Vernal Pools. Uncommon.

**Poa annua.* Thick Soils, Shaded Soils, Wet Margins. Common.

Poa scabrella. Thin Soils, Outcrop Edges, Cliff Faces. Uncommon.

Poa tenerrima. Vernal Pools. Uncommon at the mesa's northern pools. Munz (1968) lists it in El Dorado and Ventura Cos., but it is common in Butte and Tehama Cos. Rare but not endangered in California (Smith et al. 1980).

**Polypogon monspeliensis.* Vernal Pools. Common.

Scribneria bolanderi. Low Mounds, Thick Soils. Uncommon.

Stipa pulchra. Rare, only known from herbarium collection.

**Taeniatherum caput-medusae* (L.) Nevski. [=*Elymus caput-medusae* L.]. Thick Soils. Occasional

Vulpia microstachys (Nutt.) Benth. [=*Festuca microstachys* Nutt.]. Thin Soils, Outcrop Edges, Dry Cobbles. Common.

Vulpia microstachys (Nutt.) Benth. var. *ciliata* (Beal) Lonard & Gould [=*Festuca grayi* (Abrams) Piper and *F. eastwoodae* Piper]. Thin Soils, Outcrop Edges, Dry Cobbles.

Vulpia microstachys (Nutt.) Benth. var. *confusa* (Piper) Lonard & Gould [=*Festuca confusa* Piper and *F. tracyi* Hitchc.]. Thin Soils, Outcrop Edges, Dry Cobbles.

Vulpia microstachys (Nutt.) Benth. var. *pauciflora* (Beal) Lonard & Gould [=*Festuca pacifica* Piper and *F. reflexa* Buckl.]. Thin Soils, Outcrop Edges, Dry Cobbles.

**Vulpia myuros* (L.) C. C. Gmelin [=*Festuca myuros* L.]. Thin Soils, Outcrop Edges, Dry Cobbles, Low Mounds.

**Vulpia myuros* (L.) C. C. Gmelin var. *hirsuta* Hack [=*Festuca megalura* Nutt.]. Dry Cobbles, Low Mounds, Thick Soils. Common.

TAXA NOT OBSERVED BY THE AUTHOR

Limnanthes floccosa Howell subsp. *californica* Arroyo (Limnanthaceae). This very rare and endangered species has been collected on Table Mountain (*C. T. Mason 1254* and *T. Niehaus 371*) as recently as 1965; it is cited by Arroyo (1973) in the description of the subspecies and is listed as rare and endangered by the California Native Plant Society (Smith et al. 1980). This species may possibly have been extirpated here by grazing livestock.

Medicago praecox DC. (Fabaceae). According to the notes of L. Ahart, J. T. Howell (California Academy of Sciences) has collected this species on the mesa.

Polypogon australis Bongr. (Poaceae). Rubtzoff (1961) cites a collection from Table Mountain.

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VASCULAR PLANTS OF RICHVALE VERNAL POOLS, BUTTE COUNTY, CALIFORNIA

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Abstract

The Richvale Vernal Pools site in the Sacramento Valley of northern California is a 32.4 hectare grassland with 120 vernal pools of varying sizes occurring on its alluvial soils. The flora contains 45 families, 131 genera and 184 species of vascular plants, all flowering plants except for two. Annuals comprise 74.5% of the species. As is typical of annual grasslands in lowland California, a portion of the flora consists of introduced plants: the flora occurring in vernal pools is 93% natives, while the grassland matrix between pools is 67% natives. The largest family, Poaceae, contributes the most non-natives (i.e., 22 introduced, 6 native grasses). Asteraceae is also well represented, but mainly by natives (5 introduced, 18 native). Richvale Vernal Pools is important as a diverse remnant of grassland/vernal pool ecosystems in a region almost entirely cultivated in rice.

Richvale Vernal Pools occurs as a 32.4 hectare remnant of grassland in the northern Sacramento Valley, 31.5 km south of Chico, California (Fig. 1). This land is surrounded on the north, west, and south by cultivated ricelands, and on the east by California Highway 99 and a reservoir, the Thermalito Afterbay. This parcel of land has never been plowed and has suffered only relatively minor disturbance. A low hill in the east-central portion bears remains of a small grove of osage-orange and fig trees. More marked disturbances are the drainage ditch running east–west across the parcel (Fig. 1), the revegetated mounds of soil along this ditch, and several adjacent ditches that dry completely each year and harbor native vegetation. There was grazing here by 3 to 5 horses in 1979 and 1980. As in grasslands throughout northern California at present (Heady 1977), the regions between the vernal pools contain many naturalized annual grasses. Within this grassland matrix is found the largest known assemblage of vernal pools remaining in the northern Central Valley of California (Sanders 1981).

At Richvale, as is usual within groups of vernal pools that have been studied (e.g., Jain 1976), the flora of adjacent pools differs. Detailed examples of species frequency, density, and cover in nearby pools at Richvale are reported elsewhere (Schlising and Sanders 1982). The variation in size, depth, substrate, and flora in the large number of adjacent pools make the Richvale site very valuable. The isolation and the remnant nature of this land in an agricultural area also make Richvale Vernal Pools and its biota uniquely important.

Elevation at the site ranges from about 33.5 to 38.1 m above sea

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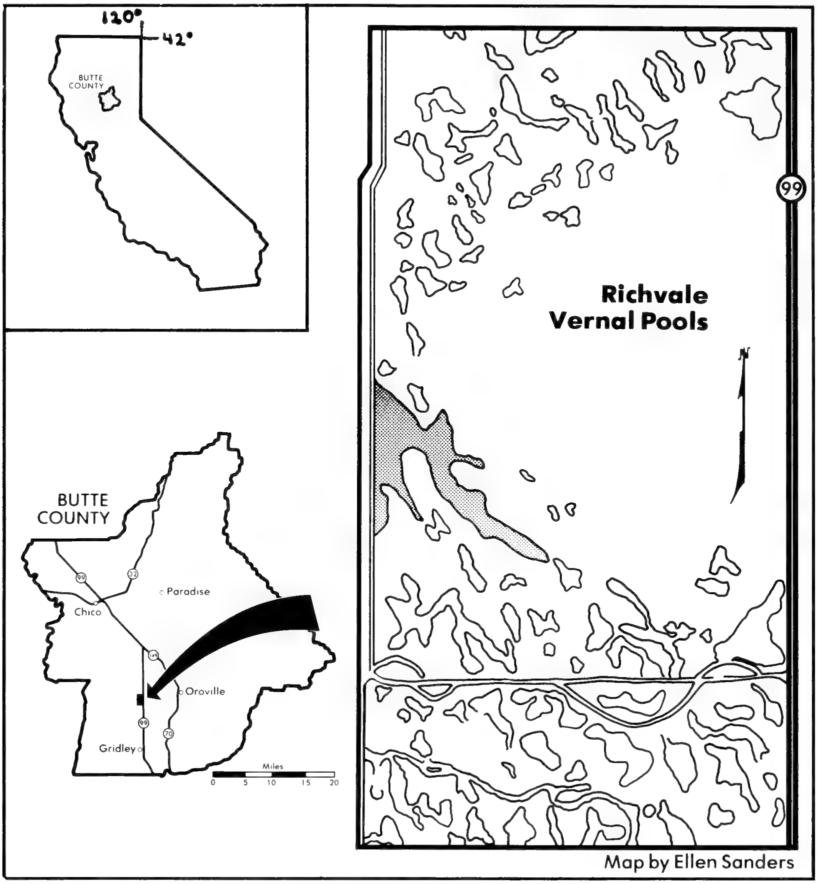

FIG. 1. Location and details of Richvale Vernal Pools, Butte County (T19N, R2E, section 24), California. High-water line of the pools in 1980 is shown; the border of the shaded pool is at 33.5 m above sea level (pool map from Sanders 1981).

level. Precipitation data taken at the Richvale Rice Experiment Station, 4 km to the southwest, show a mean of 48.89 cm annually from 1931 through 1961; more recent records are incomplete (Calif. Resources Agency 1980). Climate maintaining these typical grassland and vernal pool habitats is Mediterranean. The rainy winters fill the pools that have cemented hardpans below them. The rising temperatures and lack of precipitation in spring cause the drydown of the pools and the mostly vernal flowering of their largely endemic flora (Schlising and Sanders 1982).

There are about 120 depressions and pools at Richvale that vary in area from several m^2 to 7293 m^2 (Sanders 1981). Soils have developed from alluvium, and are red, gravelly loams of the San Joaquin series, which generally have an iron silicate hardpan within a meter of the soil surface (Holland 1978). However, the largest pool (shown shaded in Fig. 1) has a different, probably older substrate with a markedly higher clay content. This lower area has a flora somewhat different from the remainder of the 32.4 ha. (At least 6 taxa are found here only: *Evax caulescens, Hemizonia luzulaefolia* subsp. *rudis, Navarretia heterandra, N. nigellaeformis, Tuctoria* (*Orcuttia*) *greenei,* and *Trifolium variegatum*.) This large (but very shallow) pool is referred to as the "largest pool" in the checklist that follows.

The vascular plant flora contains 45 families, 131 genera and 184 species (plus four additional subspecies). With the exception of one species of fern and one quillwort (*Isoetes*), these are all flowering plants. Of the total flora, 137 species (74.5%) are annuals and 123 species (66.8%) are native to California.

When the flora is considered roughly by habitat, 93% of the species typically found in the vernal pools are natives. Within the grassland matrix about 67% of the species are natives. Along, as well as in, the ditches and on the hilltop (comprising a relatively small area of the Richvale site), the native component in the flora drops to 45% of the species.

The families best represented are: Poaceae (6 native species/28 total species), Asteraceae (17/23), Fabaceae (8/14), Scrophulariaceae (8/9), Polemoniaceae (7/7), Boraginaceae (7/7), Brassicaceae (5/7), Amaryllidaceae (6/6), Caryophyllaceae (2/6), Juncaceae (5/5), Onagraceae (5/5), and Ranunculaceae (4/5). Thirty-two percent of the introduced species present are in the Poaceae. Of the nine grasses found in the vernal pools, one, *Tuctoria* (*Orcuttia*) *greenei,* is a rare plant protected by legislation in the state of California.

This list of vascular plants from the pools and from the grassland matrix among the pools was prepared by observation and collecting from 1978 through 1983. Names follow Munz (1968); recent nomenclature is based on an unpublished checklist ("Flora Buttensis") by M. S. Taylor. Voucher specimens are in the Herbarium at California State University, Chico (CHSC). Species are classified relatively as rare, infrequent, frequent, common, or abundant. Species found in vernal pools are marked with a #; introduced species are marked with an asterisk.

LYCOPHYTA

Isoetaceae

#*Isoetes nuttallii*. Perennial, common in vernal pools.

PTEROPHYTA

Marsileaceae

#*Pilularia americana*. Perennial, frequent in vernal pools.

ANTHOPHYTA—DICOTYLEDONEAE

Aizoaceae

**Mollugo verticillata*. Introduced annual, infrequent in deep ditches that dry in summer, but not in vernal pools.

Apiaceae

#*Eryngium vaseyi* var. *vallicola*. Perennial, common in pools and moist areas between pools.

Lomatium humile. Perennial, frequent in higher areas away from pools.

Sanicula bipinnatifida. Biennial or perennial, infrequent in higher areas away from pools.

Asteraceae

#*Achyrachaena mollis*. Annual, common in shallow pools, pools margins and moist slopes.

#*Blennosperma nanum*. Annual, infrequently found near pools.

**Centaurea solstitialis*. Annual, frequent on mounds along ditches and in heavily disturbed flatter areas.

**Conyza canadensis*. Annual, infrequent on mounds and sides of ditches.

#*Evax caulescens*. Annual, common in largest pool and adjacent clayey flats.

Filago californica. Annual, infrequent in grasslands.

Gnaphalium chilense. Annual or biennial, frequent on moist sides of ditches.

Grindelia camporum. Perennial, with one population on mound by ditch.

#*Hemizonia fitchii*. Annual, common throughout area, including some pools.

#*Hemizonia luzulaefolia* subsp. *rudis*. Annual, abundant in largest pool and adjacent clayey flats.

#**Hypochoeris glabra*. Annual, common throughout grasslands and frequent in some shallow pools.

**Lactuca serriola* var. *serriola*. Annual, infrequent in grasslands.

**Lactuca serriola* var. *integrata*. Annual, rare in grasslands.

Lagophylla glandulosa subsp. *glandulosa*. Annual, frequent throughout area between pools.

Lagophylla glandulosa subsp. *serrata*. Annual, rare in area; considered an early-flowering ecotype.

#*Lasthenia fremontii*. Annual, abundant in pools.

#*Lasthenia glaberrima*. Annual, known in one southeastern pool.

#*Layia fremontii*. Annual, common throughout area, including shallow pools.

Micropus californicus. Annual, infrequent throughout grasslands.

#*Microseris douglasii*. Annual, common throughout, including shallow pools.

#*Psilocarphus brevissimus*. Annual, abundant in vernal pools throughout.

#*Psilocarphus oregonus*. Annual, infrequent in shallow pools.

#*Psilocarphus tenellus* var. *tenuis*. Annual, known in one shallow southeastern pool.

**Senecio vulgaris*. Annual, infrequent in disturbed areas.

Solidago occidentalis. Perennial, rare in ditch along west side.

Boraginaceae

Amsinckia intermedia. Annual, rare on hill near Highway 99.

Plagiobothrys fulvus var. *campestris*. Annual, common between pools and especially on hill.

#*Plagiobothrys greenei*. Annual, common in shallow pools, pool margins and low areas.

#*Plagiobothrys leptocladus*. Annual, known in several pools near cross ditch.

Plagiobothrys nothofulvus. Annual, rare in areas between pools.

#*Plagiobothrys stipitatus* var. *stipitatus*. Annual, abundant in largest pool and adjacent clayey flats.

#*Plagiobothrys stipitatus* var. *micranthus*. Annual, common in deeper pools throughout area.

Brassicaceae

**Capsella bursa-pastoris*. Annual, rare on hill.

Cardamine oligosperma. Annual, rare in grasslands.

#*Lepidium nitidum*. Annual, common at pool margins and in low areas.

Rorippa palustris subsp. *occidentalis*. Annual, rare in ditches.

**Sisymbrium officinale*. Annual, in heavily trampled areas under trees on hill.

Thysanocarpus radians. Annual, infrequent between pools.

Tropidocarpum gracile. Annual, rare on hill.

Callitrichaceae

#*Callitriche longipedunculata*. Annual, in deeper vernal pools and ditches.

#*Callitriche marginata*. Annual, in deeper pools and ditches.

Campanulaceae

#*Downingia bella*. Annual, abundant in vernal pools throughout.

#*Downingia bicornuta*. Annual, common in vernal pools throughout.
#*Downingia ornatissima*. Annual, common in vernal pools throughout and in adjacent moist areas.
Githopsis specularioides. Annual, rare in higher areas.

Caryophyllaceae

**Cerastium glomeratum* [*C. viscosum*]. Annual, infrequent in disturbed areas.
**Petrorhagia velutina* (Gussone) Ball and Heywood [*Tunica prolifera, Kohlrauschia velutina*]. Annual, infrequent in grasslands.
#*Sagina apetala* Ard. [*S. apetala* var. *barbata*]. Annual, infrequent in shallow pools and low areas.
#*Sagina decumbens* (Ell.) Torr. & Gray subsp. *occidentalis* (Wats.) Crow [*S. occidentalis*]. Annual, infrequent in shallow pools and low areas.
**Silene gallica*. Annual, infrequent in disturbed areas.
**Stellaria media*. Annual, infrequent in disturbed areas.

Convolvulaceae

**Convolvulus arvensis*. Perennial, rare in trampled area under trees on hill.

Crassulaceae

#*Crassula aquatica* (L.) Schonl. [*Tillaea aquatica*]. Annual, common in shallow pools, in horse trails and other low or open areas.
Crassula erecta (H. & A.) Berger [*Tillaea erecta*]. Common in low areas.
**Crassula muscosa* (L.) Roth [*Tillaea muscosa*]. Common in low areas.

Cuscutaceae

#*Cuscuta howelliana* Rubtzoff. Annual, common throughout (especially in southwest corner) in pools and at pool margins; fruiting mostly on *Eryngium*.

Euphorbiaceae

#*Eremocarpus setigerus*. Annual, common throughout, especially in shallow pools.
#*Euphorbia ocellata*. Annual, infrequent in shallow pools.

Fabaceae

Lotus purshianus. Annual, abundant near cross ditch.
Lotus subpinnatus. Annual, infrequent near ditches.
Lupinus bicolor subsp. *pipersmithii*. Annual, common between pools.
**Medicago polymorpha* var. *polymorpha* [*M. hispida*]. Annual, infrequent in disturbed areas.

**Medicago polymorpha* var. *brevispina* [*M. hispida* var. *confinus*]. Annual, infrequent in disturbed areas.

#Trifolium depauperatum. Annual, common in some shallow pools and in flat areas.

**Trifolium dubium*. Annual, infrequent near cross ditch.

**Trifolium hirtum*. Annual, common throughout between pools.

Trifolium microcephalum. Annual, frequent throughout grasslands.

**Trifolium subterraneum*. Annual, infrequent at margins of area.

#Trifolium tridentatum. Annual, infrequent in shallow pools.

#Trifolium variegatum. Annual, common in and near largest pool.

**Vicia angustifolia*. Annual, infrequent near cross ditch.

**Vicia sativa*. Annual, infrequent, especially in heavily disturbed areas near Hwy 99.

**Vicia villosa*. Annual or biennial, infrequent along ditches.

Gentianaceae

#Centaurium floribundum. Annual, in several pools, including largest, and along ditches.

#Cicendia quadrangularis. Annual, frequent in shallow pools, flat areas and horse trails in higher areas.

Geraniaceae

**Erodium botrys*. Annual, common throughout grasslands, especially lower areas between pools.

**Erodium moschatum*. Annual, rare under trees on hill.

**Geranium dissectum*. Annual, infrequent in grasslands.

**Geranium molle*. Annual, rare under trees on hill.

Haloragaceae

Myriophyllum exalbescens Fern. [*M. spicatum* subsp. *exalbescens*]. Perennial, common in irrigation ditch on west side.

Hypericaceae

**Hypericum perforatum*. Perennial, infrequent along cross ditch.

Lamiaceae

#Pogogyne zizyphoroides. Annual, common in shallower pools and margins of deeper pools throughout.

#Trichostema lanceolatum. Annual, common throughout area, including vernal pools.

Lycopus americanus. Perennial, common in cross ditch.

Lentibulariaceae

Utricularia gibba. Annual, rare in cross ditch.

Limnanthaceae

#*Limnanthes alba*. Annual, common in most pool margins and in adjacent low areas.

Lythraceae

#*Lythrum hyssopifolia*. Annual, common in pools and low areas throughout.

Malvaceae

**Malva neglecta*. Annual, rare under trees on hill.
#*Sidalcea diploscypha*. Annual, rare on slopes and at pool margins.
#*Sidalcea hirsuta*. Annual, in large pool and rare in other pools.

Moraceae

**Ficus carica*. Few trees on hill.
**Maclura pomifera*. About twelve decrepit trees on hill.

Onagraceae

#*Boisduvalia cleistogama*. Annual, rare in widely separated pools.
#*Boisduvalia stricta*. Annual, common at pool margins and in low areas.
#*Clarkia purpurea* subsp. *quadrivulnera*. Annual, common between pools and at pool margins.
Epilobium paniculatum. Annual, rare in cross ditch.
Ludwigia peploides. Perennial, abundant in cross and west ditches.

Papaveraceae

Eschscholzia lobbii. Annual, frequent between pools, especially in south portion.

Plantaginaceae

**Plantago lanceolata*. Perennial, infrequent along ditches.

Polemoniaceae

Linanthus bicolor. Annual, frequent between pools throughout area.
#*Navarretia heterandra*. Annual, found only in largest pool and adjacent clayey flats.
Navarretia intertexta. Annual, collected in 1978 (*M. S. Taylor 1611*), but not relocated.
#*Navarretia leucocephala*. Annual, abundant in pools throughout.
#*Navarretia nigellaeformis*. Annual, common in largest pool and adjacent clayey flats.
Navarretia pubescens. Annual, infrequent in grasslands.
#*Navarretia tagetina*. Annual, common throughout at pool margins and in grasslands between pools.

Polygonaceae

**Rumex crispus*. Perennial, scattered throughout grasslands, especially near ditches.

**Rumex pulcher*. Perennial, infrequent, especially near ditches.

Polygonum punctatum. Perennial, common in cross ditch.

Portulacaceae

Calandrinia ciliata var. *menziesii*. Annual, rare between pools.

Claytonia perfoliata subsp. *perfoliata*. Annual, infrequent on hill among trees.

Montia fontana L. subsp. *chondrosperma* (Fenzl.) Walt. [*M. verna, M. minor*]. Annual, common throughout in low areas and along horse trails.

Primulaceae

**Anagallis arvensis*. Annual, rare in largest pool.

#*Anagallis minima* [*Centunculus minimus*]. Annual, infrequent in pools.

Ranunculaceae

Delphinium variegatum. Perennial, infrequent in higher grassland.

#*Myosurus minimus*. Annual, infrequent in pools.

#*Ranunculus bonariensis* var. *trisepalus*. Annual, rare in cross ditch and several pools.

Ranunculus aquatilis var. *hispidulus*. Perennial, in deeper ditches.

**Ranunculus muricatus*. Annual or perennial, infrequent in cross ditch.

Rubiaceae

**Galium tricorne*. Annual, common in southeast corner.

Salicaceae

Populus fremontii. Few saplings in ditch on west side.

Salix gooddingii. Few plants in ditch on west side.

Salix hindsiana. Few plants in ditch on west side.

Scrophulariaceae

#*Gratiola ebracteata*. Annual, common in pools.

Lindernia dubia (L.) Penn. var. *anagallidea* (Michx.) Cooperrider [*L. anagallidea*]. Annual, rare on banks of cross ditch.

#*Mimulus guttatus*. Annual, infrequent in cross ditch and in some pools.

#*Mimulus tricolor*. Annual, infrequent in pools.

Orthocarpus attenuatus. Annual, frequent in areas between pools.

#*Orthocarpus campestris*. Annual, infrequent in pools throughout.

#*Orthocarpus erianthus*. Annual, common in lower areas and at pool margins.

Verbascum blattaria. Biennial, rare on bank of cross ditch.

#*Veronica peregrina* subsp. *xalapensis*. Annual, uncommon in pools throughout.

Solanaceae

**Lycium halimifolium*. One shrub near trees on hill.

ANTHOPHYTA—MONOCOTYLEDONEAE

Alismataceae

Alisma triviale. Perennial, in cross ditch.

Sagittaria calycina Engelm. [*S. montevidensis* subsp. *calycina*]. Perennial, infrequent in cross ditch.

Amaryllidaceae

#*Allium amplectens*. Perennial, common throughout in low areas and in many shallow pools.

Brodiaea coronaria. Perennial, infrequent on higher ground.

#*Brodiaea minor*. Perennial, common between, and sometimes in pools.

Dichelostemma multiflorum (Benth.) Heller [*Brodiaea multiflora*]. Perennial, common between pools.

Dichelostemma pulchellum (Salisb.) Heller [*Brodiaea pulchella*]. Perennial, infrequent between pools.

#*Triteleia hyacinthina* (Lindl.) Greene [*Brodiaea hyacinthina*]. Perennial, common between pools and in margins of shallow pools.

Cyperaceae

Cyperus eragrostis. Perennial, infrequent along ditches.

#*Eleocharis macrostachya* Britton. Perennial, infrequent as dense clumps in deeper pools.

Scirpus acutus. Perennial, in central part of cross ditch.

Hydrocharitaceae

Elodea canadensis. Perennial, in ditches.

Juncaceae

Juncus acuminatus. Perennial, infrequent in ditches.

#*Juncus bufonius*. Annual, common in pools, in low areas, and on horse trails.

#**Juncus capitatus*. Annual, frequent in pools throughout.

#*Juncus oxymeris*. Perennial, rare in a few pools.

#*Juncus uncialis*. Annual, frequent at pool margins, especially on pocket gopher soil-mounds.

Liliaceae

Calochortus luteus. Perennial, rare near center of area.

Chlorogalum angustifolium. Perennial, common throughout grassland area.

Poaceae

**Aegilops triuncialis*. Annual, infrequent as dense populations in grassland.

**Agrostis avenacea*. Perennial, infrequent in cross ditch.

**Aira caryophyllea*. Annual, common throughout grassland area.

#*Alopecurus saccatus*. Annual, common in some pools.

**Andropogon glomeratus*. Perennial, rare in ditches.

#*Aristida oligantha*. Annual, frequent throughout, in pools and low areas.

**Avena barbata*. Annual, frequent throughout grassland.

**Briza minor*. Annual, common throughout grassland.

**Bromus diandrus* [*B. rigidus*]. Annual, infrequent throughout grassland.

**Bromus mollis*. Annual, the most abundant grassland species throughout.

**Bromus rubens*. Annual, common throughout grassland.

**Cynodon dactylon*. Perennial, infrequent near cross ditch.

#*Deschampsia danthonioides*. Annual, common in pools, especially at margins.

#**Gastridium ventricosum*. Annual, frequent throughout, sometimes in pools.

**Hordeum geniculatum* [*H. hystrix*]. Annual, infrequent.

**Hordeum glaucum* [*H. stebbinsii*]. Annual, common in grassland.

#**Hordeum leporinum*. Annual, common in grassland and in some pools.

**Lolium multiflorum*. Annual, common in grassland.

**Paspalum dilatatum*. Perennial, common along ditches.

**Poa annua*. Annual, infrequent in disturbed areas like ditch banks.

#**Polypogon maritimus*. Annual, common in distrubed areas and frequent in many vernal pools.

#*Phalaris lemmonii*. Annual, infrequent in some pools.

#**Phalaris paradoxa*. Annual, infrequent in some pools.

Setaria geniculata. Perennial, infrequent at ditch margins.

**Taeniatherum caput-medusae* (L.) Nevski [*T. asperum*]. Annual, infrequent as dense populations in grassland.

#*Tuctoria greenei* (Vasey) J. Reeder [*Orcuttia greenei*]. Annual, known only from one small population in the largest pool.

**Vulpia bromoides* (L.) S. F. Gray [*Festuca dertonensis*]. Annual, infrequent along ditch banks and in areas between pools.

Vulpia microstachys (Nutt.) Benth. var. *microstachys* [*Festuca microstachys*]. Annual, infrequent in grassland.

**Vulpia myuros* (L.) Gmelin var. *hirsuta* Hack. [*Festuca megalura*]. Annual, infrequent along ditch banks and in areas between pools.

Pontederiaceae

**Heteranthera limosa*. Perennial, infrequent in cross ditch.

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VASCULAR FLORA OF THE MUDDY MOUNTAINS, CLARK COUNTY, NEVADA

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ABSTRACT

The Muddy Mountains are located 42 km northeast of Las Vegas, Nevada. In this study, the area covered is nearly 1684 km^2 and includes Muddy Mountain, North Muddy Mountain and several small rural communities. The elevation range is from 365 m to 1646 m. A flora of 435 species in 266 genera and 68 families is present in the range. Seventy-six non-indigenous species were collected in rural areas, comprising 17.6% of the total flora. There were no endemic species.

The mountains of southern Nevada, Utah, and northwestern Arizona have interested many botanists because they lie in the broad transition corridor between the Mojave and Great Basin Deserts. Clokey (1951) describes the Charleston Mountains as ". . . a meeting ground for the invasion of plants from both the north and south during the advances and retreats of the Ice Age."

An incomplete flora (Tidestrom 1925) exists for Nevada and checklists are available for only a few isolated ranges within the state. Taxonomic and ecological studies have been made in the transition zone of southern Nevada by Armstrong (1969) in the Virgin Mountains, Beatley (1976) on the Nevada Test Site, Bostick (1973) in the McCullough Mountains, Clokey (1951) in the Spring Mountains, Higgins (1967) in the Beaver Dam Mountains, Utah, and Meyer (1976) for Washington County, Utah.

The Muddy Mountains offer a wide diversity of substrates. The earliest exposed rocks date from Cambrian time, and the majority of these formations are carbonate. Other exposed substrates include limestone, sandstone, micaceous shales, mudstone, volcanic tuff, colemanite, gypsum, caliche, eolian sands, and alkali sinks. Current geological information (Bohannon 1977, 1979; Longwell et al. 1965) of the Muddy Mountain area suggests that much of the area is complex and still poorly described.

The climate is characterized by temperature extremes and sporadic precipitation. Seasons are well-defined with summer temperatures above 38°C and winter temperatures frequently below freezing. Snow at any elevation is uncommon. Based on a 38-year annual average (Ruffner and Bair 1977) for Las Vegas, precipitation is nearly 102 mm, and occurs as rain mainly during winter months. Summer thundershowers are occasional, intense, and strongly localized.

Permanent water sources are mostly confined to the Muddy River

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drainage. Five small springs located on the east side of Muddy Mountain are associated with faulting. At its source the Muddy River is fed by many small thermal springs. Within 13 km of its source, the river becomes charged with a heavy mineral and silt load. The unusually high percentage of non-native plants (Swearingen 1981) reflects the presence of well established agrarian communities in the Moapa Valley at the north end of the study area.

Patterns of association among plants in the Muddy Mountains are complex, reflecting the effects of climate, substrate, and physiography. Plant distribution appears to be controlled primarily by climate and secondarily by edaphic factors. Many plants are characteristic of specific substrates associated with the highly varied geology. Thus, the vegetation is divided into a mosaic of plant communities. Regional zones described by Billings (1951) overlap in ecotones; however, communities are more sharply defined based on specific factors, e.g., soil or topographic preference. Zones and communities were qualitatively assessed in the study area. Within the Muddy Mountains, four of Billings (1951) regional zones apply: Creosote Bush Zone, Shadscale Zone, Sagebrush Zone, and Azonal. Community descriptions within the zones are based on Thorne (1976). Eight communities within the Creosote Bush Zone are: Alkaline Sink Scrub, Alkaline Meadow and Aquatic Herb, Arroyo Woodland, Creosote Bush Scrub, Desert Holly Scrub, Desert Rural Ruderal, Dune Sand Barren, Gypsum Barren, and Oasis Woodland. The Blackbrush Scrub community represents the Shadscale Zone, and Sagebrush Scrub community represents the Sagebrush Zone. The Azonal region has one community, the Mixed Cliff Semishrub.

Nomenclature follows that of Kartesz and Kartesz (1980), hence authorities are not given. Voucher specimens are deposited in the UNLV Herbarium. The checklist is based on field observations from January 1979 through November 1980. Specimens documented from the UNLV Herbarium were included along with citations from literature. Species abundance was rated as very rare, rare, uncommon, common, abundant, or ubiquitous based upon Braun-Blanquet (Mueller-Dombois and Ellenberg 1974). Three non-native categories defined by Lawrence (1958) were used: (1) naturalized, (2) introduced, and (3) adventive.

Annotated Checklist of Vascular Plants

Pterophyta

Adiantaceae

Cheilanthes parishii. Uncommon; in limestone crevices.
Notholaena jonesii. Rare; in limestone crevices.
Notholaena parryi. Common; in crevices of sandstone formations.

CONIFEROPHYTA

Ephedraceae

Ephedra fasciculata. Uncommon; in wash gravels.
Ephedra nevadensis. Uncommon; in washes.
Ephedra torreyana. Common; on desert pavement and wash gravels.

ANTHOPHYTA—DICOTYLEDONEAE

Aizoaceae

Sesuvium verrucosum. Rare; adventive in rural area.

Amaranthaceae

Amaranthus albus. Common; naturalized around rural areas.
Amaranthus fimbriatus. Uncommon; in gravels or washes.
Amaranthus palmeri. Common; naturalized around rural areas.
Amaranthus powellii. Uncommon; adventive in disturbed habitats.
Tidestromia oblongifolia. Common; in disturbed habitats.

Anacardiaceae

Rhus trilobata var. *anisophylla.* Uncommon to rare; on gravel slopes or disturbed gravels of washes.

Apiaceae

Apium graveolens. Uncommon; introduced along irrigation canals.
Hydrocotyle verticellata. Rare; in alkaline pools of thermal springs.
Lomatium parryi. Uncommon; on sandstone.
Lomatium scabrum. Uncommon; on limestone cliffs at high elevation.

Apocynaceae

Apocynum cannabinum var. *glaberrimum.* Locally common; in disturbed soils along drainage ditches in rural areas.

Asclepiadaceae

Asclepias erosa. Rare; in gravels.
Asclepias subulata. Uncommon; in washes.
Cynanchum utahense. Rare; in loose sands derived from sandstone outcrops.
Sarcostemma cynanchoides subsp. *hartwegii.* Rare; in sandy soils.
Sarcostemma hirtellum. Rare; on limestone slopes, entwined in *Ephedra.*

Asteraceae

Acamptopappus shockleyi. Common; on alluvial fans and in washes.
Acamptopappus sphaerocephalus. Common; on bajadas and in washes.

Ambrosia dumosa. Abundant; usually co-dominant with *Larrea tridentata* on sandy plains, washes, and micaceous shales.

Ambrosia eriocentra. Common in wash gravels.

Amphipappus fremontii subsp. *spinosus.* Common; in gravels and washes.

Artemisia ludoviciana subsp. *albula.* Locally common; on limestone outcrops and talus at higher elevations.

Artemisia tridentata subsp. *tridentata.* Abundant; on limestone at higher elevations.

Aster pauciflorus. Locally common; along irrigation canals and the Muddy River.

Aster spinosus. Rare; adventive along irrigation ditches.

Atrichoseris platyphylla. Locally common; on desert pavement.

Baccharis brachyphylla. Rare; in wash gravels.

Baccharis glutinosa. Common; on the banks of the Muddy River.

Baccharis sarothroides. Common; along the Muddy River.

Baccharis viminea. Common; along the Muddy River.

Baileya multiradiata. Common; on most disturbed habitats.

Baileya pleniradiata. Common; on sandy disturbed soils.

Bebbia juncea. Common; in washes.

Brickellia atractyloides. Uncommon; on rock outcrops at lower elevations.

Brickellia longifolia. Rare; usually on ledges and washes.

Brickellia multiflora. Common; in washes and on steep slopes at higher elevations.

Centaurea melitensis. Uncommon; naturalized on disturbed habitats.

Centaurea repens. Locally abundant; naturalized along margins of fields and Muddy River drainage.

Chaenactis carphoclinia. Common; on desert pavement.

Chaenactis fremontii. Common and ubiquitous.

Chaenactis macrantha. Uncommon; on desert pavement or gravels.

Chrysothamnus nauseosus subsp. *leiospermus.* Common; at higher elevations on rocky limestone slopes and outcrops.

Chrysothamnus paniculatus. Common; in washes and disturbed habitats.

Cirsium neomexicanum. Uncommon; in washes and moist alkaline soils.

Conyza canadensis. Locally common; naturalized in disturbed habitats of rural areas.

Conyza coulteri. Locally common; naturalized in disturbed habitats of rural areas.

Dicoria canescens subsp. *canescens.* Common; on loose sands.

Dyssodia cooperi. Uncommon; in sands and washes.

Dyssodia pentachaeta. Common; on limestone outcrops and in washes.

Encelia farinosa. Common; on cliff walls and limestone outcrops.

Encelia virginensis subsp. *virginensis*. Common; in disturbed habitats, typically on gravels.

Enceliopsis argophylla var. *grandiflora*. Abundant; on gypsiferous and micaceous substrates.

Erigeron divergens. Rare; in sands of washes.

Eriophyllum lanulosum. Common; in washes and on desert pavements.

Geraea canescens. Common; on sand, desert pavement and shales.

Gutierrezia microcephala. Common; on alluvial slopes at higher elevations.

Gutierrezia sarothrae. Common; on gravels and deep alluvium.

Haplopappus acradenius var. *eremophilus*. Common; on alklaine flats, gypsum, and micaceous shales.

Haplopappus gooddingii. Common; on crevices, rocky cliffs and limestone outcrops.

Hazardia brickellioides. Locally common; on sheer limestone cliffs.

Helianthus annuus subsp. *lenticularis*. Common; introduction in disturbed habitats.

Helianthus petiolaris var. *canescens*. Uncommon; introduction in disturbed habitats.

Heterotheca echioides. Common; in sands and gravels of washes.

Hymenoclea salsola var. *salsola*. Common; in washes and somewhat alkaline soils.

Lactuca serriola. Common; on disturbed habitats.

Lygodesmia exigua. Common; on alluvium and desert pavement.

Machaeranthera leucanthemifolia. Common; on sand dunes and sandy plains.

Machaeranthera tortifolia. Common; on rocky outcrops and along wash embankments.

Malacothrix glabrata. Common; on sand, alluvium, washes, and desert pavement.

Monoptilon bellidiforme. Common; in wash gravels at low elevations.

Monoptilon bellioides. Common; in wash gravels at low elevation.

Onopordum acanthium. Rare; but locally abundant adventive in a fallow field.

Palafoxia arida. Common; in sandy localities.

Pectis papposa. Common; after summer rains.

Perityle emoryi. Common; on cliffs and crevices.

Perityle megalocephala var. *intricata*. Locally common; on steep limestone cliffs.

Peucephyllum schottii. Common; on rocky cliffs and outcrops.

Pleurocoronis pluriseta. Common; on rock crevices and at the base of outcrops.

Pluchea odorata var. *odorata*. Uncommon; along alkali water courses and adjacent to springs at low elevations.

Porophyllum gracile. Uncommon; along washes and disturbed roadside gravels.

Prenanthella exigua. Uncommon; in sandy alluvial soils.

Psathyrotes pilifera. Common; during summer months on gypsum.

Psathyrotes ramosissima. Common; during late summer on gypsum and heavy mineral clay flats.

Psilostrophe cooperi. Common; on alluvial slopes and washes.

Rafinesquia neomexicana. Uncommon; growing in shade or under shrub canopy.

Senecio douglasii var. *monoensis.* Common; along wash beds.

Silybum marianum. Rare; adventive along disturbed access road.

Solidago confinus. Common; in alkaline soils of springs, seeps, and irrigation ditches.

Sonchus asper. Common; naturalized in moist alkaline soils.

Stephanomeria exigua. Uncommon; on alluvial slopes and in washes.

Stylocline micropoides. Uncommon; in sand, alluvium, and desert pavement.

Tessaria sericea. Common; along irrigation canals, springs, seeps, and Muddy River.

Trichoptilium incisum. Uncommon; on limestone and desert pavement.

Xanthium strumarium var. *canadense.* Abundant; along drainage courses, seeps, and springs.

Bignoniaceae

Chilopsis linearis. Common; along washes and intermittent stream beds.

Boraginaceae

Amsinkia intermedia. Common; in washes.

Amsinkia tesselata. Common; on sandy soils and gravels.

Cryptantha angustifolia. Common; on sands and disturbed gravels.

Cryptantha barbigera. Common; in sands and disturbed soils.

Cryptantha circumscissa. Common; on sandy soils.

Cryptantha confertiflora. Uncommon; on limestone outcrops.

Cryptantha decipiens. Common; in sand or gravels.

Cryptantha holoptera. Rare; on rocky slopes at low elevations.

Cryptantha inaequata. Rare; on rocky outcrops.

Cryptantha maritima. Common; in sands and washes.

Cryptantha micrantha subsp. *micrantha.* Common; on sands.

Cryptantha nevadensis var. *nevadensis.* Common; on sands and wash gravels.

Cryptantha pterocarya. Common; in sands and gravels.

Cryptantha racemosa. Rare; on rocky outcrops.

Cryptantha recurvata. Rare; on sandy soils.

Cryptantha virginensis. Common; on rocky slopes and outcrops.

Heliotropium convolvulaceum var. *californicum.* Very rare, but locally abundant; in wet years on sand dunes.

Heliotropium curassavicum var. *oculatum.* Abundant; on moist saline or alkaline soils.

Lappula redowskii. Locally common; in sands of washes.

Pectocarya heterocarpa. Common; in washes and sands.

Pectocarya platycarpa. Common; in disturbed soils.

Tiquilia canescens var. *pulchella.* Common; on desert pavement and rocky outcrops.

Tiquilia hispidissima. Common; on dunes of sandy alluvium.

Tiquilia plicata. Common; on dune sands.

Brassicaceae

Arabis perennans. Rare; on rocky slopes and boulder outcrops.

Capsella bursa-pastoris. Abundant; naturalized in lawns and disturbed habitats.

Cardaria pubescens. Locally common; adventive in alfalfa fields.

Descurainia pinnata subsp. *glabra.* Common; naturalized on disturbed soils.

Descurainia sophia. Common; naturalized on disturbed soils.

Dithyrea californica. Common; on sand dunes or sandy alluvium.

Draba cuneifolia. Uncommon; on sandy soils.

Eruca sativa. Rare; adventive on disturbed soils.

Lepidium campestre. Rare; adventive along fallow fields.

Lepidium dictyotum. Rare; in sandy soils.

Lepidium fremontii. Common; and widespread.

Lepidium lasiocarpum. Common; on sandstone, washes and desert pavement.

Lepidium montanum. Rare; on alluvial slopes.

Lesquerella tenella. Common; on sandy alluvium and dune sand.

Malcolmia africana. Abundant; naturalized on sandy soils.

Sisymbrium altissimum. Uncommon; in disturbed fields.

Sisymbrium irio. Uncommon; in fallow fields.

Sisymbrium officinale. Uncommon; on disturbed soils.

Stanleya pinnata subsp. *pinnata.* Uncommon; on alkaline soils.

Streptanthella longirostris. Common; on alluvium.

Thelypodium integrifolium subsp. *affine.* Rare; adventive along cultivated fields.

Thelypodium lasiophyllum var. *utahense.* Common; among shrubs and in washes.

Thysanocarpus curvipes var. *eradiatus.* Common; on grassy outcrops and alluvium.

Cactaceae

Echinocactus polycephalus. Locally common; on rocky slopes and outcrops of limestone.

Echinocereus engelmannii var. *chrysocentrus*. Common; on limestone cliffs and gravelly slopes.

Ferocactus acanthodes. Locally common; on rocky slopes and steep limestone cliffs.

Mammillaria tetrancistra. Rare; on dry slopes at low elevations.

Neolloydia johnsonii. Rare; on dry rocky outcrops.

Opuntia acanthocarpa. Common; in washes.

Opuntia basilaris. Common; on alluvium and outcrops.

Opuntia echinocarpa var. *echinocarpa*. Locally common; in washes and on alluvial fans.

Opuntia ramosissima. Uncommon, but locally abundant; on sandy soils.

Campanulaceae

Nemacladus glanduliferus var. *orientalis*. Common; in sands and between pebbles of desert pavements.

Caprifoliaceae

Symphoricarpos longiflorus. Locally common; in protected limestone canyons and crevices of higher altitudes.

Caryophyllaceae

Achyronychia cooperi. Common; in dune sands and alluvium.

Arenaria macradenia var. *parishiorum*. Common; on many substrates.

Scopulophila rixfordii. Common; on limestone cliffs.

Spergularia marina. Rare; on moist alkaline soils.

Celastraceae

Mortonia utahensis. Abundant; on sandstone and around dune sands.

Chenopodiaceae

Allenrolfea occidentalis. Locally abundant; on moist alkaline soils.

Atriplex canescens subsp. *canescens*. Common; on alluvium and washes.

Atriplex confertifolia. Uncommon; on alkaline soils.

Atriplex elegans subsp. *fasciculata*. Rare; on alkaline soils.

Atriplex hymenelytra. Locally common; on mudstone and shales.

Atriplex lentiformis subsp. *lentiformis*. Abundant; on moist alkaline soils.

Atriplex polycarpa. Abundant; on moist, clay, alkaline soils.

Atriplex semibaccata. Locally common; naturalized on alkaline soils disturbed by farming practices.

Bassia hyssopifolia. Common; adventive on moist alkaline soils.

Ceratoides lanata. Common; on alluvial fans and in washes.

Chenopodium album. Common; adventive along fallow fields.

Chenopodium berlandieri var. *sinuatum*. Common; adventive in disturbed soils.
Cycloloma atriplicifolium. Uncommon; adventive on disturbed soils.
Grayia spinosa. Uncommon; on alluvium and in washes.
Kochia californica. Uncommon; adventive on alkaline soils.
Kochia scoparia. Common; adventive on disturbed habitats.
Salsola paulsenii. Common; widespread and naturalized.
Suaeda torreyana var. *ramosissima*. Locally common; on alkaline soils.

Convolvulaceae

Convolvulus arvensis. Locally common; in fallow fields.
Cuscuta californica. Abundant; on many shrubs.
Cuscuta salina. Common; on plants of alkali, moist soils.
Cressa truxillensis. Rare; but locally common on alkali soils.

Cucurbitaceae

Cucurbita foetidissima. Uncommon; in sands and washes.

Elaeagnaceae

Elaeagnus angustifolia. Rare; escaping cultivation in rural areas.

Euphorbiaceae

Argythamnia neomexicana. Rare; in alkali, moist clay soils.
Croton californicus var. *mohavensis*. Common; on sandy soils.
Euphorbia albomarginata. Abundant; on disturbed soils.
Euphorbia incisa. Common; on sandstone and in washes.
Euphorbia micromera. Locally abundant; on sand dunes.
Euphorbia parryi. Common; on dune sands.
Euphorbia polycarpa var. *hirtella*. Uncommon; in washes.
Euphorbia setiloba. Uncommon; in disturbed soils.

Fabaceae

Acacia greggii. Common; in washes.
Astragalus amphioxys var. *amphioxys*. Common; on sandy soils.
Astragalus flavus var. *candicans*. Rare; in disturbed habitats adjacent to roads.
Astragalus geyeri var. *triquetrus*. Very rare; on sandy plains.
Astragalus lentiginosus var. *fremontii*. Common; on sandy plains and washes.
Astragalus newberryi var. *newberryi*. Rare; on rocky slopes and limestone cliffs.
Astragalus nyensis. Rare; on alluvium and gravelly slopes.
Astragalus nuttallianus var. *imperfectus*. Common; on alluvium, in washes and on fire disturbed soils.
Astragalus preussii var. *preussii*. Common; on alkaline clays and gypsum-micaceous shales.

Astragalus sabulonum. Rare; on sandy plains and in washes.
Cassia armata. Common; in only one arroyo.
Dalea mollissima. Uncommon; in sandy soils.
Lotus corniculatus. Rare; adventive in disturbed habitats.
Lotus rigidus. Uncommon; in washes and canyon bottoms.
Lotus tomentellus. Common; on sandy slopes.
Lupinus flavoculatus. Common; on sandy alluvial fans and wash gravels.
Medicago sativa. Common; introduction in disturbed habitats.
Melilotus alba. Uncommon; introduction on disturbed soils.
Melilotus indicus. Common; introduction on disturbed soils.
Prosopis juliflora var. *torreyana.* Abundant; in washes and on dune sands.
Psoralea castorea. Rare; on sands.
Psorothamnus fremontii var. *fremontii.* Common; on alluvial fans and desert pavement.
Psorothamnus polydenius var. *polydenius.* Locally common; on heavy clays (bentonite).

Geraniaceae

Erodium cicutarium. Abundant; in most disturbed communities.
Erodium texanum. Uncommon; on sandy soils.

Hydrophyllaceae

Eucrypta micrantha. Common; in crevices and sandy areas.
Eucrypta chrysanthemifolia var. *bipinnata.* Uncommon; under boulders and in shady, protected areas.
Nama demissum var. *demissum.* Uncommon; on sand.
Phacelia crenulata. Common; on alluvium and wash gravels.
Phacelia distans. Uncommon; in gravels of washes.
Phacelia fremontii. Common; in sands and gravels.
Phacelia ivesiana. Rare; in washes.
Phacelia palmeri. Common; on gypsum soils.
Phacelia pedicellata. Uncommon; in washes and canyons.
Phacelia perityloides var. *jaegeri.* Rare; on limestone cliffs and crevices.
Phacelia pulchella var. *gooddingii.* Common; on alkaline soils and gypsum-micaceous shales.
Phacelia rotundifolia. Rare; on rocky cliffs and in crevices.
Phacelia vallis-mortae. Rare; on rocky limestone ledges.
Tricardia watsoni. Rare; under boulders and rock crevices.

Krameriaceae

Krameria grayi. Common; in sands and alluvium.
Krameria parvifolia var. *glandulifera.* Common; on sands and alluvium.

Lamiaceae

Hedeoma nanum subsp. *californicum*. Common; on loose limestone at high elevation.

Monardella linoides subsp. *linoides*. Common; in washes at high elevations.

Salazaria mexicana. Abundant; in washes and canyons at low elevation.

Salvia columbariae var. *columbariae*. Common; on disturbed habitats and alluvial fans.

Salvia dorrii. Rare; on alluvial slopes and in washes.

Loasaceae

Eucnide urens. Common; on cliffs and rock outcrops.

Mentzelia albicaulis. Rare; in washes.

Mentzelia dispersa. Rare; in wash sands.

Mentzelia oreophila. Rare; in disturbed roadside gravels.

Mentzelia puberula. Common; on sandstone cliffs.

Mentzelia pumila. Rare; in sands and gravels.

Mentzelia tricuspis. Common; on sand and roadside embankments.

Petalonyx parryi. Common; on gypsum and micaceous shales.

Petalonyx thurberi. Uncommon; in washes and sandstone areas.

Loganiaceae

Buddleja utahensis. Uncommon; on limestone crevices and outcrops.

Malvaceae

Eremalche exilis. Rare; in sands.

Eremalche rotundifolia. Rare; on disturbed habitats.

Malva parviflora. Common; naturalized along rural roads.

Malvella leprosa. Rare; in moist alkaline soils.

Sphaeralcea ambigua subsp. *ambigua*. Abundant; on disturbed soils.

Sphaeralcea angustifolia subsp. *cuspidata*. Uncommon; along disturbed rural roads.

Moraceae

Cannabis sativa. Rare; introduced along Muddy River.

Morus alba. Rare; introduction along irrigation canals.

Nyctaginaceae

Abronia villosa var. *villosa*. Common; in sandy soils.

Allionia incarnata. Common; to sands and desert pavement.

Anulocaulis leiosolenus. Common; on gypsiferous soils.

Boerhaavia wrightii. Rare; in gravelly washes.

Mirabilis bigelovii var. *aspera*. Rare; in washes and outcrops.

Mirabilis bigelovii var. *retrorsa*. Rare; on sandstone.

Selinocarpus diffusus. Uncommon; on desert pavement.
Tripterocalyx micranthus. Rare; on sandy soils.

Oleaceae

Fraxinus anomala. Locally common; in canyons.
Fraxinus velutina var. *coriacea.* Common; on moist alkaline soils and at springs.
Menodora spinescens. Uncommon; on alluvial fans and in washes.

Onagraceae

Camissonia boothii subsp. *condensata.* Common; in wash gravels.
Camissonia brevipes subsp. *pallidula.* Abundant; on alluvium and in washes.
Camissonia multijuga. Uncommon; in canyon and wash bottoms.
Camissonia refracta. Uncommon; on sandy soils and alluvium.
Camissonia walkeri subsp. *tortilis.* Common; on rock outcrops.
Gaura coccinea. Uncommon; in washes and disturbed soils.
Oenothera cavernae. Locally common; on steeply faulted limestone of Muddy Peak Formation.
Oenothera deltoides. Abundant; in sandy habitats.

Orobanchaceae

Orobanche cooperi. Very rare; on *Hymenoclea salsola, Chilopsis,* and *Larrea tridentata* mainly in loose sands.
Orobanche ludoviciana. Very rare; on *Hymenoclea* in loose sands.
Orobanche multiflora var. *arenosa.* Very rare; on *Ambrosia* in loose sands.

Papaveraceae

Arctomecon californica. Abundant; on gypsum and micaceous soils.
Argemone munita. Uncommon; on limestone substrates.
Eschscholzia glyptosperma. Uncommon; but locally abundant on alluvium and gravels.

Plantaginaceae

Plantago insularis var. *fastigiata.* Abundant and ubiquitous.
Plantago lanceolata. Locally common; naturalized in disturbed soils.

Polemoniaceae

Eriastrum diffusum. Uncommon; usually in sands.
Eriastrum eremicum. Common; on sandy substrates.
Gilia clokeyi. Common; on sandy substrates.
Gilia hutchinsifolia. Common; on sandy substrates.
Gilia latifolia. Abundant; on shales and conglomerates.
Gilia leptomeria. Uncommon; on sands.
Gilia scopulorum. Common; in washes and alluvium.

Gilia transmontana. Rare; on sand substrates.

Langloisia schottii. Uncommon; on sand substrates.

Langloisia setosissima. Common; on sand substrates.

Leptodactylon pungens. Common; in washes and rocky slopes.

Linanthus demissus. Rare; in washes.

Polygonaceae

Chorizanthe brevicornu subsp. *brevicornu*. Abundant; on gravels and desert pavement.

Chorizanthe rigida. Common; on alluvium and desert pavements.

Eriogonum brachypodum. Uncommon; in washes.

Eriogonum corymbosum var. *glutinosum*. Rare; in wash gravels.

Eriogonum deflexum subsp. *deflexum*. Common; in sand and washes.

Eriogonum fasciculatum subsp. *polifolium*. Common; on alluvium.

Eriogonum heermannii subsp. *sulcatum*. Common; on sandstone.

Eriogonum inflatum. Common; on disturbed substrates.

Eriogonum insigne. Common; on disturbed soils with clay.

Eriogonum maculatum. Locally common; on limestone ridges.

Eriogonum microthecum var. *foliosum*. Common; on steep alluvium at high elevations.

Eriogonum thomasii. Common; in disturbed soils.

Eriogonum trichopes. Common; in washes, alluvium, and roadside gravels.

Eriogonum viscidulum. Locally common; in deep sands.

Oxytheca perfoliata. Rare; on sandy substrates.

Polygonum argyrocoleon. Common; adventive in rural areas.

Polygonum lapathifolium. Locally common; along cultivated fields.

Pterostegia drymarioides. Common; under ledges and in protected areas.

Rumex crispus. Common; naturalized, in deep sands of disturbed habitats.

Rumex hymenosepalus. Common; on dune sands.

Primulaceae

Samolus parviflorus. Common; along alkali springs and moist soils.

Ranunculaceae

Anemone tuberosa. Very rare; on limestone in protected, shady areas.

Delphinium parishii subsp. *parishii*. Common; on alluvial slopes.

Resedaceae

Oligomeris linifolia. Common; on alkali, moist soils.

Rosaceae

Cercocarpus intricatus. Common; on rocky limestone slopes of higher elevation.

Coleogyne ramosissima. Abundant; in Hidden Valley only.

Cowania mexicana var. *stansburiana.* Locally common; on north-facing washes at higher elevations.

Fallugia paradoxa. Locally common; in washes at high elevation.

Petrophytum caespitosum. Rare; on limestone outcrops at high elevation.

Prunus fasciculata. Common; in washes at low elevation.

Rubiaceae

Galium stellatum subsp. *eremicum.* Common; on rocky outcrops.

Rubia tinctoria. Very rare; adventive in disturbed habitats.

Rutaceae

Thamnosma montana. Uncommon; on sandstone substrates.

Salicaceae

Populus fremontii var. *fremontii.* Common; in moist areas and along river drainages.

Salix gooddingii var. *variabilis.* Uncommon; along irrigation canals and Muddy River.

Saururaceae

Anemopsis californica. Ubiquitous; in moist alkaline soils.

Scrophulariaceae

Antirrhinum filipes. Uncommon; in shrubbery at low elevation.

Castilleja chromosa. Uncommon; on alluvial slopes.

Mimulus bigelovii. Common; in washes and alluvial slopes.

Mohavea breviflora. Locally common; in gravels some years.

Mohavea confertiflora. Uncommon; on gravels.

Penstemon ambiguus. Common; on dune sands.

Penstemon bicolor subsp. *roseum.* Uncommon; in wash gravels.

Penstemon eatonii. Uncommon; on outcrops and gravels.

Penstemon palmeri. Common; on disturbed soils.

Solanaceae

Datura meteloides. Uncommon; in washes and disturbed areas.

Lycium andersonii. Uncommon; on alluvium or disturbed soils.

Lycium cooperi. Uncommon; in washes.

Lycium torreyi. Common; along Muddy River drainage.

Nicotiana glauca. Rare; introduction.

Nicotiana palmeri Uncommon; under rock outcrops.

Nicotiana trigonophylla. Uncommon; in outcrops and under crevices.

Physalis angulata var. *lanceifolia.* Rare; adventive in rural area.

Physalis crassifolia var. *crassifolia.* Rare; on outcrops.

Physalis lobata. Rare; in wash gravels.

Solanum elaeagnifolium. Common; naturalized in rural areas.

Tamaricaceae

Tamarix aphylla. Uncommon; on moist alkali soils.
Tamarix aralensis. Uncommon; in moist habitats.
Tamarix parviflora. Common; along alkaline habitats.
Tamarix ramosissima. Uncommon; on moist soils.

Urticaceae

Parietaria floridana. Uncommon; in shady rock crevices.

Verbenaceae

Lippia nodiflora. Rare; introduced in disturbed soils.

Viscaceae

Phoradendron californicum. Common; on *Prosopis* and *Acacia.*

Vitaceae

Vitis arizonica. Locally abundant; around springs and seeps.

Zygophyllaceae

Fagonia laevis. Locally common; on limestone outcrops.
Larrea tridentata. Ubiquitous and on many substrates.
Tribulus terrestris. Common; naturalized in disturbed soils.

ANTHOPHYTA—MONOCOTYLEDONEAE

Agavaceae

Agave utahensis var. *nevadensis.* Uncommon; on steep limestone cliffs at high elevation.
Yucca brevifolia. Introduction within the study area.
Yucca schidigera. Rare; on alluvial fans.
Yucca elata var. *utahensis.* Very rare; in protected wash.

Amaryllidaceae

Androstephium breviflorum. Rare; in sands.

Arecaceae

Washingtonia filifera. Common; at springs and seeps.

Cyperaceae

Cladium californicum. Rare; in alkali spring soils.
Cyperus strigosus. Uncommon; but locally dense along irrigation canals and Muddy River drainage.
Eleocharis macrostachya. Locally abundant; in alkaline meadows.
Eleocharis rostellata. Locally common; in alkaline meadows.
Scirpus maritimus. Common; in alkaline marshes and meadows.

Scirpus olneyi. Uncommon; on moist alkaline soils.
Scirpus robustus. Uncommon; on moist alkaline soils.

Hydrocharitaceae

Vallisneria americana. Abundant; in slow, thermal waters.

Iridaceae

Sisyrinchium bellum. Rare; in alkaline soils.

Juncaceae

Juncus balticus. Common; in moist habitats.

Liliaceae

Asparagus officinalis. Rare; introduced in rural areas.
Calochortus flexuosus. Uncommon; on limestone substrates.

Najadaceae

Najas marina. Rare; in thermal waters of springs.

Poaceae

Agropyron elongatum. Rare; adventive along alfalfa fields.
Aristida adscensionis. Uncommon; on disturbed habitats.
Aristida glauca. Rare; in disturbed areas.
Aristida parishii. Rare; on gravels and boulders.
Aristida purpurea. Uncommon; in gravels and sands.
Arundo donax. Common; naturalized along Muddy River drainage.
Avena fatua. Uncommon; introduced along fallow fields.
Avena sativa. Rare; introduced along fallow fields.
Bothriochloa barbinodis. Rare; on sandstone.
Bouteloua aristidoides. Common; on disturbed soils.
Bouteloua barbata. Common; in washes.
Bouteloua trifida. Rare; on alluvial slopes.
Bromus rigidus. Uncommon; adventive in disturbed habitats.
Bromus rubens. Abundant throughout the range.
Bromus tectorum. Abundant throughout the range.
Cenchrus pauciflorus. Uncommon; adventive, but spreading in rural areas.
Cynodon dactylon. Common; naturalized in rural areas.
Digitaria sanguinalis. Common; introduction, escaping from lawns.
Distichilis spicata var. *stricta.* Abundant; in alkaline meadows.
Echinochloa crus-galli. Common; adventive in rural areas.
Elymus triticoides. Rare; introduction, in alfalfa fields.
Enneapogon desvauxii. Uncommon; in sands.
Eragrostis cilianensis. Uncommon; in sands of wash.
Eriochloa contracta. Rare; adventive in rural area.
Eriochloa gracilis. Uncommon; adventive on disturbed soils.

TABLE 1. SUMMARY OF THE VASCULAR PLANT TAXA OF THE MUDDY MOUNTAINS, INCLUDING THE TEN LARGEST FAMILIES (LISTED IN DECREASING NUMBER, BY SPECIES).

Group	Number of families	Number of genera	Number of species	Number of non-natives
Vascular Cryptogams	1	2	3	0
Gymnosperms	1	1	3	0
Angiosperms	66	263	429	76
Total all groups	68	266	435	76
Dicots				
Asteraceae		55	78	
Fabaceae		11	23	
Brassicaceae		15	23	
Polygonaceae		6	20	
Chenopodiaceae		10	18	
Polemoniaceae		5	12	
Cactaceae		6	9	
Nyctaginaceae		7	8	
Rosaceae		6	6	
Monocots				
Poaceae		35	52	

Erioneuron pulchellum. Common; on desert pavement and washes.
Hilaria rigida. Common; in sandy soils.
Hordeum geniculatum. Common; introduction in rural areas.
Hordeum glaucum. Common; introduced in alfalfa fields.
Hordeum leporinum. Uncommon; introduced in pastures.
Hordeum vulgare. Common; introduction in rural waste places.
Muhlenbergia asperifolia. Rare; in alkaline soils.
Muhlenbergia porteri. Common; on alluvial slopes.
Oryzopsis hymenoides. Common; on sandy soils.
Paspalum distichum. Rare; adventive in alfalfa fields.
Phalaris caroliniana. Common; adventive in fallow fields.
Phragmites australis. Common; naturalized in moist soils.
Poa arida. Uncommon; in arroyos.
Polypogon monspeliensis. Common; naturalized along irrigation canals and Muddy River.
Schismus arabicus. Common; on disturbed soils.
Schismus barbatus. Common; on disturbed soils, especially sands.
Setaria lutescens. Common; adventive in pastures.
Sitanion hystrix. Uncommon; on alluvial slopes.
Sitanion jubatum. Common; on alluvial slopes.
Sorghum bicolor. Rare; introduction along farm roads.
Sorghum halepense. Common; introduced in disturbed soils.
Sporobolus airoides. Common; on moist alkaline meadow soils.
Sporobolus flexuosus. Uncommon; in wash gravels.

TABLE 2. GROWTH FORMS OF TAXA FOUND IN THE MUDDY MOUNTAINS, CLARK COUNTY, NEVADA.

Growth form	No. of species	% of total flora
Annual	184	42.3
Biennial	8	1.8
Perennial herb	146	33.6
Stem succulent	9	2.1
Shrub	71	16.3
Sub-tree to tree	17	3.9
Totals	435	100.0

Stipa speciosa. Rare; in washes.
Tridens muticus. Uncommon; on sandstone.
Triticum aestivum. Rare; introduced in disturbed habitats.
Vulpia octoflora. Common; on many substrates.

Potamogetonaceae

Potamogeton pectinatus. Common; in thermal alkaline waters.
Ruppia maritima. Common; in thermal alkaline waters.

Typhaceae

Typha angustifolia. Abundant; in alkaline waters.

Zannichelliaceae

Zannichellia palustris. Common; in quiet thermal waters.

DISCUSSION

A summary of the vascular flora of the Muddy Mountains is given in Table 1. The 76 non-indigenous species comprise 17.6% of the total flora. The ten largest families (Table 1) represent 57% of the total flora, with Asteraceae comprising 18%. Growth forms for the Muddy Mountain flora are listed in Table 2. The flora is dominated by annuals (42%) and perennial herbs (34%). Excluding introduced taxa, no trees occur in the range. An analysis of vegetation distribution patterns was made based on edaphic versus topographic control. Edaphic and topographic subdivisions were based on field notes, along with Beatley (1976), Munz (1974), and Thorne et al. (1981). Final assignment of a taxon to a substrate was often arbitrary and was done with some hesitation. Because of the transitional location of the study area, some species specific to one substrate elsewhere, were not so restricted in the Muddy Mountains. For example, Munz (1974) and Beatley (1976) list *Mortonia utahensis* as a calciphile. In the Muddy Mountains it occurs only on Aztec sandstone and its derived soils.

Edaphic categories include borates, alkali, sandstone, eolian sand, carbonates and semi-aquatic. Topographic categories include cliff, desert pavement, boulder outcrops (providing shade) and three types of perturbation: alluvium-talus, washes and human. Some conditions tend to occur together and share significant portions of the data. For example, many cliffs are limestone, and 14 taxa are restricted to limestone cliffs. Low-lying areas were often both alkaline and semi-aquatic; those habitats support 21 taxa not found elsewhere. About 6% of the flora shows little influence of substrate and topography on its distribution. Gypsum, sandstone, and eolian sands, however, support a large number of edaphically restricted species accounting for a total of 20% of the total flora.

The transitional nature of the Muddy Mountain flora becomes more apparent when one looks at species distributions that extend beyond their known ranges. Three legumes, *Cassia armata, Dalea mollis,* and *D. mollissima* reach northward into the area, presumably protected by the warm Colorado River corridor and south-facing exposures.

Some Great Basin taxa appearing to reach their southern limits include *Astragalus flavus* var. *candicans, Psorothamnus polydenius, Enneapogon desvauxii,* and *Yucca elata* var. *utahensis. Yucca elata* var. *utahensis,* apparently a Texas-Plains species, is found in southwest Utah (Meyer 1976, Higgins 1967) and in northern Arizona (Kearney and Peebles 1960) along the Grand Canyon, but does not extend farther west in Nevada or California. This species may also owe its existence to the protection of the Virgin River–Colorado River gorge. *Psoralea castorea,* a northern Rocky Mountain species, extends just to the northern boundary of the Muddy Mountains.

Taxa of Pacific Coast/Cismontane California (Thorne et al. 1981) that reach beyond the Kingston Range into the Muddy Mountains are *Bouteloua aristidoides, Sarcostemma cynanchoides* var. *hartwegii, S. hirtellum,* and *Trichoptilium incisum.* The first three extend at least as far as the McCullough Range in Nevada and occur on sandy soils. *Trichoptilium* is reported in gravels, washes, and bajadas in Thorne et al. (1981) and Kearney and Peebles (1960). It occurs throughout the Muddy Mountains usually on limestone rock.

Apparently unique to the Muddy Mountains are the sympatric distributions of *Psorothamnus fremontii* with *P. polydenius* and *Acamptopappus shockleyi* with *A. sphaerocephalus.* Although the two *Psorothamnus* species occur together, *P. fremontii* flowers earlier than *P. polydenius.* Along Gale Hills, at the southern end of Muddy Mountain, *P. polydenius* shows preference for heavy, lacustrine deposits and is somewhat spatially segregated from *P. fremontii. Psorothamnus polydenius* is not known farther south. *Acamptopappus shockleyi* and *A. sphaerocephalus* hybridize and are often difficult to identify. *Acamptopappus shockleyi* occurs on the Nevada Test Site (Beatley 1976), in the Spring Mountains (Clokey 1951), and in the Beaver Dam Mountains (Higgins 1967), and is known from the Mormon and Virgin

Mountains (pers. observ.). It does not occur with *A. sphaerocephalus* in any of these nearby ranges. This sympatry is unknown in the McCullough Range just 20 km south of the Muddy Mountains.

The overall flora is not significantly similar to other Great Basin or Sonoran floras. Great Basin elements become evident at higher elevations in the Muddy Mountains; however, they are only expressed as a sagebrush belt. There is no occurrence of *Yucca brevifolia* at the *Coleogyne* interface anywhere in the range nor is there a single true arborescent form, i.e., no *Juniperus* or *Pinus monophylla,* excluding introduced taxa. This is particularly interesting because *Yucca brevifolia* occurs in a dense stand only 10 km north of the range. Nearby rat midden analysis at Gypsum Cave at 610 m indicates significant amounts of pine and juniper pollen and macrofossils dated at 12,000 yrs B.P., as well as an ". . . abundance of leaf fragments of the Joshua Tree, which no longer grows in the vicinity of the cave . . ." (Wells and Berger 1967). Because all three species occur in surrounding areas and occurred historically within the range itself (Wells and Berger 1967), their current paucity is not a dispersal failure. Precipitation requirements for establishment of seedlings may contribute to the anomaly. Possibly orographic effects may be instrumental. The Muddy Mountains are under rainshadow effects of the Spring and Sheep Ranges on the west and the Virgin Mountains to the southeast. The Virgin Mountains, with a maximum elevation of 2317 m, form a significant barrier for summer showers (pers. observ.). Despite relatively low elevation, the Virgin Mountains support a relict population of *Abies concolor* and *Pinus ponderosa* (Armstrong 1967). Characteristic woodland shrub species such as *Artemisia tridentata, Cercocarpus intricatus, Cowania mexicana* var. *stansburiana, Fallugia paradoxa, Symphoricarpos longiflorus* and *Petrophytum caespitosum* still persist at high elevation in the Muddy Mountains. According to Wells and Berger (1967), pinyon-juniper woodlands descended to approximately 1100 m on limestone and co-existed with semidesert shrubs during the late Pleistocene. A midden in the North Muddy Mountains at 550 m (Wells and Berger 1967) contained abundant *Juniper* and associated woodland shrub species but had no pinyon pine remains. Comparison of land masses above 1100 m shows 40.3 km^2 and 5.2 km^2 respectively, for the Virgin and Muddy Mountains. In the Muddy Mountains, the land mass at 1100 m and above may have been too small to support a confined woodland population in the increasingly warm Pleistocene climate.

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FLORISTIC CHECKLIST FOR THE HEADWATERS BASIN AREA OF THE NORTH FORK OF THE AMERICAN RIVER, PLACER COUNTY, CALIFORNIA

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ABSTRACT

A species list of vascular plants was compiled for an 80 km^2 area, at elevations of 1770–2745 m, on the west slope of the central Sierra Nevada Mountains. The basin area is topographically and geologically diverse, and it supports a rich flora of more than 500 taxa. The area is relatively undisturbed and includes protected portions suitable for long-term research.

The headwaters of the North Fork of the American River, and of its tributary, Onion Creek, arise in an 80 km^2 basin in Placer County, centering on 39°15′N latitude and 120°20′W longitude. The basin is geologically and topographically diverse, with elevations ranging from 1770 m to 2745 m (Fig. 1). Slopes are typically 10–40%. Geological substrates include Mesozoic granitics of Jurassic or Triassic age, and Tertiary lavas (Burnett and Jennings 1962).

The basin contains two protected areas that have potential for long-term study. One is the Onion Creek Experimental Forest, about 13 km^2 in area, which is administered by the United States Forest Service's Pacific Southwest Forest and Range Experiment Station. This forest has been listed by The Institute of Ecology–UC Davis (1977, 1981) as an Experimental Ecological Reserve, one of 96 in the nation and 11 in California. These Reserves have been chosen on the basis of site quality, protection, stability, and depth of background information available. The National Science Foundation has begun a program to encourage long-term research in this network of Reserves. The other is the Chickering-American River, 7 km^2 in area, which recently has been added to the University of California's Natural Land and Water Reserve System, as well as the Institute of Ecology's system. The University encourages long-term studies on such properties.

Mr. Sherman Chickering has been compiling a flora for part of the basin for many years. From 1979 to 1982, the authors have been extending that work, collecting throughout the eastern and northern ⅔ of the basin, >1770 m, with particular attention to the two protected areas identified above.

GENERAL SITE DESCRIPTION

Although the span of elevation and microenvironment makes a climatic summary difficult, data from nearby weather stations allow one

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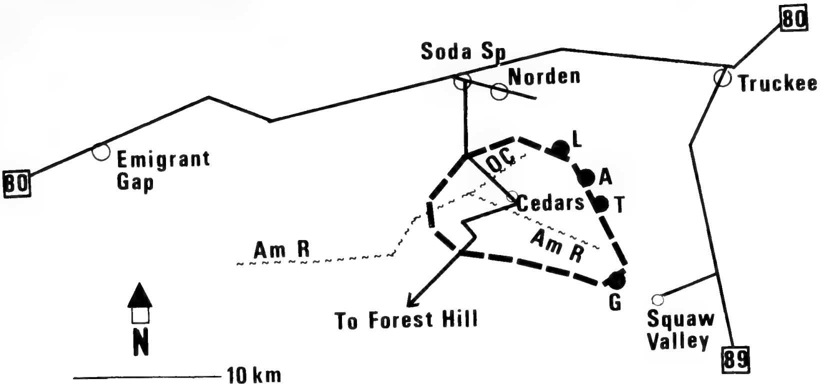

FIG. 1. Headwaters basin area of the North Fork of the American River (Am R) and of its tributary, Onion Creek (OC), as shown by dashed lines. The crest of the Sierra Nevada runs along the eastern edge of the basin, and major peaks are abbreviated: L for Mt. Lincoln (2555 m), A for Anderson Peak (2646 m), T for Tinkers Knob (2727 m), and G for Granite Chief (2745 m). The western edge of the basin corresponds to Heath Springs at an elevation of 1555 m, but for the purposes of the checklist we used a minimum elevation of 1770 m.

to make some climatic generalizations. The United States Forest Service currently maintains a Central Sierra Snow Laboratory at Soda Springs, 6 km north of the basin at an elevation of 2100 m. Using weather data from that station (Smith 1978a, b), from the National Climatic Center (Anonymous 1981), and from a review by Major (1977), we generalize as follows:

Mean annual precipitation is 129 cm, more than 90% of which falls from mid-October to early June; much of this falls as snow. Average snowpack duration is 192 days, and average snowpack depth is 310 cm. Half the years of record show two peak periods of precipitation—early December and mid-March—and half the years show a single peak in early January. Mean annual temperature is 5°C, mean daily maximum for July is 28°C, and mean daily minimum for January is −10°C.

Judging from the recent Forest Service draft of a third order soil survey of the basin (Sutter 1981) and published soil surveys of the adjacent Tahoe Basin (Rogers 1974), major soil series include: 1) Tinker and Tallac on glacial till; 2) Ahart, Meiss, and Waca on volcanics; and 3) Skeletal Granitic Rock Land types. Tinker and Tallac are Inceptisols, well-drained, brown loams, slightly acid (pH 6), 50–150 cm in depth. Meiss is an Inceptisol on slightly weathered volcanic rock, and is a pale brown, neutral sandy loam. Ahart and Waca are Inceptisols on weathered tuff, 59–100 cm in depth, and are brown, acidic, sandy loams. These volcanics are well- to excessively well-drained.

Major forest communities in the basin include white fir-mixed conifer forest, red fir forest, and lodgepole pine forest. Narrow riparian bands with *Populus trichocarpa, P. tremuloides, Alnus tenuifolia,* and *Salix* spp., or wet meadows dominate drier sites. The red fir and red fir-white fir forests have been quantitatively described for Onion Creek Experimental Forest by Talley (1977); all other communities are similar to those described for the Sierra as a whole by Rundel et al. (1977).

About half the area within the basin is part of Tahoe National Forest. About 25% of the area is held by private home owners who are seasonally present, their homes clustered in a central area called "The Cedars" (Fig. 1). About 10% of the area is in the University of California's Chickering-American River Reserve, and the remainder is owned by American Forest Products and the Southern Pacific Company.

Overall, the effects of human disturbance on the basin have been modest. Logging has occurred in two sections. Some jeep trails and weirs have been constructed in the Onion Creek Experimental Forest and a few other roads exist throughout the basin. Sheep began to graze in the basin in the 19th century, and they still graze in some sections in some years. The Cedars homesites have been present since the start of this century. Old photographs from that time show a more open, pine-dominated forest at 2000 m than the dense, fir-dominated forest at present. Visitors are attracted to the basin for recreational purposes by: 1) the Pacific Crest Trail, which skirts the southeastern portion of the basin; 2) by two unimproved campsites near Onion Creek that are occupied during deer hunting season; and 3) by a dirt road that runs through the basin, connecting Soda Springs to Forest Hill, about 45 km apart.

THE CHECKLIST

Families, genera, and species are listed as in Munz (1959). Nomenclature follows Munz (1959, 1968). The notation "chk" following a taxon means that a specimen is deposited only in the personal collection of Sherman Chickering. All other taxa have voucher specimens deposited with the herbarium of the Botany Department at the University of California, Davis (DAV). After each listed taxon found above 2050 m we have noted floristic affinities according to Stebbins (1982): "1" represents circumboreal, "2" for Lowland California, "3" for Great Basin Desert, and "4" for Old Cordilleran element. We found that 359 out of our complete list of 547 taxa could be associated this way. Of these 359 taxa, 83 (23%) have circumboreal affinities, 91 (26%) Lowland California, 42 (12%) Great Basin, and 142 (39%) Old Cordilleran affinities. This is roughly comparable to the proportions from the whole Sierra Nevada flora cited by Stebbins, except that the Lowland California element is better represented, and the Great Basin Desert less so (OC = 39%, CB = 26%, LC = 19%, GB = 16%) (Stebbins 1982).

Nine species of rare and endangered plants have been determined as potentially occurring within the basin, according to California Natural Diversity Data Base maps: *Berberis sonnei, Elodea brandegeae, Erigonum umbellatum* var. *torreyana, Glyceria grandis, Lewisia pygmaea* subsp. *longipetala, Rorippa subumbellata, Silene invisa, Veronica cusickii,* and *Viola tomentosa.* However, only one of these, *Veronica cusickii,* has been collected in the basin in recent years. Its status is listed as rare in California but common elsewhere. We have not yet found any other of the nine species, but it is possible, given the high plant diversity in the Headwaters Basin, that further searches may result in discovery of new populations.

We have no doubt that the checklist is incomplete, and that additional taxa will be found by others in the future. Nevertheless, we believe that the great majority of all taxa are recorded in this list. A total of 61 families of vascular plants are found—one-third of all families in California—with 240 genera and 547 taxa of specific or subspecific rank. Table 1 lists the 13 largest families and the 17 largest genera. The nine largest families acccounted for more than half of all taxa, and the 18 largest genera accounted for over one-fourth of all taxa. Considering that there are about 5000 taxa in the entire state of California (Raven 1977), an area of about 40,500,000 ha, we can conclude that this 8000 ha basin is exceptionally rich. This richness is paralleled by the basin's animal diversity. More than 100 species of birds have been observed in this area (Beedy 1981), and preliminary observations indicate a high diversity of reptiles, amphibians, and insects (Barry, Daley, and Shapiro, pers. comm.).

LYCOPHYTA

Selaginellaceae

Selaginella watsoni 4.

SPHENOPHYTA

Equisetaceae

Equisetum arvense.
Equisetum funstoni.

PTEROPHYTA

Pteridaceae

Athyrium alpestre var. *americanum* 1 chk.
Cheilanthes gracillima 3.
Cryptogramma acrostichoides 1.
Onychium densum 4 chk.
Pellaea brachyptera.
Pellaea breweri 4 chk.
Pellaea bridgesii.
Pteridium aquilinum var. *pubescens* 1.

Aspidiaceae

Cystopteris fragilis 1.

TABLE 1. THE 13 LARGEST FAMILIES AND THE 17 LARGEST GENERA OF THE VASCULAR PLANT FLORA OF THE HEADWATERS BASIN AREA.

Families with 12 or more taxa		Genera with more than 5 taxa	
Family	Taxa	Genus	Taxa
Asteraceae	81	*Carex*	14
Poaceae	39	*Eriogonum*	12
Scrophulariaceae	38	*Viola*	11
Polygonaceae	28	*Arabis*	11
Brassicaceae	25	*Epilobium*	10
Fabaceae	24	*Polygonum*	10
Polemoniaceae	22	*Penstemon*	9
Cyperaceae	21	*Lupinus*	8
Rosaceae	20	*Mimulus*	8
Saxifragaceae	20	*Ribes*	8
Onagraceae	17	*Arnica*	8
Ranunculaceae	15	*Trifolium*	7
Apiaceae	12	*Poa*	7
		Artemisia	6
		Potentilla	6
		Allium	6
		Ranunculus	6

Total taxa for the Headwaters Basin: 540.
Total genera for the Headwaters Basin: 241.
Total families for the Headwaters Basin: 62.

CONIFEROPHYTA

Pinaceae

Abies concolor.
Abies magnifica 4.
Pinus albicaulis 4.
Pinus jeffreyi 4.
Pinus lambertiana.
Pinus monticola 1.
Pinus murrayana 4.
Pseudotsuga menziesii.
Tsuga mertensiana 4.

Cupressaceae

Calocedrus decurrens.
Juniperus occidentalis 3.

ANTHOPHYTA—MONOCOTYLEDONEAE

Amaryllidaceae

Allium amplectens.
Allium campanulatum 2.
Allium obtusum 2.
Allium parvum chk.
Allium platycaule.
Allium tribracteatum 3.
Brodiaea elegans.
Brodiaea hyacinthina 2.
Brodiaea lutea var. *analina* 2.

Cyperaceae

Carex athrostachya 4.
Carex aquatilis 1.
Carex exserta 4.
Carex heteroneura 1.
Carex jonesii 4.
Carex multicostata 4.
Carex nervina 4.
Carex nigricans 1.
Carex raynoldsii 1.
Carex rossii 4.
Carex scopulorum 1.
Carex straminiformis 4.
Carex vernacula 1.
Scirpus congdoni 1.

Iridaceae

Iris missouriensis 2 chk.
Sisyrinchium idahoense 3 chk.

Juncaceae

Juncus chlorocephalus 4.
Juncus drummondii 4.
Juncus mexicanus 4.
Juncus orthophyllus 2.
Juncus parryi 4.
Luzula subcongesta 1 chk.

Liliaceae

Calochortus leichtlinii 2.
Chlorogalum pomeridianum.
Fritillaria atropurpurea 2 chk.
Fritillaria recurva chk.
Lilium parvum 2.
Lilium pardalinum chk.
Lilium washingtonianum.
Smilacina racemosa var. *amplexicaulis* 4.
Smilacina stellata 1.
Veratrum californicum 1.
Zigadenus venosus 4.

Orchidaceae

Corallorhiza maculata 4.
Corallorhiza striata.
Goodyera oblongifolia.
Habenaria dilatata var. *leucostachys* 1.
Habenaria sparsiflora 1.
Habenaria unalascensis 1.
Spiranthes romanzoffiana 1 chk.

Poaceae

Agropyron trachycaulum 4.
Agrostis scabra 4.
Agrostis variabilis 4.
Bromus marginatus 2.
Bromus orcuttianus.
Bromus suksdorfii 2.
Bromus tectorum.
Calamagrostis canadensis 1.
Dactylis glomerata.
Danthonia californica 2.
Danthonia unispicata.
Deschampsia danthonioides 2.
Deschampsia elongata.
Elymus glaucus 4.
Glyceria elata 4.
Glyceria striata 4.
Hordeum brachyantherum 1.
Hordeum californicum.
Lolium perenne.
Melica stricta 4.
Muhlenbergia filiformis 4.
Panicum pacificum.
Phleum alpinum 1.
Poa ampla.

Poa bolanderi 2.
Poa epilis 4.
Poa fendleriana 4.
Poa incurva 4.
Poa palustris.
Poa pratense 1.
Sitanion hystrix 4.
Stipa californica 3.
Stipa columbiana 3.
Stipa lemmonnii.
Stipa occidentalis 3.
Stipa williamsii.
Trisetum cernuum var. *canescens* 1.
Trisetum spicatum 1.
Triticum aestivum.

ANTHOPHYTA—DICOTYLEDONEAE

Aceraceae

Acer glabrum 1.

Apiaceae

Angelica breweri 1.
Cicuta douglasii 1.
Heracleum lanatum 1.
Ligusticum grayi 1.
Lomatium dissectum chk.
Osmorhiza chilensis 2.
Perideridia bolanderi 2.
Perideridia parishii 2.
Pteryxia terebinthina var. *californica* 3.
Sanicula graveolens 2.
Sanicula tuberosa 2.
Sphenosciadium capitellatum 2.

Apocynaceae

Apocynum androsaemifolia 4 chk.
Apocynum pumilum.

Asclepiadaceae

Asclepias cordifolia chk.

Asteraceae

Achillea lanulosa 1.
Adenocaulon bicolor.
Agoseris glauca var. *laciniata* 4 chk.
Agoseris glauca var. *monticola* 4 chk.
Agoseris grandiflora chk.
Agoseris retrorsa.
Anaphalis margaritacea 1.
Antennaria alpina var. *media* 4 chk.
Antennaria rosea 4.
Antennaria umbrinella chk.
Arnica amplexicaulis 4 chk.
Arnica chamissonis.
Arnica cordifolia 4 chk.
Arnica discoidea var. *alata.*
Arnica longifolia 4 chk.
Arnica mollis 4 chk.
Arnica nevadensis 4 chk.
Arnica parryi subsp. *sonnei* 4.
Artemisia arbuscula 3.
Artemisia cana 3 chk.
Artemisia douglasiana.
Artemisia ludoviciana 3.
Artemisia rothrockii 3.
Artemisia tridentata 3.
Aster alpigenus subsp. *andersonii* 4 chk.
Aster ascendens chk.
Aster integrifolius 4 chk.
Aster occidentalis 4.

Aster radulinus chk.
Balsamorhiza sagittata 4.
Brickellia grandiflora 3 chk.
Brickellia greenei.
Chaenactis douglasii 4.
Chaenactis nevadensis 4 chk.
Chrysopsis breweri 4.
Chrysopsis villosa var. *hispida.*
Chrysothamnus nauseosus 3.

Circium andersonii 3.
Circium californicum chk.
Circium vulgare.
Crepis acuminata 4 chk.
Crepis modocensis 4 chk.
Crepis occidentalis subsp. *conjuncta* 4 chk.
Erigeron coulteri 4 chk.
Erigeron peregrinus subsp. *callianthemus* 4.
Erigeron barbellulatus 4 chk.
Erigeron philadelphicus.
Eriophyllum lanatum 2.
Eupatorium occidentale 4.
Gnaphalium californicum.
Gnaphalium palustre 2.
Haplopappus acaulis 3 chk.
Haplopappus bloomeri 4 chk.
Haplopappus suffruticosus 4 chk.
Helianthella californica var. *nevadensis.*
Hieracium albiflorum 4.
Hieracium gracile 4.
Hieracium horridum chk.
Lagophylla ramosissima.
Machaeranthera canescens 3 chk.
Machaeranthera shastensis var. *glossophylla* chk.
Madia elegans 2.
Madia glomerata chk.
Madia gracilis chk.
Madia minima 2.
Microseris nutans 4.
Nothocalais alpestris 4 chk.
Raillardella argentea 4 chk.
Senecio canus 4 chk.
Senecio integerrimus var. *major* 4.
Senecio triangularis 4.
Solidago californica 1.
Solidago canadensis subsp. *elongata* 1 chk.
Solidago multiradiata chk.
Stephanomeria lactucina 3.
Taraxacum laevigatum.
Taraxacum officinale.
Tragopogon dubius.
Whitneya dealbata.
Wyethia mollis 2.

Brassicaceae

Arabis breweri.
Arabis divaricarpa chk.
Arabis drummondii chk.
Arabis hirsuta.
Arabis holboellii var. *pendulocarpa.*
Arabis holboellii var. *retrofracta* 4.
Arabis lemmonii chk.
Arabis lyallii 4.
Arabis platysperma 4.
Arabis puberula chk.
Arabis rectissima chk.
Athysanus pusillus chk.
Barbarea orthoceras.
Cardamine breweri 4.
Cardamine lyallii.
Descurainia richardsonii 3.

Draba densifolia 4 chk.
Erysimum capitatum.
Erysimum perenne 2 chk.
Lepidium densiflorum.
Lepidium virginicum var. *pubescens.*
Lesquerella occidentalis chk.
Phoenicaulis cheiranthoides 3.
Streptanthus tortuosus 3.
Thysanocarpus curvipes.

Betulaceae

Alnus tenuifolia 1.

Boraginaceae

Cryptantha nubigena 3.
Cryptantha simulans.
Cryptantha torreyana 2.
Hackelia jessicae 4.
Hackelia longituba 4.
Hackelia nervosa chk.
Plagiobothrys cognatus.
Plagiobothrys hispidulus 2.

Caprifoliaceae

Lonicera conjugialis 1.
Sambucus caerulea 1.
Sambucus microbotrys 1 chk.
Symphoricarpos acutus 2.
Symphoricarpos parishii 4.
Symphoricarpos vaccinoides 4.

Caryophyllaceae

Arenaria douglasii chk.
Arenaria kingii var. *glabrescens* 4.
Arenaria nuttallii subsp. *gracilis* 4 chk.
Arenaria pumicola var. *californica* 4 chk.
Silene douglasii 2.
Silene menziesii 4.
Silene montana.
Spergularia rubra.
Stellaria longipes 1.

Chenopodiaceae

Chenopodium atrovirens 3.
Chenopodium incognitum 3.

Convolvulaceae

Convolvulus malacophyllus chk.

Cornaceae

Cornus occidentalis × *C. californica* 1.
Cornus stolonifera 1.

Crassulaceae

Sedum lanceolatum 4.
Sedum obtusatum 4.
Sedum rosea subsp. *integrifolium.*

Cuscutaceae

Cuscuta californica 2.

Ericaceae

Arctostaphylos nevadensis 2.
Arctostaphylos patula 2.
Cassiope mertensiana 1.
Kalmia polifolia var. *microphylla* 1.
Ledum glandulosa 1 chk.
Leucothoe davisiae 4.
Phyllodoce breweri 1.

Euphorbiaceae

Euphorbia serpyllifolia

Fabaceae

Astragalus austinae chk.
Astragalus whitneyi 3.
Lotus crassifolius 2.
Lotus nevadensis 2.
Lotus oblongifolius 2.
Lotus pinnatus chk.
Lotus purshianus 2.
Lupinus albicaulis 2.
Lupinus andersonii var. *apertus* 2.
Lupinus arbustus subsp. *silvicola* 4 chk.
Lupinus caudatus 3.
Lupinus latifolius chk.
Lupinus lyallii 4 chk.
Lupinus meionanthus 4 chk.
Lupinus polyphyllus subsp. *superbus* 2.
Medicago lupulina chk.
Medicago sativa.
Trifolium cyathiferum 2.
Trifolium longipes 4.
Trifolium microcephalum 2.
Trifolium monanthum var. *parvum* 2.
Trifolium pratense chk.
Trifolium productum 4.
Trifolium repens chk.

Fagaceae

Chrysolepis sempervirens 2.
Quercus chrysolepis var. *nana* × *Q. vaccinifolia.*
Quercus kelloggii.
Quercus vaccinifolia 2.

Fumariaceae

Dicentra uniflora 4.

Hydrophyllaceae

Draperia systyla.
Hesperochiron pumilus 3 chk.
Hydrophyllum capitatum var. *alpinum.*
Hydrophyllum occidentale 3.
Nama lobbii.
Nemophila spatulata 2.
Phacelia frigida subsp. *dasyphylla* chk.
Phacelia hydrophylloides 2 chk.
Phacelia marcescens.
Phacelia mutabilis 2.
Phacelia ramosissima.

Hypericaceae

Hypericum anagalloides 2.

Lamiaceae

Agastache urticifolia 2.
Monardella odoratissima subsp. *glauca* 2.
Monardella odoratissima subsp. *pallida* chk.
Prunella vulgaris subsp. *lanceolata* chk.
Scutellaria californica.
Stachys rigida 2 chk.
Trichostema oblongum.

Linaceae

Linum perenne subsp. *lewisii*.

Loasaceae

Mentzelia dispersa chk.

Loranthaceae

Arceuthobium douglasii.

Malvaceae

Sidalcea glaucescens 2 chk.
Sidalcea oregana.
Sidalcea oregana subsp. *spicata* 2.

Onagraceae

Boisduvalia densiflora 2 chk.
Circaea alpina var. *pacifica*.
Epilobium adenocaulon 4.
Epilobium angustifolium 4.
Epilobium brevistylum chk.
Epilobium glaberrimum 4 chk.
Epilobium glandulosum chk.
Epilobium hornemannii chk.
Epilobium obcordatum 4.
Epilobium oregonense 4.
Epilobium paniculatum.
Epilobium pringleanum 4.
Gayophytum diffusum 4.
Gayophytum humile 4.
Gayophytum nuttallii chk.
Zauschneria californica subsp. *latifolia* 2.

Orobanchaceae

Orobanche californica var. *corymbosa* chk.
Orobanche fasciculata chk.
Orobanche grayana.
Orobanche uniflora var. *purpurea* chk.
Orobanche uniflora var. *sedi* chk.

Paeoniaceae

Paeonia brownii 4.

Plantaginaceae

Plantago lanceolata.
Plantago major.

Polemoniaceae

Allophyllum integrifolium 2.
Allophyllum violaceum chk.
Collomia grandiflora 2.
Collomia linearis 2 chk.
Collomia tinctoria 2.
Gilia capillaris 2.
Gilia leptalea 2.
Gilia leptalea subsp. *bicolor*.
Ipomopsis aggregata chk.
Ipomopsis aggregata subsp. *attenuata* 4 chk.
Ipomopsis congesta subsp. *montana* 4 chk.
Leptodactylon pungens subsp. *pulchriflorum* 2.
Linanthus ciliatus 2.
Linanthus montanus.

Navarretia breweri 2.
Navarretia divaricata 2.
Navarretia minima.
Navarretia propinqua.
Phlox diffusa 3.
Phlox gracillis chk.
Polemonium californicum 4.
Polemonium pulcherrimum 4 chk.

Polygonaceae

Eriogonum incanum.
Eriogonum lobbii 4.
Eriogonum marifolium chk.
Eriogonum nudum 2.
Eriogonum nudum var. *deductum*.
Eriogonum ovalifolium subsp. *vineum* 3 chk.
Eriogonum rosense chk.
Eriogonum spergulinum var. *reddingianum* 2.
Eriogonum umbellatum subsp. *covillei* 4.
Eriogonum umbellatum var. *umbellatum* 4.
Eriogonum ursinum chk.
Eriogonum wrightii subsp. *subscaposum* 3.
Oxyria digyna chk.
Polygonum bistortoides chk.
Polygonum davisiae 1.
Polygonum douglasii 1.
Polygonum douglasii var. *johnstonii* chk.
Polygonum kelloggii 4.
Polygonum lapathifolium.
Polygonum minimum 4.
Polygonum phytolaccaefolium 1.
Polygonum shastense 1.
Polygonum spergulariaeforme chk.
Rumex acetosella chk.
Rumex angiocarpus.
Rumex crispus chk.
Rumex paucifolius 1.
Rumex triangulivalvis.

Portulacaceae

Calyptridium umbellatum.
Claytonia lanceolata 4 chk.
Lewisia nevadensis 4.
Lewisia triphylla 4.
Montia chamissoi 4 chk.
Montia parvifolia 4 chk.
Montia perfoliata.
Montia perfoliata var. *depressa*.

Primulaceae

Dodecatheon alpinum subsp. *majus* 4.
Dodecatheon jeffreyi 4 chk.

Pyrolaceae

Allotropa virgata chk.
Chimaphila menziesii.
Pleuricospora fimbriolata 2.
Pterospora andromedea 4.
Pyrola asarifolia var. *purpurea* 1 chk.
Pyrola picta 1.
Sarcodes sanguinea 4.

Ranunculaceae

Aconitum columbianum 1.
Anemone drummondii 4 chk.
Anemone occidentalis 1 chk.
Aquilegia formosa 4.
Caltha howellii 1.
Delphinium depauperatum 2.
Delphinium sonnei.
Ranunculus alismaefolius var. *alismellus* 4 chk.
Ranunculus alismaefolius var. *hartwegii* chk.
Ranunculus cymbalaria chk.

Ranunculus eschscholtzia 4 chk.
Ranunculus occidentalis var. *ultramontanus* 2.
Ranunculus uncinatus.
Thalictrum fendleri 1.

Rhamnaceae

Ceanothus cordulatus 2.
Ceanothus fresnensis × chk.
Ceanothus integerrimus.
Ceanothus prostratus chk.
Ceanothus velutinus.

Rosaceae

Amelanchier pallida 1.
Fragaria californica chk.
Geum canescens 4.
Holodiscus boursieri 4.
Horkelia fusca subsp. *parviflora* 2.
Horkelia fusca subsp. *pseudocapitata* 2 chk.
Ivesia shockleyi 3.
Potentilla breweri 1.
Potentilla flabellifolia 1 chk.
Potentilla fruticosa 1.
Potentilla glandulosa subsp. *glandulosa* chk.
Potentilla glandulosa subsp. *nevadensis*.
Potentilla gracilis.
Prunus emarginata 1.
Purshia tridentata 3.
Rubus parviflorus 4.
Sibbaldia procumbens 1 chk.
Sorbus californica 1 chk.
Spiraea densiflora 1.

Rubiaceae

Galium aparine.
Galium bifolium 4.
Galium grayanum.
Galium hypotrichium chk.
Galium trifidum var. *pusillum*.
Galium triflorum.
Kelloggia galioides 4.

Salicaceae

Populus tremuloides 1.
Populus trichocarpa 1.
Salix eastwoodiae 1.
Salix jepsonii 1.
Salix lemmonii 1.
Salix orestera 1.
Salix scouleriana 1.

Saxifragaceae

Heuchera micrantha var. *erubescens*.
Heuchera rubescens var. *glaucescens* chk.
Lithophragma bulbifera chk.
Lithophragma glabrum 2.
Lithophragma parviflora.
Mitella breweri 1.
Parnassia fimbriata chk.
Parnassia palustris 1 chk.
Ribes cereum.
Ribes inebrians 4.
Ribes lasianthum 2.
Ribes montigenum 4 chk.
Ribes nevadense 2 chk.
Ribes roezlii 2.

Ribes viscosissimum 4.
Ribes viscosissimum var. *halli.*
Saxifraga aprica 2.
Saxifraga bryophora 1.
Saxifraga nidifica 2.
Saxifraga odontoloma 1 chk.

Scrophulariaceae

Castilleja applegatei 2.
Castilleja miniata 4.
Castilleja nana 3.
Castilleja piersonii chk.
Castilleja pilosa 3.
Castilleja pruinosa 3.
Collinsia parviflora 2.
Collinsia torreyi var. *torreyi* chk.
Collinsia torreyi var. *wrightii* 2.
Cordylanthus pilosus subsp. *bolanderi.*
Cordylanthus tenuis.
Mimulus breweri 3.
Mimulus cardinalis.
Mimulus guttatus 2.
Mimulus lewisii 4.
Mimulus microphyllus chk.
Mimulus moschatus 4.
Mimulus primuloides 4.
Mimulus tilingii 2.
Mimulus torreyi 2.
Orthocarpus copelandii var. *cryptanthus* 3.
Orthocarpus hispidus 2.
Pedicularis attolens 1.
Pedicularis groenlandica 1.
Pedicularis semibarbata 1.
Penstemon deustus 4.
Penstemon gracilentus.
Penstemon heterodoxus 4 chk.
Penstemon laetus.
Penstemon laetus subsp. *roezlii* 2 chk.
Penstemon lemmonii.
Penstemon newberryi 4.
Penstemon oreocharis 4.
Penstemon speciosus 3 chk.
Scrophularia californica.
Verbascum thapsus.
Veronica cusickii 1 chk.
Veronica serpyllifolia var. *humifusa* 1.

Solanaceae

Solanum xantii var. *montanum* chk.

Urticaceae

Urtica holosericea.

Valerianaceae

Valeriana capitata subsp. *capitata* 1 chk.

Verbenaceae

Verbena hastata chk.
Verbena officinalis.

Violaceae

Viola adunca chk.
Viola bakeri 4.
Viola beckwithii 3 chk.
Viola glabella 2.

Viola lobata chk.
Viola macloskeyi 1.
Viola purpurea 2.
Viola purpurea subsp. *integrifolia*.
Viola purpurea subsp. *mesophyta*.
Viola purpurea subsp. *xerophyta*.
Viola sheltonii.

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ADDITIONS TO THE NATIVE VASCULAR FLORA OF THE OLYMPIC PENINSULA, WASHINGTON

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ABSTRACT

Although Olympic Peninsula plants were among the first in the Pacific Northwest to be seen by a European botanist (Archibald Menzies, May 1792), comparatively little botanical attention has been given to the area since then. This paper notes the addition of more than a hundred native taxa that are not attributed to the Peninsula in standard floras of the area (Piper 1906, Piper and Beattie 1915, Frye 1934, Jones 1936, Abrams and Ferris 1940–1960, Hitchcock et al. 1955–1969, Hitchcock and Cronquist 1974) or in other floras whose ranges sometimes include or closely approach the Peninsula (Henry 1915, Hultén 1968, Welsh 1974, Fernald 1970). A number of these additions are included in the regionally published catalog of vascular plants of this area (Buckingham and Tisch 1979).

The Olympic Peninsula is that part of the northwest corner of Washington lying north of the Chehalis River and the southern reach of Puget Sound, but omitting the Kitsap Peninsula. Within its 15,500 km^2 are the Olympic Mountains, with peaks to 2400 m. The climate is oceanic, but with a drastic precipitation gradient from 40 cm in the rain shadow to 600 cm on Mt. Olympus. Endemism, disjunction, and deviations from the described parameters of many taxa are characteristic of the flora, resulting, in part from isolation and the presumed existence of glacial refugia.

The area challenges many aspects of botanical investigation. Most of the Olympic Mountains, plus the extensive Ocean Strip, comprise the Olympic National Park. The world-wide ecological significance of this Park has led to its designation as a World Heritage Site and a Biosphere Reserve. The floristically rich eastern and southern Olympics are managed and protected by the Olympic National Forest. The authors hope that this paper will stimulate the interest of botanists in this isolated, but readily accessible region.

The known Olympic Peninsula distribution is given for all plants. When the presence of the plant is considered somewhat exceptional, in view of general ranges stated in the floras, additional data are provided. These include pertinent parts of the general range and [in brackets] closer occurrences of which we are aware through herbarium

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and literature search. Nomenclature follows Hitchcock and Cronquist (1974), except where authorities are listed.

All herbarium citations represent Olympic Peninsula collections. Specimens of all listed taxa are in the personal herbarium of the senior author or that of the Olympic National Park, unless one or both are specifically excepted. Both are accessible by appointment or inquiry. Other herbarium specimens of listed plants are cited. Those herbaria not included in the Index Herbariorum are indicated by the use of lower case letters, as follows: (nmb)—Nelsa M. Buckingham, Port Angeles, WA; (onp)—Olympic National Park, Port Angeles, WA; (pc)—Peninsula College, Port Angeles, WA; (plu)—Pacific Lutheran University, Tacoma, WA; (smc)—St. Martin's College, Olympia, WA; (ups)—University of Puget Sound, Tacoma, WA.

Certain frequently recurring geographical areas are abbreviated as follows: BC—British Columbia; Cas—Cascades; OM—Olympic Mountains; OP—Olympic Peninsula; VI—Vancouver Island.

LYCOPHYTA

Lycopodiaceae

Lycopodium annotinum. Moist, cool forest and forest openings, northeast OM, 915–1372 m: (pc, WTU). [Cas.]

Lycopodium complanatum. Moist open woods, northeast OM, 685–1402 m: (pc). [Cas.]

Lycopodium inundatum var. *inundatum.* Shore of Lk. Ozette, 11 m: (WS, not at onp).

Isoetaceae

Isoetes maritima Underw. In water, Lk. Ozette, 10.5 m: (not at onp). South along the coast to Alberni, central VI. The taxonomy of the genus in BC is under study by D. M. Britton and A. and O. Ceska. The Ceskas have determined that three taxa are represented in our OP collections, as follows: *Isoetes echinospora* Dur. sensu lato (incl. *I. muricata* Dur.); *I. flettii* (A. A. Eaton) Pfeiffer; *I. maritima* Underw. The first two are apparently the plants referred to as *Isoetes braunii* Dur. and *I. piperi* A. A. Eaton in Jones (1936). *Isoetes maritima* is apparently a first collection for the OP.

SPHENOPHYTA

Equisetaceae

Equisetum × *ferrissii.* Upper beach, dunes, and sandy bluffs, Mukkaw Bay, Lk. Ozette, and Discovery Bay, 5 to 50 m: (WS).

Equisetum variegatum var. *variegatum.* Lake shores and boggy meadows, north to east OM, 1082–1645 m: (pc, WS). [Southern VI (Taylor 1963).]

PTEROPHYTA

Ophioglossaceae

Botrychium boreale. Subalpine meadow above Silver Lk., 1830 m, and moist woods, Copper Cr., 1295 m. [Cas.]

Polypodiaceae

Dryopteris filix-mas. Mt. Olympus, 1830 m: (WTU, not at nmb or onp). [Mt. Rainier (Frye 1934).]

Polypodium hesperium. Lang (1969) divides this taxon into two entities: *Polypodium hesperium,* occurring only east of the Cas, and *P. amorphum* Suksd. (*P. montense* Lang) to the west. *Polypodium amorphum* is common on the OP, but *P. hesperium* has been collected on the base of a tree trunk at Whiskey Cr., 10 m, and on seastacks, northwest OP, 5–24 m: (WS, not at onp).

ANTHOPHYTA—MONOCOTYLEDONEAE

Alismataceae

Sagittaria latifolia. Wet places near Sequim Bay, in the Satsop drainage, and at Lk. Ozette, 6–100 m: (WS, WTU).

Cyperaceae

Carex aperta. Seasonally flooded meadows, southeast OP, 67 and 245 m: (pc). [Skamania Co. and Kittitas Co. (Standley 1981).]

Carex aquatilis. Wet places, north and southeast OP, 11–780 m. Generally in and east of the Cas.

Carex disperma. Bogs and streambanks, northeast OM, 790–1495 m: (pc). Generally east of the Cas crest.

Carex interior. Wet sedge meadows, north and east sides of the OP, 230–960 m.

Carex interrupta. River banks, south and northwest OP, 37–46 m: (WTU). Generally lower Columbia R. and south. [Duncan, VI (Henry 1915); lower Fraser R., BC, and Thurston Co. (Standley 1981).]

Carex lasiocarpa var. *americana.* Boggy margin of Wentworth Lk., Ozette area 25 m. [VI (Henry 1915); Seattle (Piper 1906).]

Carex limnophila. Wet places, north and central OM, 790–1400 m: (pc). [North Cas (Douglas et al. 1973).]

Carex neurophora. Wet meadows and streambanks, east OM, 1280–1495 m: (WS, WTU). [Mt. Rainier.]

Carex obtusata, Dry ridges, northeast OM, 1675–2027 m: (pc, WTU).

East of the Continental Divide in the U.S. [Bridge Cr., Fraser R., BC (Henry 1915).]

Carex unilateralis. Seasonally flooded meadows, north and southeast OP, 60 and 245 m: (WS, WTU).

Carex vulpinoidea. Muddy sandbar, Lower Skokomish R. ,25 m. Generally east of the Cas crest. [Goldstream, VI.]

Cyperus aristatus. Lake shore, Shelton area, 60 m: (pc, V).

Eleocharis acicularis. Wet lake margins, northwest and southeast OP, 10.5 and 60 m: (WTU).

Eriophorum polystachion. Lake shores and bogs, N. Fork Quinault, upper Dungeness, and Lake Cr. drainages, 1220–1645 m: (plu).

Scirpus cyperinus var. *brachypoda.* Wet areas, southeast OP, Quinault Res., and Lk. Ozette, 15–229 m. Southeast BC and east. [Whatcom Co. (Taylor et al. 1973); southwest BC, including VI.]

Scirpus subterminalis. Shallow pond, Lk. Ozette, 11 m.

Hydrocharitaceae

Elodea nuttallii. Drainage channel, Copalis area, 9 m. [Hick's Lk., Thurston Co.]

Juncaceae

Juncus supinus. Extensive, dense population on margins, spring-fed gravelly flat, and in moving water of long-abandoned gravel pit about 9.6 km southeast of Neilton; present also on pond margin of old gravel pit about 6 km west, 45 m: (V, WS, WTU). Apparently known in U.S. only from near Duvall, Snohomish Co. [Near Sultan, Snohomish Co. (Taylor et al. 1978).]

Orchidaceae

Habenaria greenei. Dry bank, Lk. Crescent, 180 m, and "cliff, Port Crescent, Clallam Co.": (WS).

Poaceae

Agropyron caninum subsp. *majus* var. *andinum.* Dry subalpine meadows, Mt. Angeles area, 1525 and 1675 m: (WTU).

Agropyron caninum subsp. *majus* var. *latiglume.* Dry subalpine meadows, northeast OM, 1675–1965 m (pc, WTU). Generally east of the Cas. [Southern VI.]

Glyceria borealis. Margin of Sandy Shore Lk., northeast OP, 120 m.

Glyceria striata var. *stricta.* Sandbar, Satsop R., 30 m: (not at onp). [Whatcom Co.]

Hierochloe odorata. Streamsides and wet meadows, northeast OM, 1370–1645 m. [Burlington, Skagit Co.]

Panicum capillare var. *occidentalis.* Wet places, Shelton area, 60 m: (pc, V).

Poa grayana. Olympic plants key most closely to this taxon. Subalpine rock outcrops and moist meadows, north and east OM, above 1495 m: (pc, WTU). Cas.

Poa nervosa var. *wheeleri*. Steep, thinly forested west-facing slope, Royal Basin, 1615 m: (pc, not at nmb or onp). Cas.

Poa rupicola. Alpine area, vicinity of Buckhorn Pass, 1905–1983 m: (WTU). Generally in Rocky Mt. area. [Chowder Ridge, Mt. Baker (Douglas and Taylor 1970).]

Puccinellia pumila. Sand and *Salicornia* mats, Crescent Beach and mouth of Waatch R.: (WS, WTU).

Stipa lemmonii var. *lemmonii*. South-facing hillsides, north OP, 183 and 550 m. Generally east of the Cas. [Comox Sandspit, VI (Hubbard 1955); San Juan Island.]

Potamogetonaceae

Potamogeton amplifolius. Lakes on north, east, and south sides of OP, 10.5–165 m: (WS, WTU).

Potamogeton berchtoldii. Widely distributed in suitable habitats on the OP, 10.5–945 m: (WS, WTU).

Potamogeton illinoensis. Deep water, Lk. Crescent, 176 m: (WTU).

Potamogeton obtusifolius. Shallow water, Lk. Arrowhead, 100 m. West to Minn.; also southern BC. [Minkler Lk., Skagit Co., is the only other Wash. collection seen.]

Sparganiaceae

Sparganium fluctuans. Deep water, Lk. Ozette, 10.5 m: (WS, WTU). [Idaho (Davis 1955).]

Sparganium minimum. Pond, Lilliwaup Swamp area, 229 m. [Mt. Rainier.]

Zosteraceae

Phyllospadix serrulatus Rupr. Mid-tidal pools, northwest OP: (WS, WTU). [From just west of Kodiak Island to Coos Bay, Oreg. (Phillips 1979).]

Phyllospadix torreyi. Sub-tidal, northwest OP: (smc, WS). [VI to Baja Calif. (Phillips 1979).]

ANTHOPHYTA—DICOTYLEDONEAE

Asteraceae

Antennaria umbrinella. Subalpine and alpine screes, northeast OM, 1770–1950 m: (WS, WTU).

Aster radulinus. Subalpine woods margin and meadow, northeast OM, 1295 and 1370 m: (pc). Olympic plants could be keyed alternatively to *A. sibiricus* var. *meritus,* a taxon that would also be new to the OP.

Bidens cernua. Wet places, northeast OP, 5 and 425 m.

Crocidium multicaule. Open mossy bench on rock outcrop, Elwha Valley, 180 m: (pc).

Eriophyllum lanatum var. *achillaeoides.* Dry open places, lowland to subalpine; most common on the east side, but occurring on gravel bars and dry sites on the western OP: (pc). Lane Co., Oreg., and south.

Psilocarphus elatior. Dried margins and bottoms of vernal pools and on sandbars, Calawah drainage, 55–268 m.

Taraxacum olympicum G. N. Jones. This epithet has been reduced to synonymy with *T. eriophorum* Rydb. in Hitchcock et al. (1955–1959). Olympic material does not, however, conform to the description of *T. eriophorum* and merits further study. For the present, these plants should probably retain the G. N. Jones epithet. Blue Mt. to Mt. Angeles, 1570–1845 m: (WTU).

Balsaminaceae

Impatiens capensis. Moist woods margins, southwest Grays Harbor Co., 5–15 m. Rare in the Pacific Northwest (Ornduff 1967). [Ladner, BC; Whatcom Co.] Two hybrid forms resulting from the crossing of *Impatiens capensis* with *I. ecalcarata* (Ornduff 1967) occur here in the presence of the parent species. These represent the spurless-spotted form and the spurred-spotless form. Both are represented at (nmb).

Betulaceae

Alnus incana subsp. *rugosa* var. *occidentalis.* Wet to flooded streambanks, John's Cr., Mason Co., 73 m: (pc). Generally east of the Cas. crest. [Near Tacoma.]

Betula glandulosa var. *hallii.* Partially drained boggy area, Port Angeles, about 60 m: (pc, V, WS).

Brassicaceae

Arabis hirsuta var. *glabrata.* Rock outcrops and dry open slopes, north and east OM, 270–1740 m. [Mostly in and east of the Cas. (R. C. Rollins, pers. comm., 27 Jan. 1981).]

Arabis holboellii var. *retrofracta.* Rock outcrops and scree in dry areas of the northeast OM, 855–2070 m. Generally east of the Cas.

Athysanus pusillus. Dry, often grassy places, north OP, 4–548 m: (pc).

Cardamine bellidifolia var. *bellidifolia.* Mt. Ellinor, 1465 m: (WTU, not at nmb or onp). Cas. of Wash., north and east. [Golden Hinde, VI.]

Draba cana Rydb. Dry rocky soil, Mt. Tyler, 1770 m: (pc, not at onp). R. C. Rollins states, “This is what has been called *D. lanceolata* Royle, but Mulligan, who has seen the type of *D. lanceolata,* a plant of central Asia, claims that the material does not fit that species. The next name in line is that of Rydberg." (Pers. comm., 14 Apr. 1981.) In the U.S., Idaho and east. [Cathedral Ridge, BC (Taylor et al. 1973).]

Draba prealta. Dry scree meadows in northeast OM, 1767–1830 m: (pc). [Mt. Baker (Taylor and Douglas 1978).]

Thysanocarpus curvipes. Dry rock outcrops above Elwha R., 548–640 m: (pc, WTU). Mostly east of the Cas. [Victoria area, VI (Szczawinski and Harrison 1973); Tacoma.]

Campanulaceae

Downingia yina var. *major*. Shores of small lakes, southern Mason Co., about 60 m: (pc, V, WS).

Caryophyllaceae

Stellaria nitens. Rock outcrops and dry hillsides above Elwha R., 76–545 m.

Ceratophyllaceae

Ceratophyllum echinatum Gray. Lk. Ozette, 10.5 m, and Lk. Arrowhead, 100 m: (V, WS, WTU). West to Minn. (Fernald 1970). [Southern VI (A. and O. Ceska 1980).]

Cornaceae

Cornus unalaschkensis Ledeb. Although this taxon is reduced to synonymy with *C. canadensis* L. in Hitchcock et al. (1955–1969), Bain and Denford (1979) establish that *C. unalaschkensis* must be treated as a species. Olympic plants, occurring widely in montane habitats, conform to *C. unalaschkensis*. We have not seen specimens of *C. canadensis* from the OP.

Crassulaceae

Sedum lanceolatum var. *rupicolum*. Dry open areas and rocks, northeast OM, 915–2060 m: (pc). Wenatchee Mts.

Sedum roseum. Cliffs, Mt. Pershing area, 1524 m. [Mt. Rainier.]

Tillaea aquatica. Exposed mud, shore of Lk. Ozette, 10.5 m: (WS). [Lower Fraser R.]

Ericaceae

Kalmia microphylla. Wet subalpine meadows and bogs, upper Dungeness drainage, 1675–1830 m: (pc). Cas.

Pyrola minor. Moist, usually open woods, northeast OM, 884–1464 m: (pc). [Mt. Rainer.]

Euphorbiaceae

Euphorbia serpyllifolia. Gravelly lake margin, Shelton area, 60 m: (pc, V). Generally east of the Cas. in Wash. [Yelm and Tacoma (Piper 1906).]

Fabaceae

Astragalus microcystis. Dry scree meadows, upper Dungeness drainage, 1770–1965 m: (BRY, NY, pc, WTU). The collection *J. W. Thompson 7997* of 13 Aug. 1931 (WTU), which was cited in Abrams (1940–1960), was omitted from Barneby (1964) because the OM source of the collection was considered so unlikely that a mixup of labels was suspected (R. C. Barneby, pers. comm., 8 Mar. 1979). [Extreme northeast Wash. (Barneby 1964).]

Lupinus microcarpus var. *microcarpus.* Sandy beach bluff, east side Discovery Bay, 45 m: (pc). Generally east of the Cas. Flower color of this population is reddish purple, rather than the pale yellowish characteristic of the var. *scopulorum* of southern VI and adjacent islands.

Lupinus polyphyllus var. *pallidipes.* Moist forest opening, Skokomish R., 10 m.

Grossulariaceae

Ribes triste. Wet meadows and streambanks, northeast OM, 792–1402 m: (pc). Cas.

Hydrophyllaceae

Phacelia linearis. Sandspit, Chehalis R., sandy west-facing beach bluffs, northeast OP, and from 975–1050 m on Mt. Maynard: (pc, WTU).

Lamiaceae

Lycopus americanus. Lake shore, Shelton area, 60 m: (pc, V).

Lentibulariaceae

Utricularia intermedia. Shallows, Lk. Ozette, 10.5 m (V, WS). [Southern VI (Ceska and Bell 1973).]

Utricularia minor. Shallows, Lk. Ozette, 10.5 m. [Southern VI (Ceska and Bell 1973); Olympia (Piper 1906).]

Onagraceae

Epilobium watsonii var. *parishii.* Scattered at lower elevations on the OP.

Ludwigia palustris var. *pacifica.* Gravelly seep near Lk. Ozette, 15 m: (WS).

Orobanchaceae

Orobanche californica var. *californica.* Upper beach, Pt. Wilson: (WTU).

Orobanche pinorum. Dry open woods, Elwha Valley, 550 m: (pc, not at nmb or onp). [Cowichan Lk., VI.]

Oxalidaceae

Oxalis suksdorfii. Seaward edge of eroding high beach meadow, Mukkaw Bay, a solitary find that may not represent an established population: (not at onp). Generally southern Wash. and south. [Kitsap Co. (WNHP, 1981).]

Plantaginaceae

Plantago major var. *pachyphylla.* High beach, north shore, Grays Harbor.

Polemoniaceae

Microsteris gracilis var. *humilior.* Dry open places, east half of OP, 75–915 m. Generally east of the Cas. crest. [Lacey, Thurston Co.]

Polygonaceae

Polygonum majus. Patch of bare soil on hillside above Copper Cr., 1315 m. [Marblemount, Skagit Co. (D. B. and R. W. Naas, pers. comm.).]

Polygonum viviparum. Wet meadows and seeps, northeast OM, 1403–1996 m: (pc). [Forbidden Plateau, VI (Hardy 1954).]

Portulacaceae

Calandrinia ciliata. Open south-facing hillside, north OP, 183 m.

Montia chamissoi. Boggy meadow, Blue Mt., 1630 m. Generally in or east of the Cas. [Roy, Pierce Co. (Piper 1906).]

Montia linearis. "Wet land, Sequim": (WTU, not at nmb or onp).

Montia spathulata (Dougl.) Howell. High beach and sand dunes, southwest and northeast OP.

Ranunculaceae

Anemone deltoidea. Vernally wet shrubby meadow, Mt. Ellinor, 1375 m: (ups, not at nmb or onp).

Caltha biflora var. *rotundifolia.* Wet forest opening with north exposure, Pine Mt. area, 885 m. Occasional in the Cas. [Jordan Meadows, VI.]

Ranunculus glaberrimus var. *ellipticus.* Dry scree meadows, northeast OM, 1676–1830 m: (pc). East of the Cas.

Ranunculus verecundus. Alpine meadows and talus, northeast OM, 1738–2010 m: (pc, WTU). Cas.

Rosaceae

Sanguisorba sitchensis. Big Cr. Prairie, 45 m, and Mink Lk. and sedge meadow above, 945 and 960 m: (WS, WTU). Mink Lk. plants in Buckingham collection were growing with *S. menziesii* and with intermediate plants (both at nmb). Cas. and east. [Forbidden Plateau, VI (Hardy 1954).]

Spiraea betulifolia var. *lucida*. Mt. Walker and Mt. Jupiter, 260–1370 m: (pc, not at onp). Generally in and east of the Cas. [Olympia.]

Rubiaceae

Galium bifolium. "One-half mile above Dose Meadows along Lost Pk. trail, growing in old elk trail at 4000 feet" (1220 m): (WTU, not at nmb or onp). Generally east of the Cas. [Hart's Pass.]

Galium kamtschaticum. Moist forest, upper Humptulips drainage, 590 m: (pc, not at onp). In western U.S. known only from Stevens Pass, Cas.

Kelloggia galioides. Dry open woods at 1675 m, and consolidated talus at cliff base, 1830 m, upper Dungeness drainage: (pc). Generally east of the Cas. crest.

Salicaceae

Salix brachycarpa var. *brachycarpa*. North-facing rocky meadow, Maiden Pk., 1905 m: (V, WS). Kittitas Co.

Salix geyeriana var. *meleiana*. Swamps, John's Cr. area near Shelton, 70 m: (pc).

Saxifragaceae

Lithophragma bulbifera. Subalpine rocks and scree meadows, northeast OM, 1650–1740 m. Generally east of the Cas. crest. [Southern VI.]

Parnassia palustris var. *neogaea*. Wet rocks and subirrigated meadows to 930 m, southwest OM: (smc). Generally north of Wash. [Lillooet area, BC.]

Saxifraga debilis. Damp cliffs and rock crevices, northeast OM, above 1740 m: (WTU). Cas.

Tiarella trifoliata var. *laciniata*. Morse Cr. drainage, 1188 m, and Skokomish drainage, 580 m: (pc).

Scrophulariaceae

Lindernia anagallidea. Wet potholes near Shelton airport, 60 m. [Mt. St. Helens.]

Scrophularia lanceolata. Satsop R. banks, 58 m: (WS, WTU).

Tonella tenella. Open woods and rock outcrops above Elwha R., 305–457 m. Generally south of the Columbia R. [Saltspring Island, BC (Douglas and Douglas 1978).]

Umbelliferae

Osmorhiza depauperata. Margins of subalpine fir clumps, north OM, about 1830 m: (WTU). Generally east of the Cas. crest.

Sanicula bipinnatifida. Consolidated upper beach, Marrowstone Pt., 3 m, and sandy beach bluff, east side Discovery Bay, 45 m: (pc).

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THE ALPINE VASCULAR FLORA OF ARIZONA

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ABSTRACT

The Arizona alpine, 5.18 km^2, is restricted to the summits of the three highest peaks of the San Francisco Mountain near Flagstaff. Forty-nine vascular species were formerly known for this very southern tundra. Eighty vascular taxa are now known for the Arizona alpine. This study includes and confirms most additions since 1941 and reports as new nineteen taxa.

The San Francisco Mountain, a single massif of recent volcanic origin located just north of Flagstaff, supports the only known alpine tundra in Arizona. This small alpine (ca. 5.18 km^2 [2 mi^2]; Little 1941, Moore 1965) is restricted to the summits of the three highest peaks of the caldera; Humphrey 3853 m, Agassiz 3761 m, and Fremont 3639 m. Radiodated andesitic extrusives (Holm, pers. comm.) indicate that Agassiz, the peak of intermediate position and oldest of the three, was formed about seven hundred thousand years ago.

An open irregular krumholtz of *Pinus aristata* and *Picea engelmannii* marks the lower limits of the alpine. This "band" of conifers fluctuates above and below 3505 m, depending on slope and substrate stability. Extremely dwarf specimens of *Pinus aristata* and *Picea engelmannii* can be found in protected locations within the tundra to above 3658 m.

Moisture is provided by melt of the snowpack and by the usually frequent and heavy summer (July–mid September) thundershowers, the Arizona "monsoon." A protective snow cover is usually established in December or late November, though this can be interrupted by midwinter thaw. Snow accumulations are greatest in late winter and early spring. The tundra is largely free of snow by mid-May, though it may be snow-free as early as late April or as late as mid-June. Streams provided by permanent or late season snowbanks are unknown, as are other aquatic habitats. When snowfall is light or almost absent and thundershowers infrequent, anthesis of later-flowering taxa is drastically curtailed. When snowfall is adequate and the thundershowers of normal duration and intensity, a second anthesis period may occur in the fall for earliest blooming constituents.

Previous investigations in the Arizona alpine were made by Merriam (1890), Little (1941), and Moore (1965). Merriam reported twenty species for his "alpine zone," nine from the "bleak and storm-beaten summit,"

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and eleven other above-timberline taxa. Little (1941), in the most extensive previous study, listed forty-nine vascular species for the area. Moore (1965) suggested two additional taxa for the region, but failed to list either. My search of ASC revealed a collection of *Polemonium pulcherrimum* var. *delicatum, Moore s.n.* (ASC 12618), apparently from near the summit of Humphrey Peak. The other addition remains unknown.

During this investigation, thirty-four collecting trips were made into the Arizona alpine from April to October of 1968 and 1969. All collections were made well above the krumholtz ecotone. Collections were not made where the krumholtz was abnormally depressed because of extreme snow accumulation and/or substrate mobility.

Eighty taxa of fifty genera in twenty-three families are now known for the Arizona alpine. This listing includes all known reports of Little (1941) and Moore (1965) and confirms most of the thirteen additional records in Kearney and Peebles (1964) and McDougall (1973). Nineteen taxa are reported new to the Arizona alpine. Most of these additions were previously known from lower elevations on the mountain, but two reports for the genus *Carex* were new for the state (Schaack 1979).

Of these new reports, *Agrostis idahoensis* and *Dugaldia hoopesii* are suggested as recent advents to the tundra. Both, as they are now known, are restricted to a limited portion of the favorable south-facing slopes of Agassiz Peak. Dispersal appears to have been directly upward, in increments, from the subalpine or krumholtz ecotone. This staircase-like movement from below results in a striking reduction in stature, especially dramatic in *Dugaldia hoopesii*. At highest elevation, ca. 3658 m, this species is represented only by its basal leaf rosette. Anthesis is apparently not possible for *Dugaldia* at this altitude. Total lack of flowering upon entrance into the alpine is known only for *Epilobium angustifolium*. Buds are formed but apparently desiccate, and anthesis is not realized.

Vascular taxa include two cryptogams (2.5%). Of the phanerogams, four (5.0%) are either annual, biennial, or short-lived perennials, six (7.5%) are woody perennials, and the remainder (85%) are perennial herbs (69.1% dicots and 30.9% monocots). Two taxa are endemic, *Packera franciscana* and *Ranunculus inamoenus* subsp. *subaffinis*. The others, of varying phytogeographic affinities, are generally agreed (Little 1941, Moore 1965, Schaack 1970) to have moved to the San Francisco Mountain from the main Rocky Mountain chain during Pleistocene time when treeline was greatly depressed and alpine stations were more continuous.

The primary dispersal corridor used by these alpine taxa to reach the San Francisco Mountain is hypothesized (Schaack 1970) as the continuous area of high elevation to the east and north beginning with the main Rocky Mountain chain of Colorado and New Mexico. From here, the suggested pathway is to the White Mountains of Arizona via the adjacent western mountains of New Mexico, then from the connecting Mogollan escarpment to the San Francisco Mountain. That this might be the primary corridor is suggested by the southern distribution of *Besseya plantaginea.* This mid- to high-mountain species of limited dispersal capabilities is known as far north as southern Wyoming and is restricted to the eastern flanks of the Rockies through most of Colorado. Its westerly station is on or near the San Francisco Mountain. Its apparent absence from Utah suggests that a barrier to movement of mid- or high-mountain taxa could have existed to the north.

PLANT COMMUNITIES

Little (1941) recognized two major communities for this tundra: the alpine rockfield and the alpine meadow.

The alpine rockfield or fellfield occupies most of this alpine. Substrate stability and composition vary greatly here. Most vascular taxa are found on relatively stable substrates of pebble-sized or smaller material. Extreme areas that are highly mobile, slide areas, of large angular rock and/or small boulders support few or no vascular plants. Species restricted to or found predominantly in the fellfield are: *Arenaria fendleri, A. rubella, Silene acaulis, Draba aurea, Potentilla concinna, Polemonium viscosum, Antennaria parvifolia, A. rosulata, A. umbrinella,* and *Packera franciscana.*

Alpine meadows consist of small sod patches scattered in the tundra. These occur only on the more favorable sites and reach their best development on the south-facing slopes of Agassiz Peak. Taxa restricted to or found mainly in the alpine meadow are: *Botrychium lunaria, Bromus ciliatus, Phleum alpinum, Poa fendleriana, P. pratensis, Carex atrata* var. *erecta, C. elynoides, C. petasata, Ranunculus inamoenus* subsp. *subaffinis, Anemone multifida* var. *tetonensis, Sibbaldia procumbens, Gentianella amarella, G. barbellata, G. tenella, Pedicularis parryi, Veronica wormskjoldii* and *Dugaldia hoopesii.* Due to the large number of restricted taxa, it is the meadow that contains the greatest number of vascular constituents in this alpine.

Most of the taxa in the tundra are opportunistic. Frequently encountered monocots in both fellfield and meadow include: *Agropyron scribneri, Festuca ovina* var. *brevifolia, Poa interior, Trisetum spicatum, Carex albo-nigra, C. atrata* var. *chalciolepis, C. ebenea,* and *Luzula spicata.* Common dicots found in both fellfield and meadow are: *Cerastium beeringianum, Ranunculus pedatifidus, Thlaspi montanum, Saxifraga rhomboidea* var. *franciscana, Geum rossii* var. *turbinatum, Potentilla diversifolia, Pseudocymopterus montanus, Mertensia franciscana, Penstemon whippleanus,* and *Solidago multiradiata.*

A consistent assemblage of species can be found associated with cracks and crevices, and within rock alcoves, whereas certain others are typically from soils trapped in boulder-formed recesses or beneath shelf overhangs. Predominant crack-and-crevice species include *Cystopteris reevesiana, Heuchera versicolor, Saxifraga caespitosa, Sedum rhodanthum* (occasionally with *Primula parryi*) and, at highest elevations on the north slope of Agassiz, *Oxyria digyna.* Species most abundant in or collected only from boulder-protected areas include: *Stellaria umbellata, Saxifraga debilis, S. flagellaris, Primula parryi,* and the woody species *Ribes montigenum* and *Lonicera involucrata.*

Little (1941) suggested that the alpine meadow of the Arizona alpine was the climax community. He hypothesized that pioneer plants such as *Geum rossii* var. *turbinatum, Silene acaulis,* and *Sibbaldia procumbens* spread vegetatively, forming compact mats and providing conditions that favor soil improvement and the establishment of other species. Invading mats, then, represent incipient meadows from which more extensive sods can result, a process later investigated in Colorado by Griggs (1956).

Moore (1965), apparently influenced by the dry appearance of the alpine, thought that succession here was of the retrogressive type described by Churchill and Hanson (1958). He suggested that should this environment become more adverse (drier and warmer), this vascular flora would become less vigorous and diverse.

Results of this floristic study are contrary to Moore's hypothesis. Species diversity is greater than was previously known, and evidence suggests that certain species (*Agrostis idahoensis* and *Dugaldia hoopesii*) are recent advents to this alpine. Mat invasion, as hypothesized by Little (1941) and elucidated by Griggs (1956), appears to be occurring, though it is uncertain that this is the sole mechanism of meadow formation. It has no doubt played a role in the formation of many of the existing sods. Numerous species listed in Schaack (1970) that are alpine in Colorado (Harrington 1954) are found at lower elevations on the San Francisco Mountain; many of these reach the subalpine. It is possible that certain of these will follow the stepwise upward dispersal displayed by *Dugaldia hoopesii* and *Agrostis idahoensis.*

The number of vascular taxa of this small, isolated, geologically young alpine compares favorably with that of other alpine "islands" (Hall 1967, Bell and Johnson 1980). The eighty-two species in fifty-six genera and twenty-eight families reported for Mt. Hood by Hall is almost an exact match for findings of this study. Previous comparisons of the Arizona alpine with the older, larger, and more continuous Colorado alpine (Little 1941, Moore 1965) are inappropriate.

In the following list an asterisk indicates taxa not recognized as entering the alpine (above 3505 m) by Kearney and Peebles (1964) and McDougall (1973). Brief comments, where appropriate, are provided on relative abundance, habitat preference, altitudinal limits, and phytogeographic affinities.

By and large, the nomenclature presented is that of Hitchcock et

TABLE 1. PHYTOGEOGRAPHIC ABBREVIATIONS AND NUMBERS OF TAXA.

Category	Abbreviation	Number of taxa
American alpine	AA	3
American boreal	AB	1
Circumboreal	CB	2
Circumpolar	CP	19
Cordilleran widespread	CW	1
Endemic	E	2
Plains species	P	2
Rocky Mountain	RM	10
Southern Rocky Mountain	SRM	14
Southwestern	SW	7
Western cordilleran	WC	16
Widespread introduced	WI	3

al. (1955–1969), Hitchcock and Cronquist (1973), Lehr (1978), and Lehr and Pinkava (1980, 1982). Phytogeographic affinities were derived from Hitchcock et al. (1955–1969), Hultén (1971), and Polunin (1959). Phytogeographic abbreviations and numbers of taxa for each category are found in Table 1. Complete or partial vouchers are in ARIZ, ASC, MNA, MONTU and US.

PTEROPHYTA

Ophioglossaceae

Botrychium lunaria. Rare. Known for the alpine from a single collection, alpine meadow, 3566 m. CP.

Polypodiaceae

Cystopteris reevesiana. Common. Cracks and crevices, alpine meadow, to 3761 m. SW.

CONIFEROPHYTA

Cupressaceae

**Juniperus communis* (ours referred to as var. *depressa*). Rare. Found to about 3615 m on the south slopes of Agassiz. CP.

Pinaceae

**Abies lasiocarpa* var. *arizonica*. Rare. Known only from the most protected areas on the south slopes of Agassiz, to 3627 m. SW.

Picea engelmannii. Uncommon. Dwarf specimens in protected areas on south slopes to above 3658 m. WC.

Pinus aristata. Uncommon–fairly common. Dwarf specimens scattered above treeline, most common on protected south slopes, a few to above 3749 m. SW.

ANTHOPHYTA—MONOCOTYLEDONEAE

Cyperaceae

Carex albo-nigra. Common. Alpine meadow and fellfield, to 3658 m. WC.

Carex atrata var. *chalciolepis.* Common. Alpine meadow or fellfield, to above 3658 m. SRM.

**Carex atrata* var. *erecta.* Common. Alpine meadow to 3658 m, first state record (Schaack 1979). WC.

Carex bella. Common. Alpine meadow and fellfield, to 3749 m or more. RM.

Carex ebenea. Common. Alpine meadow and fellfield, to above 3658 m. SRM.

**Carex elynoides.* Rare. Alpine meadow, known only from a single collection at about 3612 m on Agassiz, first state record (Schaack 1979). SRM.

**Carex petasata.* Rare. Alpine meadow, at about 3566 m. WC.

Juncaceae

Juncus drummondii. Rare. Alpine meadow, reported from a single meadow by Little (1941). RM.

Luzula spicata. Common. Alpine meadow or fellfield, to above 3658 m. CP.

Poaceae

Agropyron scribneri. Common. Fellfield or alpine meadow, to above 3658 m. RM.

Agropyron trachycaulum var. *latiglume.* Uncommon. Alpine meadow, cracks and crevices, known from the south-facing slopes of Agassiz, to 3658 m. WC.

**Agrostis idahoensis.* Uncommon. Alpine meadow and fellfield, south slopes of Agassiz, to near 3658 m. WC.

**Bromus ciliatus.* Uncommon. Alpine meadow and favorable fellfield areas, most common on the south slopes of Agassiz, to near 3627 m. AB.

Festuca ovina var. *brevifolia.* Common. Alpine meadow and fellfield, to above 3658 m. CP.

Phleum alpinum. Rare. Alpine meadow, to 3658 m. CP.

**Poa fendleriana.* Rare. Alpine meadow, ca. 3597 m. WC.

Poa interior. Common. Alpine meadow and fellfield, to above 3658 m. P?

**Poa pratensis.* Rare. Alpine meadow, known only from a single collection, ca. 3566 m. WI?

Poa reflexa. Uncommon. Alpine meadow and areas of boulder accumulation on the south slopes of Agassiz, to 3658 m. RM.

Poa rupicola. Common. Alpine meadow, fellfield, and areas of boulder accumulation, to 3658 m. WC.

Trisetum spicatum. Common. Alpine meadow, fellfield and areas of boulder accumulation, to above 3658 m. CP.

ANTHOPHYTA—DICOTYLEDONEAE

Apiaceae

Pseudocymopterus montanus. Very common. Alpine meadow or fellfield, above 3658 m. SRM.

Asteraceae

Antennaria parvifolia. Common. Fellfield, to above 3658 m. P.

Antennaria rosulata. Rare. Fellfield? Reported for the alpine by McDougall 1973, to 3658 m. SRM.

Antennaria umbrinella. Rare–uncommon. Fellfield, to above 3658 m. CB.

**Dugaldia hoopesii.* Rare. Alpine meadow on protected south slopes of Agassiz, to above 3658 m. WC.

Erigeron compositus. Rare. Alpine meadow and cliffs, reported for Arizona alpine by Little (1941). CP.

Erigeron simplex. Rare. Alpine meadow, collected at 3658 m. RM.

Packera franciscana. Relatively common. Fellfield, often on rubble or scree substrate, to above 3658 m. E.

Solidago multiradiata var. *scopulorum.* Common. Fellfield or alpine meadow, to above 3658 m. RM.

Taraxacum laevigatum. Uncommon. Alpine meadow, southern slopes of Agassiz below 3627 m. WI.

Taraxacum lyratum. Uncommon. Alpine meadow and fellfield, to 3658 m. CP.

**Taraxacum officinale.* Rare. Alpine meadow, known only from a single collection, ca. 3597 m. WI.

Boraginaceae

**Mertensia franciscana.* Rather common. Alpine meadow, cracks, and crevices, and occasionally fellfield, to 3658 m. SRM.

Brassicaceae

Draba aurea. Common. Fellfield, to above 3658 m. AA.

Draba crassifolia. Rare. Alpine meadow, to 3658 m. CP.

Thlaspi montanum. Common. Fellfield or meadow, to above 3658 m. RM?

Caprifoliaceae

**Lonicera involucrata.* Rare. Only one plant found above treeline, boulder-protected area, ca. 3566 m. CW.

Caryophyllaceae

Arenaria fendleri (includes var. *fendleri,* var. *porteri,* and var. *tweedyi*). Rare. Fellfield, at ca. 3658 m. SRM.

Arenaria lanuginosa subsp. *saxosa.* Common. Typically a fellfield plant, occasionally in meadows, to above 3658 m. SW.

Arenaria obtusiloba. Uncommon. Fellfield or alpine meadow, collected at 3658 m. AA.

Arenaria rubella. Common. Generally of the fellfield, to above 3658 m. CP.

Cerastium beeringianum. Common. Alpine meadow or fellfield, to above 3749 m. WC.

Sagina saginoides. Apparently known for the area only from a collection by Knowlton (Little 1941). CP.

Silene acaulis subsp. *subcaulescens.* Common. Usually of fellfield but also of alpine meadow, to above 3658 m. SRM.

Stellaria umbellata. Common. Tangled mats in crevices provided by overlapping boulders, to above 3658 m. CP.

Crassulaceae

Sedum rhodanthum. Common. Cracks and crevices, alpine meadow or fellfield, to above 3658 m. WC.

Gentianaceae

**Gentianella amarella* subsp. *heterosepala.* Rare. Alpine meadow, one collection, at about 3566 m. SW.

Gentianella barbellata. Uncommon. Alpine meadow or occasionally fellfield, to 3658 m. SRM.

Gentianella tenella. Rare. Alpine meadow, often in mats of other plants, to 3658 m. CP.

Onagraceae

**Epilobium angustifolium.* Uncommon. Fellfield or alpine meadow, noticed only on the south-facing slopes of Agassiz, to 3658 m. CP?

Polemoniaceae

**Polemonium pulcherrimum* var. *delicatum.* Rare. Known for the alpine from a single collection, *Moore s.n.* (ASC 12618), apparently made at or near the summit of Humphrey Peak, 3853 m. SRM.

Polemonium viscosum. Very common. Fellfield or occasionally alpine meadow, to above 3658 m. WC.

Polygonaceae

Oxyria digyna. Uncommon. Cracks and crevices, boulder-protected at lower elevations, growing more exposed on the highest north-facing slopes of Agassiz, to 3749 m or more. CP.

Primulaceae

Androsace septentrionalis. Common. Alpine meadow or fellfield, to above 3658 m. CP.

Primula parryi. Rather common. Alpine meadow and in protective recesses provided by boulders, to above 3658 m. RM.

Ranunculaceae

Anemone multifida var. *tetonensis*. Rare. Alpine meadow, to 3658 m. SRM.

Ranunculus inamoenus subsp. *subaffinis*. Common. Alpine meadow, to 3658 m. This subspecies is endemic to the San Francisco Mountain. E.

Ranunculus pedatifidus (includes var. *affinis*). Common. Alpine meadow or fellfield, to above 3658 m. CP.

Rosaceae

**Fragaria ovalis*. Rare. Known only from one restricted area on the south slope of Agassiz, to 3627 m. SRM.

Geum rossii var. *turbinatum*. Abundant. Alpine meadow and fellfield, above 3749 m. WC.

Potentilla concinna. Uncommon. Fellfield, about 3658 m. RM.

Potentilla diversifolia. Very common. Alpine meadow or fellfield, to above 3749 m. WC.

Potentilla subviscosa. Rare. Fellfield, reported from the area by Kearney and Peebles (1964) and McDougall (1973). SW.

Sibbaldia procumbens. Uncommon. Alpine meadow, to 3658 m. CP.

Saxifragaceae

Heuchera versicolor. Common. Cracks, crevices and alcoves formed by boulders, the typical form to 3658 m; forma *pumila* to above 3749 m. SW.

**Ribes montigenum*. Uncommon. Boulder-protected areas or protected alpine meadow, to 3658 m. WC.

Saxifraga caespitosa (ours referred to as subsp. *exaratoides*). Uncommon. Cracks and crevices, fellfield and alpine meadow, to 3658 m. CP.

Saxifraga debilis. Uncommon. Boulder-protected areas, to above 3658 m. WC.

Saxifraga flagellaris. Uncommon. Boulder-protected areas, and occasionally alpine meadow, to above 3658 m. CB.

Saxifraga rhomboidea var. *franciscana*. Common. Most common in alpine meadow, to above 3658 m. RM.

Scrophulariaceae

Pedicularis parryi. Rather common. Largely of alpine meadow, to 3658 m. SRM.

Penstemon whippleanus. Common. Alpine meadow or fellfield, to above 3658 m. SRM.

Veronica wormskjoldii. Rare. Alpine meadow, to 3658 m. AA.

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ALPINE FLORA OF THE SWEETWATER MOUNTAINS, MONO COUNTY, CALIFORNIA

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ABSTRACT

The Sweetwater Mountains of Mono County, California, lie along the transition between Sierra Nevada and Great Basin floras. The alpine zone of the range, defined as the area above that dominated by shrubby *Artemisia* species of the section Tridentae, is 16 km^2. The zone includes persistent snowdrifts and streams, some frost-sorted soils, and four rock substrates: rhyolite, andesite, granite, and quartz monzonite. The alpine flora includes 173 species of vascular plants. Many taxa show considerable preference for a single substrate. Ninety-four percent of the Sweetwater alpine taxa are also found in the Sierra Nevada, 75% in the Great Basin, 52% in the southern Rocky Mountains, and 18% in the Arctic.

A comparison of alpine floristics of four ranges along the western perimenter of the Great Basin (the Sweetwater, Wassuk, White, and Spring Mountains) indicates that the Sweetwater and Wassuk alpine zones are relatively less isolated than the other islands. The unusually large flora of the Sweetwaters may be related to the range's accessibility to both Great Basin and Sierra Nevada floras and to the presence of appropriate microsites for both Great Basin xerophytes and Sierran mesophytes.

INTRODUCTION

A series of three mountain ranges in western Nevada and eastern California contain the westernmost alpine areas of the Great Basin. The floras of the southern two, the Spring Mountains (Clark County, Nevada) and the White Mountains (Mono County, California, and Esmeralda County, Nevada), have been described in detail by Clokey (1951) and Lloyd and Mitchell (1973), respectively. The alpine flora of the third, the Sweetwater Mountains (Mono County, California), has been only partially documented (Major and Taylor 1977). Although these ranges all lie along the western perimeter of the Great Basin, they form alpine islands with considerably different degrees of isolation.

The Spring Mountains are the most remote from other alpine areas because three desert ranges and four deep valleys separate them from the Sierra Nevada to the west. The nearest alpine area to the east lies on the Markagunt Plateau (Iron County, Utah), 190 km distant. Clokey (1951) found the Spring Mountain flora to have been derived from

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both the flora of the Sierra Nevada and that of southwestern Utah. The range has an exceptionally high degree of endemism, which Clokey attributed to a long period of isolation.

The White Mountains, separated from the Sierra Nevada by Owens Valley, have a much more Sierran flora than the Spring Mountains (Lloyd and Mitchell 1973). Their lower degree of isolation is also reflected in a smaller endemic flora despite a much larger area at high elevations.

The Sweetwater Mountains lie only 33 km east of the crest of the Sierra Nevada with a possible route for overland plant migration across Devil's Gate at 2281 m elevation. Immediately to the east of the Sweetwaters, the Wassuk Range (Mineral County, Nevada) contains a strong Sierran element in its alpine flora (Bell and Johnson 1980), suggesting that both ranges may be readily accessible to Sierran taxa. The Sweetwaters might, therefore, be expected to have an alpine flora heavily influenced by the Sierra Nevada, but the partial species list by Major and Taylor (1977) indicates that widespread Cordilleran and Great Basin species both outnumber Sierran taxa in the Sweetwaters. This report presents a more complete species list for the alpine zone of the Sweetwater Mountains, allowing for a more precise comparison of alpine floristics along the western perimeter of the Great Basin.

The Alpine Zone of the Sweetwater Mountains

The geology of the Sweetwater Mountains is complex and incompletely described. Surface rocks in the alpine zone are primarily Miocene rhyolite and andesite with small outcrops of Cretaceous quartz monzonite and granite (Slemmons 1966; G. F. Brem, pers. comm.). Much of the rhyolite has been silicified, and some of the andesite has undergone intense hydrothermal alteration (G. F. Brem, pers. comm.).

The alpine zone lies on a rolling upland cut by a number of deep canyons. The canyon sides are primarily unstable talus; there are few cliffs.

Soils are, for the most part, poorly developed with no organic horizons and little evidence of leaching. Exceptions are found, however, in boggy sedge meadows along a few drainages. Many of the flat upland surfaces are covered by sorted polygons, and some slopes have sorted rock stripes. Andesite-derived soils have a high clay content in many areas, and these fine-textured soils are heavily worked by pocket gophers.

The climate of the Sweetwater Mountains is, to our knowledge, undescribed. The range has a number of snowbanks that persist through the summer even in years of regional drought. Springs and seeps also furnish water in summer, despite long periods without summer rainfall. Thus, the Sweetwaters have the appearance of being more mesic than most Great Basin ranges.

The high elevation vegetation in the Sweetwaters has been partially described by Major and Taylor (1977). In a few places, scattered whitebark pines form a boundary for the alpine zone. Throughout much the range, woody *Artemisia* species of the section Tridentae are replaced at higher elevations by low shrub communities, generally dominated by *Chrysothamnus* spp., above which are barren slopes with scattered grasses and cushion plants. Seeps and protected flats support a more dense meadow vegetation; and lush sedge meadows occur along a few streams, especially Frying Pan Creek and its tributaries. In an earlier study (Bell and Johnson 1980) we suggested that the upper edge of the shrubby *Artemisia* community forms the equivalent of treeline where trees are absent in Great Basin ranges. This definition appears applicable to the Sweetwater Mountains, and plants included in this species list were all found above that boundary.

Collections were made in the Sweetwater Mountains during the summers 1976–1979 and 1982. Nomenclature follows Kartesz and Kartesz (1980). Voucher specimens are deposited in UNLV and WS. Geographical distributions are based on the following: Sierra Nevada (SN): Munz (1973), Sharsmith (1940), Taylor (1976a); White Mountains: Lloyd and Mitchell (1973); Great Basin (GB): Cronquist et al. (1972, 1977), Hansen (1956), Hunter and Johnson (unpublished data), Lewis (1971, 1973, 1975), Linsdale et al. (1952), Loope (1969), McMillan (1948), Preece (1950); southern Rocky Mountains (Ro): Harrington (1964), Weber (1976); Arctic (Ar): Polunin (1959).

ALPINE PLANTS OF THE SWEETWATER RANGE

LYCOPHYTA

Selaginellaceae

Selaginella watsonii. Uncommon; among rocks in snow accumulation areas on rhyolite. SN, GB.

PTEROPHYTA

Aspidiceae

Cystopteris fragilis. Uncommon; among rocks on north-facing slopes, under winter snow; not found on andesite. SN, GB, Ro, Ar.

Woodsia oregana. Rare; from a single rocky granite slope south of Wheeler Peak. SN, GB, Ro.

ANTHOPHYTA—MONOCOTYLEDONEAE

Cyperaceae

Carex brevipes. Locally common in small areas of dry, generally gravelly, soil; on rhyolite and granite. SN, GB, Ro.

Carex douglasii. Rare; in dry gravel flats on rhyolite. SN, GB, Ro.

Carex foetida. Very rare; in a single wet sedge meadow south of Wheeler Peak; in organic soil. SN, Ro.

Carex haydeniana. Rare; at seeps on talus slopes. SN, GB, Ro.

Carex helleri. Common; generally in deep snow accumulation areas, less common at persistent seeps on talus slopes; on various rock types. SN, GB.

Carex heteroneura var. *brevisquama.* Locally common; in moist snow accumulation areas; primarily on rhyolite. SN, GB, Ro, Ar.

Carex jonesii. Very rare; in moist gravel on the northeast slope of Wheeler Peak. SN, GB, Ro.

Carex leporinella. Extremely rare; in organic soil in a single wet meadow south of Wheeler Peak. SN.

Carex microptera. Uncommon; in wet, rocky soil of deep snow accumulation areas; generally on rhyolite. SN, GB, Ro.

Carex phaeocephala. Common; in snow accumulation areas; most common on rhyolite but also found on dacite, andesite and granite. SN, GB, Ro.

Carex scopulorum. Rare; in wet meadows below persistent snowbanks; on rhyolite. SN, GB, Ro.

Carex straminiformis. Rare; in deep gullies, generally on rocky slopes under winter snow but melting in early summer. SN.

Carex subnigricans. Dominant in flat or nearly flat meadows that remain wet and cold throughout the summer; forming deep turf. SN, GB.

Juncaceae

Juncus balticus var. *montanus.* Locally abundant, but restricted to a single slope of weathered andesite on the ridge between South Sister and the southern portion of the range. SN, GB, Ro, Ar.

Juncus orthophyllus. Rare; known from a single wet sedge meadow along Frying Pan Creek; in organic soil. SN, GB.

Juncus parryi. Moderately common; moist to dry gravel slopes; generally on rhyolite. SN, GB, Ro.

Luzula multiflora subsp. *comosa.* Uncommon; in organic soils of wet sedge meadows. SN, GB, Ro, Ar.

Luzula spicata. Uncommon; in areas of shallow snow accumulation on gravel soils of various rock types. SN, GB, Ro, Ar.

Poaceae

Agropyron pringlei. Uncommon; in loose scree; on rhyolite and dacite. SN.

Agrostis variabilis. Uncommon; very wet meadows; in organic soil. SN, GB, Ro.

Alopecurus geniculatus. Very rare; in a single persisting, shallow pool below a melting snowbank; on andesite. SN, Ro, Ar.

Calamagrostis purpurascens. Uncommon; on rocky, but stable, slopes; on all rock types. SN, GB, Ro, Ar.

Deschampsia caespitosa. Locally dominant; in wet meadows; in organic soil. SN, GB, Ro, Ar.

Elymus cinereus. Rare; on rocky, stable slopes; on grante. GB, Ro.

Festuca brachyphylla. Abundant; generally present except in deep snow accumulation areas; on rock types but more common on rhyolite. SN, GB, Ro, Ar.

Hordeum brachyantherum. Very rare; at a single site in upper Ferris Creek Canyon. SN, GB, Ro.

Koeleria cristata. Rare; on south-facing slopes; absent on andesite. SN, GB, Ro.

Leucopoa kingii. Uncommon; on stable rocky slopes in snow accumulation areas; on rhyolite. SN, GB, Ro.

Muhlenbergia richardsonis. Locally dominant in small areas, absent elsewhere; generally on level sites in gravelly or fine-textured andesite soils. SN, GB, Ro.

Oryzopsis hymenoides. Very rare; in a single site on the rocky ridge between South Sister and the plateau to the south; on andesite. SN, GB, Ro.

Phleum alpinum. Uncommon; in wet meadows; in organic soil. SN, GB, Ro, Ar.

Poa cusickii. Locally dominant; in flat to sloping meadows in fine-textured soils; usually on rhyolite. SN, GB, Ro.

Poa fendleriana. Uncommon; on rocky slopes in snow accumulation areas; most common on andesite. SN, GB, Ro.

Poa leibergii. Very rare; along the edges of wet meadows fed by persistent snowbanks; on rhyolite. SN.

Poa leptocoma. Very rare; in a wet meadow along upper Frying Pan Creek; in organic soil. SN, GB, Ro, Ar.

Poa nervosa. Rare; on steep, rocky slopes, probably under winter snow accumulation, in upper Ferris Canyon; on rhyolite. SN, GB, Ro.

Poa rupicola. Abundant and ubiquitous except in deep snow accumulation sites; most common on rhyolite, but present on other rock types. SN, GB, Ro.

Poa suksdorfii. Common; in many habitats, especially on scree and in shallow snow accumulation areas; more common on rhyolite, quartz monzonite, and granite than on andesite. SN.

Sitanion hystrix. Abundant and ubiquitous except in areas of deep snow accumulation; on all substrates except organic soil. SN, GB, Ro.

Stipa nevadensis. Rare; on rocky slopes at the head of Ferris Canyon; on rhyolite and andesite. SN, GB.

Stipa pinetorum. Rare; on a single, east-facing slope at the head of Ferris Canyon; on rhyolite. SN, GB, Ro.

Trisetum spicatum. Uncommon; in wet meadows and in some moist, rocky snow accumulation areas; on various substrates. SN, GB, Ro, Ar.

ANTHOPHYTA—DICOTYLEDONEAE

Apiaceae

Cymopterus cinerarius. Moderately common on andesite scree; rare on slopes in snow accumulation areas on rhyolite. SN.

Asteraceae

Achillea millefolium var. *alpicola.* Very rare; in moist scree at a rhyolite-andesite contact on Wheeler Peak; much more common slightly lower with *Artemisia nova.* SN, GB, Ro.

Agoseris glauca var. *monticola.* Uncommon; in snow accumulation areas on weathered andesite and dacite. SN, GB, Ro.

Antennaria alpina var. *media.* Moderately common; on rocky slopes of early-melting snow and in some wet meadows; on andesite, rhyolite and granite. SN, GB, Ro, Ar.

Antennaria corymbosa. Rare; moist meadows in organic soil. SN, GB, Ro.

Antennaria microphylla. Moderately common; on rocky areas that are probably under shallow winter snow; most common on rhyolite but present on other parent materials. SN, GB, Ro, Ar.

Antennaria umbrinella. Uncommon; gravelly to rocky soils in areas of shallow snow accumulation; on andesite. SN, GB, Ro, Ar.

Arnica longifolia. Very rare; on a single talus slope at the head of Ferris Canyon. SN, GB, Ro.

Artemisia ludoviciana subsp. *incompta.* Rare; on stable rocky rhyolite slopes near the lower edge of the alpine zone. SN, GB, Ro.

Aster alpigenus subsp. *andersonii.* Rare; in wet sedge meadows with organic soil. SN.

Chaenactis douglasii var. *rubricaulis.* Uncommon; on unstable scree and in disturbed sites on both rhyolite and andesite. SN.

Chrysothamnus parryi subsp. *monocephalus.* Moderately common; on rocky rhyolite slopes near the lower edge of the alpine zone; uncommon in similar sites at higher elevations. SN.

Chrysothamnus viscidiflorus subsp. *viscidiflorus.* Moderately common; on rocky rhyolite slopes near the lower edge of the alpine zone; uncommon in similar sites at higher elevations. SN, GB, Ro.

Crepis nana. Locally common; on andesite scree. SN, GB, Ro, Ar.

Dugaldia hoopesii. Uncommon; mostly in wet or moist meadows in organic soil; also rare on rocky andesite slopes. SN, GB, Ro.

Erigeron clokeyi. Rare; on rocky rhyolite or andesite slopes, usually on south-facing slopes near the lower edge of the alpine zone. SN.

Erigeron compositus var. *glabratus*. Uncommon; on rocky ridges on both rhyolite and andesite. SN, GB, Ro, Ar.

Erigeron petiolaris. Moderately common; on mesic scree in areas of shallow snow accumulation; mostly on rhyolite. SN.

Erigeron pygmaeus. Moderately common; on mineral soil in moist snow accumulation areas; on all rock types but more common on rhyolite. SN.

Eriophyllum lanatum var. *integrifolium*. Uncommon; in snow accumulation sites on rhyolite, granite, and altered andesite slopes. SN, GB.

Haplopappus apargioides. Locally common; on andesite scree or gravel surfaces. SN, GB.

Haplopappus macronema. Uncommon; generally on steep slopes or cliff ledges near the lower edge of the alpine zone; more abundant on andesite than on rhyolite. SN, GB, Ro.

Haplopappus suffruticosus. Rare; known from two sites on rocky rhyolite near the lower edge of the alpine zone. SN, GB.

Hulsea algida. Locally common in snow accumulation areas on deeply weathered andesite slopes; rare on rhyolite. SN, GB.

Hymenoxys cooperi var. *canescens*. Moderately common; on andesite and dacite slopes. GB.

Raillardella argentea. Uncommon; in snow accumulation areas, most commonly on east- or north-facing slopes; on gravelly rhyolite or rarely andesite. SN.

Senecio canus. Very rare; in a single snow accumulation area on stable andesite scree on the ridge connecting South Sister and the southern portion of the range. SN, GB, Ro.

Senecio integerrimus var. *exaltatus*. Rare; in flat, protected sites near the lower edge of the alpine zone; on andesite. SN, GB, Ro.

Senecio pattersonianus. Locally common; probably under at least shallow winter snow on rhyolite scree and quartz monzonite. Sweetwater and Wassuk Ranges.

Senecio werneriifolius. Locally common on gravelly slopes, most generally on east-facing slopes, in areas of shallow snow accumulation; mostly on andesite. SN, GB, Ro.

Solidago multiradiata. Very rare; known from only two sites in flat meadows. SN, GB, Ro, Ar.

Taraxacum officinale. Rare; in disturbed snow accumulation areas; mostly on andesite. SN, GB, Ro, Ar.

Townsendia condensata. Rare; in disturbed snow accumulation areas; mostly on andesite. White and Sweetwater Ranges.

Boraginaceae

Cryptantha glomeriflora. Rare; in most gravels. SN.

Cryptantha humilis. Uncommon; on rhyolite scree slopes, usually on exposed sites. SN, GB.

Cryptantha nubigena. Uncommon; on andesite slopes. SN.

Cryptantha watsonii. Rare; on a single disturbed gravel slope at the head of Ferris Canyon. SN, GB, Ro.

Brassicaceae

Anelsonia eurycarpa. Uncommon, but consistently present on loose andesite scree; rare elsewhere. SN.

Arabis inyoensis. Very rare; known from a single site on the south ridge of South Sister; in a community of low shrubs on andesite near the lower edge of the alpine zone. SN.

Arabis lemmonii var. *depauperata.* Moderately common in early-melting snow accumulation areas; on all substrates, but most common on rocky slopes. SN, GB, Ro.

Arabis lyallii. Rare; in early-melting snow accumulation areas on moist to dry rocky soils. SN, GB.

Arabis microphylla. Uncommon; in shallow snow accumulation areas, including frost-sorted polygons; principally on rhyolite. GB.

Arabis platysperma. Very rare; known from a single talus slope at the head of Ferris Canyon. SN, GB.

Barbarea orthoceras. Rare; found in two wet meadows in organic soils. SN, GB, Ro, Ar.

Descurainia richardsonii subsp. *viscosa.* Moderately common in fine-textured soils in snow accumulation areas; generally on andesite. SN, GB, Ro.

Draba albertina. Very rare; in a single moist meadow in mineral soil; on andesite. SN, GB, Ro.

Draba breweri. Locally common among rhyolite rocks, especially along the edges of fine-textured soil in frost-sorted polygons. SN.

Draba crassifolia var. *nevadensis.* Uncommon; in deep snow accumulation areas in pockets of fine-textured soil. SN, GB.

Draba densifolia. Locally abundant in gravelly soil of fellfields or shallow snow accumulation areas on both rhyolite and andesite. SN, GB, Ar.

Draba lemmonii var. *incrassata.* Very common in deep snow accumulation areas of rhyolite scree. A few individuals have completely glabrous leaves. Endemic.

Draba sierrae. Locally abundant; with *D. densifolia.* SN, GB.

Erysimum perenne. Moderately common in many habitats, especially under shallow winter snow and in subshrub communities; on both rhyolite and andesite. SN, GB.

Lesquerella cordiformis. Very rare; on dry east-facing scree on andesite. GB.

Caryophyllaceae

Arenaria aculeata. Moderately common; on well-drained scree slopes and flats; not usually on andesite. SN, GB.

Cerastium earlei. Common; in moist scree or mineral soil in shallow snow accumulation areas; generally on rhyolite. SN, GB, Ro.

Minuartia nuttallii subsp. *gracilis.* Moderately common; on well-drained scree slopes; more common on andesite, but also on rhyolite substrates. SN, GB.

Minuartia rossii. Rare; among rhyolite rocks on Mt. Patterson. SN, Ro, Ar.

Minuartia rubella. Rare; in moist mineral soil in sorted polygons; on rhyolite. SN, Ro, Ar.

Sagina saginoides. Rare; in organic soil in wet meadows. SN, GB, Ro, Ar.

Silene sargentii. Uncommon; on moist gravel slopes in snow accumulation areas on all rock types. SN.

Stellaria crispa. Uncommon; in wet sedge meadows. SN, GB.

Fabaceae

Astragalus kentrophyta var. *danaus.* Moderately common; on andesite scree slopes and gravel flats. SN.

Astragalus platytropis. Uncommon; on andesite scree slopes. SN, GB.

Astragalus purshii var. *lectulus.* Moderately common on andesite scree; rare on exposed slopes on other substrates. SN.

Astragalus whitneyi. Locally abundant in flat areas or gentle slopes among low shrubs near the lower edge of the alpine zone; on andesite; rarely present elsewhere. SN, GB.

Lupinus breweri var. *bryoides.* Locally abundant, but restricted to stable granite and quartz monzonite slopes near the lower edge of the alpine zone. SN.

Lupinus caudatus. Rare; in communities of low shrubs on andesite near the lower edge of the alpine zone. SN, GB.

Lupinus meionanthus. Rare; near the lower edge of the alpine zone in areas of shallow snow accumulation on andesite. SN.

Lupinus sellulus var. *lobbii.* Locally very abundant in many areas on flats and gentle slopes; mostly in fine-textured and disturbed soils of both rhyolite and andesite origin. In many places, there are large numbers of dead individuals heaved out of the soil, apparently by frost action. SN, GB.

Oxytropis parryi. Uncommon; restricted to andesite scree. SN, GB, Ro.

Trifolium longipes. Rare; in wet sedge meadows. SN, GB, Ro.

Trifolium monanthum. Rare; in sedge meadows and wet gravels along Frying Pan Creek. SN, GB.

Gentianaceae

Gentiana tiogana. Locally common in wet sedge meadows along the Frying Pan Creek drainage; in organic soil. SN.

Hydrophyllaceae

Phacelia frigida. Locally common on weathered andesite soils in areas of shallow snow accumulation or more exposed sites. SN.

Lamiaceae

Monardella odoratissima subsp. *parvifolia.* Rare; at a single location at the head of Ferris Canyon on rocky soil protected by shrubs. SN, GB, Ro.

Linaceae

Linum lewisii. Moderately common; on andesite scree and flats, especially near the lower edge of the alpine zone. SN, GB, Ro, Ar.

Onagraceae

Epilobium anagallidifolium. Uncommon; in wet areas along persistent streams or seeps. SN, GB, Ro, Ar.

Gayophytum racemosum. Moderately common; in open sites on gravelly soil in rhyolite and andesite. SN, GB, Ro.

Polemoniaceae

Ipomopsis congesta subsp. *montana.* Moderately common on andesite scree and less common on unstable rhyolite slopes. SN, GB.

Leptodactylon pungens subsp. *hallii.* Moderately common in communities of low shrubs on dry, rocky slopes. Some individuals approach *L. pungens* subsp. *pulchriflora.* GB; SN for *L. p. pulchriflora.*

Phlox caespitosa subsp. *pulvinata.* Abundant; in nearly all habitats except deep snow accumulation areas and steep barren scree. SN, GB, Ro.

Polemonium chartaceum. Rare; restricted to rocky rhyolite on South Sister and Mt. Patterson. White and Sweetwater Ranges.

Polemonium pulcherrimum. Uncommon; along the upper edges of snow accumulation areas; more common on andesite and dacite than on rhyolite. SN, GB, Ar.

Polygonaceae

Eriogonum anemophilum. Moderately abundant in highly weathered andesite soils, especially on exposed ridges and fellfields; uncommon to absent elsewhere. SN, GB.

Eriogonum lobbii. Locally abundant but known only from a single gentle gravel slope in a snow accumulation area along upper Frying Pan Creek. SN, GB.

Eriogonum ovalifolium var. *nivale.* Locally abundant; in fellfields on rhyolite and quartz monzonite; uncommon on rocky andesite slopes and in snow accumulation areas. SN, GB, Ro.

Eriogonum umbellatum var. *umbellatum*. Very rare; found in a single site on the northwest slope of South Sister near timberline; on rhyolite talus. SN, GB, Ro.

Oxyria digyna. Locally abundant; on wet, rocky north-facing slopes; generally on rhyolite. SN, GB, Ro, Ar.

Polygonum douglasii. Rare; in wet gravels. SN, GB, Ro.

Polygonum kelloggii. Rare; on moist soils of a few snow accumulation areas on both rhyolite and andesite. SN, GB, Ro.

Rumex californicus. Rare; in meadows that remain cold and wet throughout the summer. SN.

Rumex paucifolius subsp. *gracilescens*. Uncommon; in fine-textured soils in areas of shallow winter snow accumulation; generally on dacite. SN.

Portulacaceae

Calyptridium umbellatum. Locally abundant in fine-textured mineral soils of snow accumulation areas; found on various substrates, but most common in weathered andesite worked by pocket gophers. SN, GB.

Claytonia nevadensis. Uncommon; in moist rhyolite scree on Mt. Patterson; very rare elsewhere. SN.

Claytonia umbellata. Uncommon; in wet rhyolite scree. SN, GB.

Lewisia pygmaea. Locally common at the upper edge of some snow accumulation areas and in wet and moist meadows. SN, GB, Ro.

Montia chamissoi. Locally abundant in wet areas around springs along Frying Pan Creek and its tributaries; in organic soil on rhyolite. SN, GB, Ro.

Primulaceae

Androsace septentrionalis var. *subumbellata*. Moderately common in snow accumulation areas and moist or wet meadows; more common on rhyolite than andesite. SN, GB, Ro.

Dodecatheon alpinum. Rare; in wet sedge meadows. SN, GB.

Ranunculaceae

Ranunculus eschscholtzii var. *oxynotus*. Locally abundant in deep snow accumulation areas; most common on rhyolite scree. SN.

Rosaceae

Geum canescens. Rare; known from a single location in a moist meadow at the lower edge of the alpine zone along Frying Pan Creek. SN.

Holodiscus dumosus var. *glabrescens*. Very rare; a single individual found on an east-facing rhyolite cliff on Mt. Patterson. SN, GB, Ro.

Ivesia gordonii. Moderately common; in shallow snow accumulation areas in fine-textured soils; generally on andesite, less common on rhyolite. SN, GB, Ro.

Ivesia lycopodioides. Uncommon; on rocky, moist soils in snow accumulation areas; most common on north-facing slopes. SN.

Potentilla breweri. Locally abundant on slopes of quartz monzonite; absent elsewhere. SN, GB.

Potentilla drummondii. Rare; in deep turf of wet meadows. SN, GB.

Potentilla pensylvanica var. *strigosa.* Uncommon; on dry, stable rhyolite slopes and fellfields and in frost-sorted polygons. SN, GB, Ro, Ar.

Potentilla pseudosericea. Rare; in fine-textured mineral soil at the center of sorted polygons near Wheeler Peak; on rhyolite. SN, GB, Ro.

Sibbaldia procumbens. Locally common in areas that remain cold and moist throughout the summer; on all substrates. SN, GB, Ro, Ar.

Rubiaceae

Galium hypotrichium subsp. *hypotrichium.* Rare; on east-facing andesite scree. SN.

Salicaceae

Salix orestera. Very rare; in wet sedge meadows along streams fed by persistent snowbanks. SN, GB.

Saxifragaceae

Heuchera duranii. Uncommon; on rocky slopes of quartz monzonite and granite; generally in drier areas of early-melting snow accumulation. White, Sweetwater, Wassuk Ranges.

Ribes cereum. Moderately common; principally on stable rocky slopes of andesite or rhyolite; not present in the most exposed sites. SN, GB, Ro.

Ribes inebrians. Rare; on rocky andesite slopes. SN, GB, Ro.

Ribes montigenum. Very rare; known from a single snow accumulation area at the lower edge of the alpine zone along the south ridge of South Sister. On andesite. SN, GB, Ro.

Scrophulariaceae

Castilleja nana. Moderately common in snow accumulation areas; generally on andesite, but also on dacite and rhyolite. SN, GB.

Limosella aquatica. Rare; in a single pool of standing water in a boggy meadow in upper Frying Pan Creek. SN, GB, Ro, Ar.

Mimulus coccineus. Locally abundant in disturbed gravels; on all substrates. SN, GB.

Mimulus primuloides. Rare; in wet sedge meadows near the lower edge of the alpine zone. SN, GB.

Mimulus suksdorfii. Rare; in moist unstable gravels of deep snow accumulation areas. SN, GB, Ro.

Mimulus tilingii. Rare; on the edge of a single wet sedge meadow on the south slope of Wheeler Peak. SN, GB, Ro.

Pedicularis attollens. Rare; in wet sedge meadows. SN.

Penstemon davidsonii. Very rare; found only on an east-facing rhyolite cliff south of Mt. Patterson. SN, GB.

Penstemon heterodoxus. Rare; in fairly flat, moist, gravelly soil near the lower edge of the alpine zone; on both andesite and rhyolite. SN.

Penstemon procerus. Rare; in flat, moist gravels along Frying Pan Creek. SN, GB, Ro.

Penstemon speciosus. Very rare; at the lower edge of the alpine zone in andesite soils; much more common in nearby *Artemisia nova* communities. SN, GB.

Veronica wormskjoldii. Very rare; in wet organic soils along Frying Pan Creek. SN, GB, Ro, Ar.

Valerianaceae

Valeriana californica. Rare; in a single snow accumulation area on andesite scree on the south ridge of South Sister. SN, GB.

DISCUSSION

The alpine flora of the Sweetwater Range with 173 species of vascular plants is unusually diverse. Among Great Basin ranges, larger alpine floras have been described only in the Ruby Mountains with 189 species (Billings 1978) and the White Mountains with about 200 species (Lloyd and Mitchell 1973).

The 173 species in the alpine zone of the Sweetwaters are found in an area of only 16.0 km^2. Plant species-area curves for Great Basin montane zones predict only about 120 species in such an area (Harper et al. 1978), although the same curve accurately predicted the size of the alpine flora of the Wassuk Range, 48 km to the east of the Sweetwaters (Bell and Johnson 1980). The species-area curves of Harper et al. (1978), however, suggest that the Sweetwater flora is more like that of an island than that of a mainland. The latter would have about 300 species in a comparable area.

The richness of the Sweetwater alpine flora must result in part from the unusual diversity of habitats available in the small alpine area. These habitats range from flat meadows to cliffs, from xeric talus and scree slopes to wet meadows and ponds, from stable meadows and slopes to actively frost-mobile soils and loose scree. The geology of the range also appears to exert a highly significant influence on plant distributions within the range. The two predominant rock types, rhyolite and andesite, offer very different chemical and thermal re-

Table 1. Geographic Distribution of Alpine Plants in Four Mountain Ranges Along the Western Perimeter of the Great Basin. Distributions of SN (Sierra Nevada), BG (Great Basin), Ro (southern Rocky Mountain) and Ar (Arctic) species are based upon references cited in the text.

	Contribution to flora							
	Sweetwater		Wassuk		White		Spring	
Distribution	Number of taxa	Percent of flora	Number of taxa	Percent of flora	Number of taxa	Percent of flora	Number of taxa	Percent of flora
SN	34	19.7	5	7.1	31	17.8	1	2.4
SN, GB	38	22.0	16	22.9	27	15.5	3	7.3
SN, GB, Ro	58	33.5	28	40.0	55	31.6	8	19.5
SN, GB, Ro, Ar	27	15.6	13	18.6	28	16.1	6	14.6
GB	4	2.3	4	5.7	4	2.3	3	7.3
GB, Ro	1	0.6	1	1.4	5	2.9	2	4.9
GB, Ro, Ar	0	—	0	—	1	0.6	0	—
SN, GB, Ar	2	1.2	1	1.4	0	—	0	—
SN, Ro, Ar	3	1.7	0	—	2	1.1	1	2.4
SN, Ro	1	0.6	0	—	4	2.3	0	—
Spring, White, Sweetwater, Wassuk only	4	2.3	2	2.9	5	2.9	1	2.4
Ro	0	—	0	—	2	1.1	0	—
Ro, Ar	0	—	0	—	1	0.6	0	—
Endemic	1	0.6	0	—	3	1.7	9	22.0
Southern Utah	0	—	0	—	0	—	2	4.9
Other	0	—	0	—	4	2.3	5	12.2

gimes, and many species are clearly confined to a single rock type. Contacts between substrates generally delimit abrupt transitions between plant associations. Restriction of local plant distributions by rock type has been reported only rarely for alpine areas, and the clear examples of such limitation seen in the Sweetwaters make the range attractive for future studies of the role of edaphic factors in determining local plant distribution.

The position of the Sweetwater Mountains along the transition between the Great Basin and Sierra Nevada floras also appears to contribute to the large number of species present. To assess the significance of this location, it is helpful to compare the alpine flora of the Sweetwaters with those of the Wassuk, White and Spring Mountains. Analysis of the Wassuk flora can be derived from Bell and Johnson (1980). An alpine species list for the White Mountains was developed from Lloyd and Mitchell's (1973) flora, including all taxa listed above 3200 m and those found in wet meadows or rocky slopes devoid of trees between 3000 and 3200 m. This method identified 174 alpine taxa compared with approximately 125 strictly alpine and 75 facul-

TABLE 2. PERCENT OF FLORA IN WESTERN GREAT BASIN RANGES FOUND IN OTHER REGIONS.

Region	Percent of flora			
	Sweetwater	Wassuk	White	Spring
Sierra Nevada	94.2	90.0	85.1	46.3
Great Basin	75.1	90.0	69.0	53.7
Southern Rocky Mountains	52.0	60.0	56.3	41.5
Arctic	18.5	20.0	19.0	17.1
Endemic	0.6	0.0	1.8	22.0

tative alpine taxa cited by Lloyd and Mitchell (1973). For Mt. Charleston in the Spring Mountains a list of 41 species likely to be found in the alpine zone was derived from Clokey (1951) by including all taxa occurring above 3300 m and all timberline species. These White and Spring Mountain alpine floras were analyzed by the same methods applied to the Wassuk and Sweetwater floras.

Results of this comparison (Tables 1, 2) show that, of all the ranges along the western edge of the Great Basin, the Sweetwaters have the highest proportion of their taxa in common with the Sierra Nevada and the second highest proportion in common with the Great Basin. Thus, the proximity to both floristic provinces appears significant for the presence of an unusually diverse alpine flora.

The low degree of isolation of the Sweetwater and Wassuk ranges is also clear from the virtual absence of endemics in their alpine floras. The lower and hotter valleys between ranges to the south serve to isolate the White and especially the Spring Mountains, thereby allowing evolution of endemic taxa (Clokey 1951, Billings 1978).

The largest floristic element in all four ranges is made up of species that are widespread in western North America. This pool of widespread species (including many members of the Cyperaceae, Poaceae, and Rosaceae) appears to exhibit unusual mobility, although no common feature of seed morphology suggests an obvious mode of migration. Billings (1978) notes that Sierran plants appear to be generally poor at migrating eastward. A modest number of Great Basin taxa also appear unable to invade the Sierra Nevada from the Sweetwater or White Mountains. Taylor (1976b) reports a number of Great Basin taxa occurring in the vicinity of Carson Pass in the northern Sierra Nevada, but other species (e.g., *Elymus cinereus, Arabis microphylla, Lesquerella cordiformis*) appear to reach their western limits in the Sweetwater Mountains. These species have dispersed across the broad, low-lying valleys separating the Wassuk-Sweetwater complex from Great Basin ranges to the east. The high pass between the Sweetwaters and Sierra Nevada should be a trivial barrier by comparison. The failure of these plants to migrate further west supports Taylor's (1976b) hypothesis that competition from mesophytes in the Sierra Nevada is intolerable to some plants adapted to the more xeric conditions of the rain shadow. Although dispersal mechanisms remain unknown, the presence of very widespread taxa may reflect broad ecological tolerances rather than just some particularly effective mode of migration.

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LEAF FLAVONOID CHEMISTRY AND THE TAXONOMY OF *COREOPSIS* SECTIONS *PUGIOPAPPUS* AND *EULEPTOSYNE* (COMPOSITAE)

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Abstract

Members of *Coreopsis* sects. *Pugiopappus* and *Euleptosyne* primarily produce flavones and anthochlors (chalcones and aurones) in their leaves. No consistent chemical differences distinguish the two sections, and flavonoids support the concept that they are closely related. In several instances, a species from one section is more similar chemically to a member of the other section than it is to other members of the same section. There is, in general, nonconcordance between morphological and chemical similarity among species in the two sections. Chemical data support the hypothesis that sects. *Pugiopappus* and *Euleptosyne* are more closely related to Mexican elements than they are to any other North American *Coreopsis*.

Sections *Pugiopappus* and *Euleptosyne* of *Coreopsis* are each comprised of three species of annual diploid ($n = 12$) plants largely restricted to southern California (Sharsmith 1938, Smith 1975). Section *Pugiopappus* includes *C. calliopsidea* (DC.) A. Gray, *C. bigelovii* (A. Gray) H. M. Hall, and *C. hamiltonii* (Elmer) Sharsmith, whereas sect. *Euleptosyne* contains *C. californica* (Nutt.) Sharsmith, *C. stillmanii* (A. Gray) Blake, and *C. douglasii* (DC.) H. M. Hall.

Keys, descriptions, and geographic distributions of the six species were included in Sharsmith's (1938) paper on Californian *Coreopsis*, and the reader is referred to her publication for this information. Smith (1975) considered the two sections to be closely related. The purposes of the present study are: (1) to ascertain whether each species produces a specific leaf flavonoid profile; (2) to determine whether consistent flavonoid differences distinguish the two sections; and (3) to see if leaf flavonoid chemistry provides insight into the relationships of the two sections to other North American *Coreopsis*.

Methods and Materials

The methods employed in the present study are those described in several earlier publications (Crawford and Smith 1980, Crawford et al. 1980, Smith and Crawford 1981).

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An index of flavonoid similarity was computed for each pair of species using the formula $\frac{a}{a + b}$, where a = number of compounds common to both species, and b = the collective number of compounds exhibited individually.

Voucher specimens are deposited in OS or UARK, and a complete list of populations examined and place of deposit is available from the senior author.

RESULTS

Seventeen different flavonoids were isolated from 23 populations of the six species; identities of the compounds and their distributions among the six species are shown in Table 1. In Tables 1 and 2, the chalcone-aurone pairs coreopsin-sulfurein, marein-maritimein, butein-sulfuretin and okanin-maritimetin are treated as individual compounds because they almost invariably occur together. The index of flavonoid similarities for pair-wise comparisons of species in the two sections is presented in Table 2.

It is evident that two classes of flavonoids are common in the two sections, these being flavones and anthochlors (chalcones and aurones). A flavonol (quercetin 3-O-glycoside) was detected in relatively low quantities in one species. Among the flavones present, there is a C-glycosylflavone and one with 6-hydroxylation.

Our results for *C. bigelovii* agree with those of Nicholls and Bohm (1979) in most respects. We found what we interpret as butein 4,4′-O-diglucoside and okanin 4,4′-O-diglucoside, but we did not detect butein 4′-O-diglucoside. In addition, we were not able to detect lanceolatin with certainty in any of the species, although Nicholls and Bohm (1979) reported its occurrence in small concentrations in *C. bigelovii.* At the same time, we did find that when extracts of several species were run on polyamide thin-layer chromatograms, the smallest traces of a compound chromatographically similar to lanceolatin were detectable. Thus, our results must be considered inconclusive with respect to the presence of lanceolatin; if present, it occurs in very much lower quantities than butein. At least two flavanones appeared to occur in most species, but we did not attempt to characterize them. One of them may be 8-methoxybutin, which Nicholls and Bohm (1979) suggested occurs in *Coreopsis bigelovii.* We detected no interpopulational variation in any species; each species appears to be uniform chemically.

DISCUSSION

Members of sects. *Euleptosyne* and *Pugiopappus* share a number of features that suggest they are closely related. These include the annulate disk flowers, the corky-winged ray achenes, the annual habit, and the chromosome number of $n = 12$ (Sharsmith 1938, Smith 1975). While appearing very similar, the two sections are consistently separable by several features. In sect. *Pugiopappus* the achenes are dimorphic. Disk achenes are variously ciliate and have a pappus of two aristae; achenes of the ray flowers lack aristae. By contrast, in sect. *Euleptosyne* the achenes are monomorphic and lack aristae, and the pappus is reduced to a cupule (Sharsmith 1938, Smith 1975).

The differences between sects. *Pugiopappus* and *Euleptosyne* in leaf flavonoid chemistry are minimal. As shown in Table 1, no compound occurs in all species of one section and is invariably lacking from another. The flavonol quercetin 3-O-glycoside and the chalcone stillopsin were detected in certain species of sect. *Pugiopappus* but were not found in sect. *Euleptosyne* (Table 1). With respect to stillopsin, Seikel and Geissman (1950) reported its occurrence in floral tissues of *Coreopsis stillmanii.* We have been unable to document its presence in flowers of this species (Crawford and Smith 1983), nor did we detect it in the leaves in the present study. Leaf flavonoid chemistry supports the hypothesis that these two sections are closely related.

Two aspects of interspecific variation of leaf flavonoids are of interest. First, within each of the sections each species has a distinctive array of compounds. *Coreopsis californica* and *C. douglasii* are more closely similar than any other species pairs in a section (Tables 1 and 2). Secondly, there are pairs of species from different sections that are either as similar or more similar to each other in leaf flavonoids than are any two species within a section (Tables 1 and 2).

With regard to sect. *Pugiopappus,* each of the three species is well-differentiated chemically (Table 2). Flavonoid chemistry supports strongly Sharsmith's (1938) contention that *C. hamiltonii,* which is endemic to Mount Hamilton in Santa Clara County, is distinct from the widespread *C. bigelovii.* In sect. *Euleptosyne, C. californica* and *C. douglasii* are similar morphologically, and Sharsmith (1938) discussed in detail how the two entities had gone unrecognized by a number of botanists. The two species are very similar yet distinct chemically, differing by only two compounds, and with a similarity of 0.78 (Tables 1 and 2). Thus, within each of the sections, leaf flavonoids act as additional characters for distinguishing species.

Next, the leaf flavonoids of species in different sections will be considered. It may be noted from Tables 1 and 2 that *C. bigelovii* and *C. stillmanii* are more similar chemically than either is to any other species of either section; they lack luteolin 7-O-diglucoside, which is present in the other four species (Tables 1 and 2). Despite their very similar leaf flavonoids, the two species are very distinct

TABLE 1. NUMBER OF POPULATIONS EXAMINED AND DISTRIBUTION OF FLAVONOIDS IN LEAVES OF *Coreopsis* SPECIES.

Species	Number of populations examined	6-hydroxyluteolin 7-O-glucoside	Luteolin 7-O-glucoside	Luteolin 7-O-diglucoside	Apigenin 7-O-glucoside	Apigenin di-C-glycoside	Quercetin 3-O-glycoside	Marein-maritimein	Coreopsis-sulfurein	Stillopsin	Okanin 4,4′-O-diglucoside	Butein 4,4′-O-diglucoside	Okanin-maritimetin	Butein-sulfuretin
Sect. *Pugiopappus*														
C. bigelovii	6	+	+					+	+	+	+	+	+	+
C. calliopsidea	7		+	+	+	+	+	+	+	+			+	+
C. hamiltonii	1	+	+	+				+	+				+	+
Sect. *Euleptosyne*														
C. californica	4		+	+	+	+		+	+				+	+
C. douglasii	2	+	+	+		+		+	+				+	+
C. stillmanii	3	+	+					+	+		+	+	+	+

TABLE 2. INDEX OF FLAVONOID SIMILARITIES BETWEEN SIX SPECIES OF *Coreopsis* IN SECTIONS *Pugiopappus* AND *Euleptosyne*.

	Sect. *Pugiopappus*			Sect. *Euleptosyne*		
	C. bigelovii	*C. calliopsidea*	*C. hamiltonii*	*C. californica*	*C. douglasii*	*C. stillmanii*
C. bigelovii	X					
C. calliopsidea	0.46	X				
C. hamiltonii	0.60	0.55	X			
C. californica	0.42	0.80	0.67	X		
C. douglasii	0.55	0.64	0.75	0.78	X	
C. stillmanii	0.89	0.39	0.67	0.45	0.60	X

morphologically and there is no reason to believe, either from the literature (Sharsmith 1938) or from our own observations, that *C. bigelovii* and *C. stillmanii* are closely related.

Coreopsis calliopsidea (sect. *Pugiopappus*) and *C. californica* (sect. *Euleptosyne*) exhibit a higher index of flavonoid similarity to each other than either does to any other species in the two sections (Table 2). The two species differ in a broad range of features in addition to those separating the two sections to which they belong. These include characters of the leaves, size of capitula, nature of involucral bracts, etc. (see Sharsmith 1938 for detailed descriptions of the species). The very similar chemistries are unexpected in view of the numerous morphological features distinguishing the two species.

Coreopsis hamiltonii is more similar to *C. douglasii* in leaf flavonoids than it is to any of the other four species (Tables 1 and 2). Conversely, *C. douglasii,* except for the aforementioned high similarity to *C. californica,* is most similar chemically to *C. hamiltonii.* As with the other two species pairs from different sections with similar flavonoid chemistries, there are no morphological data to suggest that *C. douglasii* and *C. hamiltonii* are closely related (see descriptions in Sharsmith 1938).

Flavonoid variation often corresponds to taxonomic relationships inferred from other data, and flavonoid chemistry, therefore, may provide additional evidence in support of taxonomic decisions. Often, flavonoids are most useful for distinguishing entities that are recognized as distinct species on the basis of morphology and other data. Examples of this abound in the literature. That morphological differences between populations (such that they are recognizable as species) are often concordant with distinctions in flavonoid chemistry is apparently the result of divergence of genes controlling morphological features and those concerned with expression of flavonoids subsequent to the isolation of the population systems.

There is no a priori reason, however, why one would expect morphology and flavonoid chemistry to evolve together. In other words, there should be instances where morphology and chemistry are non-concordant. Few such examples appear in the literature, and it is not possible to ascertain whether such situations have been encountered rarely or simply have not been reported because the flavonoids have been viewed as of little "taxonomic value." Seeligmann and Alston (1967) described complex chemical variation in several species of *Hymenoxys* (Compositae) and suggested the flavonoid data indicated that patterns of morphological and geographical variation need to be examined thoroughly.

The situation in sects. *Pugiopappus* and *Euleptosyne* is not similar to that in *Hymenoxys* because there is no indication that the taxonomy of these two sections is confused. That is, each of the sections appears well delimited, and within each section species seem clear-cut. The thorough and careful study of Sharsmith (1938), as well as our own studies, has provided no reasons to change the taxonomy based on morphology. Morphological evidence in nearly all instances argues strongly against considering species most similar in leaf flavonoids as most closely related.

It appears, therefore, that in each of the sections, parallel evolution may account for the presence of very similar arrays of flavonoids in the leaves of morphologically distinct species.

The last point we wish to address concerns the relationships of these two sections with other North American *Coreopsis.* In an earlier paper one of us (Smith 1975) suggested that the two sections were derived from sect. *Anathysana,* which consists of suffrutescent plants occurring in Mexico. In a later publication (Crawford and Smith 1983), we suggested that the two sections may be closer phyletically to sect. *Pseudoagarista,* which consists of fruticose and suffruticose plants occurring in Mexico (also with representatives in the Andes). The latter interpretation is based primarily on achenial similarities between members of *Pugiopappus* and *Pseudoagarista.* The flavonoid data do not offer support for the affinities of these sections with *Pseudoagarista* rather than *Anathysana.* However, flavonoids do support the hypothesis that sections *Euleptosyne* and *Pugiopappus* are closer to Mexican elements collectively (Smith 1975, Crawford and Smith 1983) than to members occurring in the southeastern and eastern United States (sects. *Calliopsis, Coreopsis, Eublepharis, Palmatae*). For example, Mexican and Californian members often exhibit 6-hydroxyluteolin 7-O-glucoside, whereas this is rare in the other four sections and often is replaced by 6-hydroxyquercetin 7-O-glucoside. C-glycosylflavones occur in certain Mexican species and in half the species of the two California sections. These compounds have not been detected in other North

American *Coreopsis.* Lastly, butein glycosides are common and occur in large quantities in the sects. *Pugiopappus* and *Euleptosyne,* as well as in the woody taxa of Mexico. Lanceolatin glycosides appear to be present either in very small quantities or not at all in these plants, whereas they are often produced in large quantities in other North American *Coreopsis* (Crawford and Smith 1983).

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PHENETICS OF *MELAMPODIUM* (COMPOSITAE, HELIANTHEAE)

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ABSTRACT

Phenetic analyses of 37 species of *Melampodium* are presented using cluster analysis (UPGMA) and principal components analysis (PCA). Forty-two characters are employed, 22 of which are quantitative and 20, qualitative; 26 are from reproductive parts, 15 are of vegetative parts, and 1 is chromosome base number. Six analyses are presented: three UPGMA with all characters, reproductive characters, and vegetative characters, respectively; and three PCA with the same character sets. The UPGMA with all characters and the PCA with just reproductive characters gave the best resolution of taxonomic sections and series in correlation with the previous phyletic classification of the genus. The basic framework of classification of *Melampodium* is supported, but *M. nayaritense* shows closer affinity with series *Melampodium* than with series *Sericea. Melampodium nutans,* shown earlier by cladistic analysis to be problematical, does not relate well phenetically to any other species.

Melampodium is a genus of 37 species that are distributed widely throughout Mexico and Central America (Stuessy 1972). It can be distinguished from its close relatives in the Melampodiinae by the inner phyllaries, which completely enclose and are fused with the achenes of the ray florets and are smooth, ridged, or tuberculate (with no spines; Stuessy 1970). Chromosomes of *Melampodium* are interesting because the genus has the longest series of haploid numbers ($n = 9$, 10, 11, 12, 18, 20, 23, 25 ± 1, 27, 30, and 33) in the subtribe and one of the longest of the Heliantheae (Stuessy 1977). Chemically, the genus is interesting because it contains different types of sesquiterpene lactones (of the class melampolides) that may be used for assessing evolutionary relationships within the genus as well as within the subtribe (Seaman et al. 1980).

Relationships among taxa of *Melampodium* already have been determined in two independent investigations. One, an intuitive classification was completed with all species placed in series and/or sections (Stuessy 1972). This has served as an initial hypothesis of relationships among all the taxa that could be tested by new data and methods. Two, a cladistic analysis of all taxa was completed and results compared with those of the previous intuitive classifi-

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TABLE 1. CLASSIFICATION OF *Melampodium* (AFTER STUESSY 1972) SHOWING SECTIONS, SERIES, AND NUMERICAL CODES FOR SPECIES.

I. Section *Melampodium*
   A. Series *Melampodium*: 1, *M. americanum*; 2, *M. diffusum*; 3, *M. pilosum*; 4, *M. longipes*; 5, *M. linearilobum.*
   B. Series *Leucantha*: 6, *M. leucanthum*; 7, *M. cinereum*; 8, *M. argophyllum.*
   C. Series *Sericea*: 9, *M. sericeum*; 10, *M. pringlei*; 11, *M. strigosum*; 12, *M. longicorne*; 13, *M. nayaritense.*
   D. Series *Cupulata*: 14, *M. cupulatum*; 15, *M. appendiculatum*; 16, *M. sinuatum*; 17, *M. rosei*; 18, *M. tenellum*; 19, *M. glabribracteatum.*
   E. Series *Longipila*: 20, *M. longipilum.*
II. Section *Zarabellia*: 21, *M. longifolium*; 22, *M. mimulifolium*; 23, *M. gracile*; 24, *M. microcephalum*; 25, *M. paniculatum.*
III. Section *Serratura*: 26, *M. divaricatum*; 27, *M. costaricense*; 28, *M. dicoelocarpum*; 29, *M. tepicense*; 30, *M. sinaloense.*
IV. Section *Bibractiaria*: 31, *M. bibracteatum*; 32, *M. repens.*
V. Section *Rhizomaria*: 33, *M. montanum*; 34, *M. aureum.*
VI. Section *Alcina*: 35, *M. perfoliatum*; 36, *M. glabrum*; 37, *M. nutans.*

cation (Stuessy 1979). The two methods gave similar results, but some differences were detected, such as the placement of *M. nayaritense* and *M. nutans.*

During the past two decades, phenetics has been used with success to assess relationships of several plant groups (for reviews, see Sneath and Sokal 1973, Clifford and Stephenson 1975, Duncan and Baum 1981; see also Crisci 1974, Crisci et al. 1979). This method usually involves employing many non-weighted characters in different mathematical associations to produce more objective measures of affinity. These new relationships can then be compared with those obtained by other methods for a better understanding of a particular plant group (Crovello 1970).

Because phenetic classification has proven useful in other plant groups, its application to *Melampodium* seems a natural step for developing even better insights on relationships within the genus. In particular, resolutions are needed of differing putative affinities of taxa resulting from the use of intuitive and cladistic methods. The purposes of this paper, therefore, are to: (1) determine the phenetic relationships among species, series, and sections of *Melampodium* using different numerical techniques; and (2) compare these results with the previously described intuitive and cladistic relationships.

MATERIALS AND METHODS

The 37 species of *Melampodium* (Table 1) constitute the 37 Operational Taxonomic Units (OTUs) that were investigated. The characters and their states have been taken from Stuessy (1971a,b, 1972) and Keil and Stuessy (1975, 1977).

TABLE 2. CHARACTERS AND STATES USED IN THE PHENETIC ANALYSES OF *Melampodium*. All quantitative values are in mm unless otherwise noted.

VEGETATIVE CHARACTERS

PLANT: 1. Habit: annual (1), perennial (2); 2. Height (cm). STEM: 3. Orientation: prostrate or decumbent (1), ascendent (1.5), erect (2); 4. Diameter; 5. Vestiture: glabrous (1), strigose (2), pilose or tomentose (3), sericeous (4). PEDUNCLE: 6. Length (cm). LEAF: 7. Attachment: sessile or subsessile (1), petiolate (2); 8. Shape: linear, lanceolate, or oblanceolate (1), elliptic or oblong (1.5), ovate, obovate, or rhombic (2), deltate (3); 9. Length (cm); 10. Width (cm); 11. Apex: acute (1), variably acute to obtuse (2), obtuse (3); 12. Base: attenuate (1), attenuate-obtuse (1.5), obtuse (2), obtuse-auriculate (2.5), auriculate (3); 13. Vestiture (upper surface): glabrous (1), strigose (2), pilose or tomentose (3), sericeous (4); 15. Margin: serrate (1), entire to undulate (2).

REPRODUCTIVE CHARACTERS

HEAD: 16. Height; 17. Diam. OUTER INVOLUCRE: 18. Diam; 19. Bract Number; 20. Fusion: separate (1), slightly connate (1.5), connate (2); 21. Shape: linear to oblanceolate (1), ovate to rhombic (2); 22. Length; 23. Width; 24. Apex Shape: acuminate to acute (1), obtuse (2), rounded (3); 25. Vestiture (abaxial surface): glabrous (1), strigose (2), strigose-pilose (2.5), pilose, tomentose or villous (3); 26. Margin: herbaceous (1), slightly scarious (2), scarious (3). FRUIT: 27. Apical Appendage: absent (1), adaxial awn (2), abaxial hood (3); 28. Length. RAY FLORET: 29. Number; 30. Ligule Color: white (1), yellow or orange (2); 31. Ligule length; 32. Ligule width. DISC FLORET: 33. Number; 34. Corolla Diam; 35. Throat Length; 36. Tube Length. PALEA: 37. Apex Color: colorless (1), yellow or orange (2), purple (3); 38. Midrib: absent (1), weakly present (1.5), strongly present (2); 39. Vestiture of Midrib; glabrous (1), variably glabrous to pilose (1.5), pilose (2); 40. Length; 41. Width. CHROMOSOME NUMBER (basic, 42): 9, 10, 11, 12.

Data accumulation. The data consist of 42 characters scored for each of the 37 taxa (Table 2; the Basic Data Matrix is on deposit in the Ohio State University Herbarium). The set of characters includes 18 quantitative continuous, 4 quantitative discontinuous, and 20 qualitative characters. In all, 26 of the characters used are of reproductive parts and 15 are of vegetative parts. One additional character, chromosome number, was used (number 42). Chromosome numbers for several species are still unknown and these missing data are listed as NC in the Basic Data Matrix; they were ignored during computations.

Data processing. The computational work was done on an AMDAHL 470V/6II at The Ohio State University by using NT-SYS programs developed by Rohlf et al. (1971). The data were analyzed by two methods: cluster analysis and ordination. The BDM was standardized (BDMS) to remove unequal weights on characters imposed by the different scales of measurements. Details of these methods and computational procedures may be found in Sneath and Sokal (1973).

Cluster analysis. The BDMS was subjected to several agglomerative clustering procedures. Because the results were coincident, only one of them will be presented here. Details of these cluster analysis techniques can be found in Williams and Dale (1965), Wishart (1969), Spence and Taylor (1970), and Cormack (1971). The Pearson product-moment correlation coefficient between each pair of the 37 OTUs was calculated. The resulting OTU × OTU correlation matrix served as input in the calculation of a phenogram by the unweighted pair-group method, using arithmetic averages (UPGMA). The cophenetic correlation coefficient (r) was computed as a measurement of distortion (Sokal and Rohlf 1962). Although some criticism of this measure has been given (Farris 1969) it still seems a useful index (Sneath and Sokal 1973).

Ordination. A common technique of ordination is that of Principal Components Analysis (PCA). Accounts of the technique are given by Sneath and Sokal (1973). A character × character correlation matrix was obtained from the BDMS by calculating the Pearson product-moment correlation coefficient between each pair of the 42 characters. Principal Components Analysis was performed on the 42 × 42 character correlation matrix and the first two factors were extracted. The character factor loadings were used to calculate the factor scores or projections of OTUs in the two-factor space. To examine ordination efficiency, the Euclidean Distance between all pairs of OTUs in factor space was calculated and an OTU × OTU distance matrix was also calculated from BDMS using a Taxonomic Distance coefficient (Sneath and Sokal 1973). Both matrices were compared using the cophenetic correlation coefficient.

RESULTS

The results of the phenetic analyses will be presented within the framework of the existing classification of *Melampodium* (Stuessy 1972), with emphasis on alignment of species in sections and series. The data will be presented for UPGMA and PCA based on the numbers and kinds of characters used for the different analyses: (1) all 42 vegetative and reproductive characters; (2) 26 reproductive characters only; and (3) 15 vegetative characters only.

Vegetative and reproductive characters. UPGMA—The previously recognized sections of *Melampodium* (Table 1) are mostly distinct with this approach (Fig. 1), with some exceptions. Section *Rhizomaria* (species 33 and 34), while connecting together well, ties closely to *M. sinuatum* (16) at the 0.42 level and is not as distinct as the other sections of the genus. Several species also seem displaced, e.g., *M. nutans* (37), which has low correlation (0.08) with nearly all other taxa. *Melampodium nayaritense* (13) was put earlier (Stuessy 1972) in series *Sericea* (9–13) but clusters closer to series *Melampodium* (1–5). *Melampodium pilosum* (3) shows greater similarity with *M. longipilum* (2), which was placed in its own monotypic

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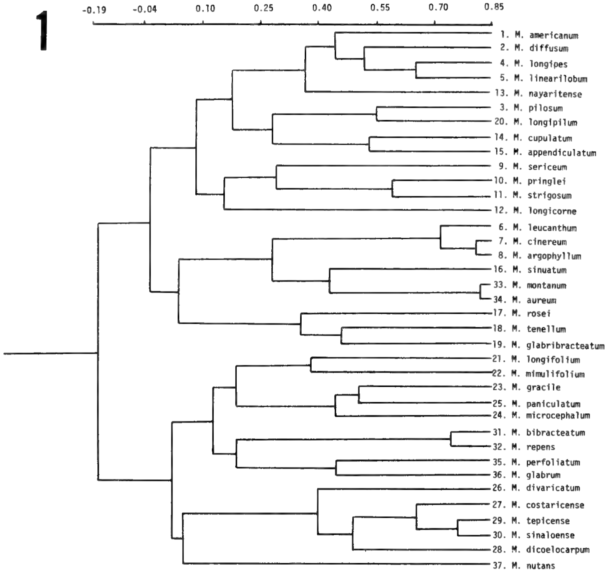

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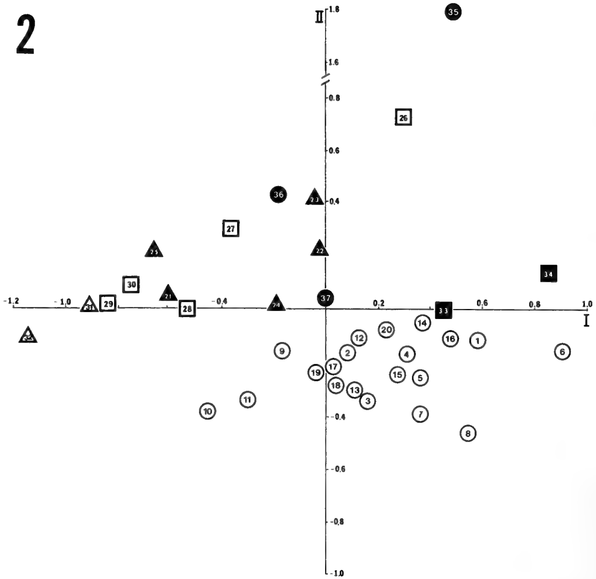

FIGS. 1 and 2. Phenetic analyses of 37 species of *Melampodium* using 42 reproductive and vegetative characters (Table 2). FIG. 1. Phenogram from UPGMA; cophenetic correlation coefficient (r) = 0.77. FIG. 2. Principal components analysis; r = 0.93.

series, rather than with its presumed position in series *Melampodium* as a close relative of *M. americanum* (1).

PCA—Three groups are reasonably distinct in this analysis (Fig. 2): sect. *Bibractiaria* (31, 32), sect. *Melampodium* (1–20), and sect. *Rhizomaria* (33, 34); the other three sections are intermixed. The characters that are most important for separating the taxa are in Axis I (24.05% of observed variation): numbers of ray florets, head height, head diameter, ligule length, number of disc florets, and ligule width. These features are all reproductive and quantitative. Axis II (16.04% of variation) contains primarily leaf width, plant height, leaf length, and stem diameter. All these characters are vegetative and quantitative.

Comparison of UPGMA and PCA—In both analyses, sects. *Bibractiaria* (31, 32), *Melampodium* (1–20) and *Rhizomaria* (33, 34) are clearly separated from the rest of the genus. Section *Alcina* (35–37) is not resolved in either [*M. nutans* (37) is out of place]. The other sections, *Serratura* (26–30) and *Zarabellia* (21–25) are poorly resolved in PCA but are very clear in UPGMA. The UPGMA analysis probably gives better discrimination of these two sections because it relies on many characters, whereas PCA relies on only a few factors that show a broad range of variation.

Reproductive characters only. UPGMA—In this analysis two small sections hold together well (Fig. 3): sects. *Bibractiaria* (31, 32) and *Rhizomaria* (33, 34). To a lesser extent series *Leucantha* (6, 7, 8) is also distinct. The other relationships, however, are extremely mixed and show few correlations with the previous intuitive classification.

PCA—The separation of the sections in this analysis (Fig. 4) is similar to the results with all characters (Fig. 2). Three sections, *Bibractiaria* (31, 32), *Melampodium* (1–20) and *Rhizomaria* (33, 34), are distinct. The first five important characters in Axis I (32.91% of variation) are exactly the same as those of Axis I in Fig. 2, and the degree of separation is approximately the same. Axis II contains a smaller amount of variation (13.17%) and includes fruit hood type, diameter of involucre, midrib vesture, bract width, and bract length. Again, the reproductive characters successfully delimit sects. *Bibractiaria, Melampodium,* and *Rhizomaria* and show essentially the same result, although with slightly better resolution of all sections, as with both reproductive and vegetative characters combined.

Comparison of UPGMA and PCA—The results of the two analyses on just reproductive features are very different. Sections *Bibractiaria* (31, 32) and *Rhizomaria* (33, 34) each have good internal cohesiveness, but the rest are intermixed. The phenogram also gives a very low cophenetic correlation coefficient (0.65), although the value for PCA is very high (0.93). In general, the phenogram is so distorted from the matrix of correlation coefficients that the portrayed relationships must be viewed dubiously.

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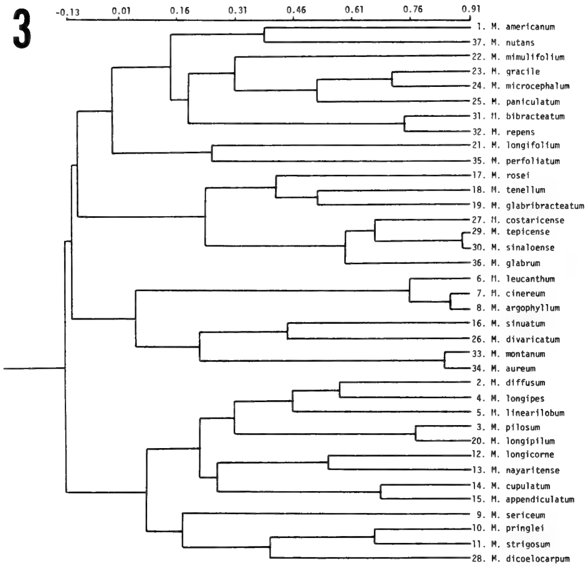

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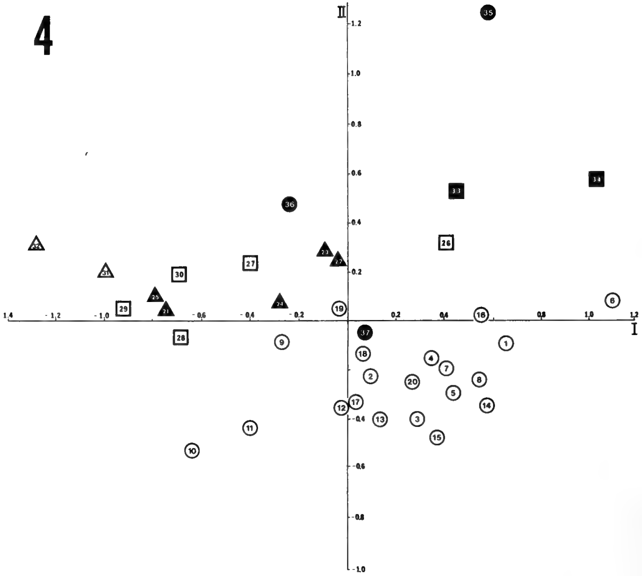

FIGS. 3 and 4. Phenetic analyses of 37 species of *Melampodium* using 26 reproductive characters. FIG. 3. Phenogram from UPGMA; r = 0.65. FIG. 4. Principal components analysis; r = 0.93.

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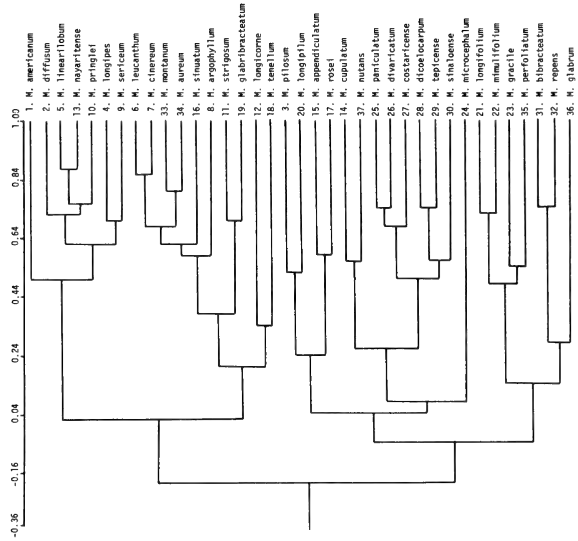

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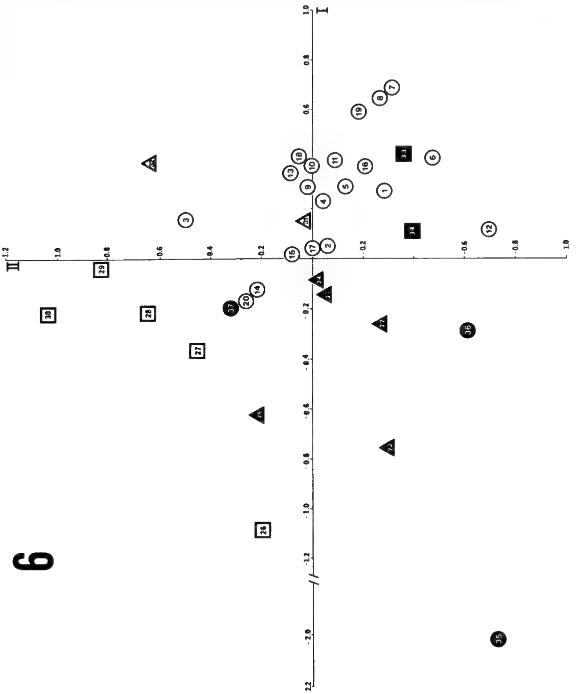

FIGS. 5 and 6. Phenetic analyses of 37 species of *Melampodium* using 15 vegetative characters. FIG. 5. Phenogram from UPGMA; r = 0.75. FIG. 6. Principal components analysis; r = 0.93.

Vegetative characters only. UPGMA—This analysis of vegetative features (Fig. 5) shows some sections more or less well resolved: *Bibractiaria* (31, 32), *Melampodium* (1–20), *Rhizomaria* (33, 34; distinct but within sect. *Melampodium*), and *Serratura* (26–30). Series *Leucantha,* however, clearly resolved in Figs. 1 and 3, is not well delimited here.

PCA—As with UPGMA, with PCA (Fig. 6) some of the sections are clear, others are not. Sections *Zarabellia* (21–25) and *Serratura* (26–30) are resolved here for the first time, indicating the importance of vegetative features in delimiting these taxa. The first four characters (all quantitative) of Axis I (27.44% variation) are the same as Axis II in Fig. 2. Characters of Axis II (16.93% variation) are all qualitative: petiolate condition of the leaves, leaf margin, stem habit, and the base of the leaves. Section *Rhizomaria* (33, 34) is for the first time not at all separated from Sect. *Melampodium* (1–20) by PCA.

Comparison of UPGMA and PCA—Both methods with vegetative data only show sects. *Serratura* (26–30), and *Zarabellia* (21–24) reasonably distinct. Sections *Melampodium* (1–20), *Bibractiaria* (31, 32), and *Rhizomaria* (33, 34), however, are better revealed in the UPGMA than in PCA (although not extremely well in either).

DISCUSSION

In attempting to relate the new data from phenetic analyses to previous work that has been done with *Melampodium* (e.g., Stuessy 1972, 1979), the need exists to select one pattern of relationship (Figs. 1–6) for comparisons. A reasonable approach is to select the result that correlates most closely with the intuitive classification, and which has a high cophenetic correlation coefficient. Of the six different phenetic analyses, the one most similar to the previously published intuitive classification of the genus (Stuessy 1972) is UPGMA of vegetative and reproductive features (Fig. 1), which also has the highest cophenetic correlation coefficient (0.77) of the three phenograms.

Relationships among the sections. Almost all of the previously recognized sections of *Melampodium* are distinct in Fig. 1, except for *Rhizomaria* (33, 34) and *Alcina* (35–37). Section *Rhizomaria* contains two morphologically very similar species, *M. aureum* (34) and *M. montanum* (33). These cluster well together, but they also relate closely to *M. sinuatum* (16) of sect. *Melampodium.* The level of attachment of sect. *Rhizomaria* to sect. *Melampodium* is not high (0.42), but it is as high as some species within well established parts of sect. *Melampodium* [e.g., *M. americanum* (1) ties to other species of series *Melampodium* at the same level; or *M. rosei* (17) and *M. tenellum* (18), extremely close morphologically and placed in the same series *Cupulata* (14–19), are united at a lower level (0.35)].

Section *Alcina* is recognized to have three species, *M. glabrum* (36), *M. perfoliatum* (35), and *M. nutans* (37). The first two species are very similar morphologically, and they do cluster close together in Fig. 1. *Melampodium nutans,* however, clusters most closely to species of sect. *Serratura* (26–30), although at a very low level (0.08). In fact, this is the lowest association of a single species to any other species in the whole genus. There is clearly a problem, however, with the placement of *M. nutans.* Chromosomally the taxon is $n = 11$ and falls most clearly in sect. *Alcina* on that basis. (Section *Rhizomaria* also has $x = 11$; but it includes perennials, woody at the base and differing in other morphological features.) Obviously the morphological affinities of *M. nutans* are still not clear.

The phenogram also shows good resolution of sect. *Melampodium* from all other sections of the genus, except for the inclusion of sect. *Rhizomaria.* The other sections as a group cluster together suggesting that only two coordinate sections or subgenera might be recognized within the genus (Robinson 1901) rather than six. Although this viewpoint has been considered seriously, we do not believe it is the best approach because (1) the level of correlation of most sections to each other is low (Fig. 1); and (2) some of the characters have surely evolved in parallel within each of the sections. The genus has in fact undergone extensive parallel evolution as shown from cladistic studies (Stuessy 1979). This could have led to association of non-homologous features, and especially at a low level of correlation, could have caused ties that are not taxonomically meaningful.

Relationships within the sections. The relationships expressed in Fig. 1 among the species within each section are very close to those of the intuitive classification (Stuessy 1972). Section *Alcina* (35–37) is a cohesive unit, except for *M. nutans.* Section *Serratura* (26–30) is very clear with *M. tepicense* (29) and *M. sinaloense* (30) being very close. Section *Bibractiaria* (31, 32) is distinct from the other groups. Section *Zarabellia* (21–25) is a good unit but it associates at a low level (0.18). *Melampodium gracile* (23), *M. microcephalum* (24), and *M. paniculatum* (25) form a tightly-knit evolutionary unit in which artificial hybridizations have been done (Stuessy and Brunken 1979), and F_1 hybrids have been obtained in crosses between each pair of species. *Melampodium longifolium* (21) is in an isolated morphological line of sect. *Zarabellia,* a placement that seems intuitively correct. *Melampodium mimulifolium* (22), known only from the type collection, is shown as the closest relative of *M. longifolium* (Fig. 1), but the former has been regarded as simply an unusually aberrant population (or individual) of *M. gracile* (Stuessy 1972). Section *Rhizomaria* shows as a good unit on the phenogram (Fig. 1), but it occurs within sect. *Melampodium.*

Section *Melampodium* (1–20), the largest of all the sections, forms a good unit except for the inclusion of sect. *Rhizomaria* (33, 34). Series *Melampodium* (1–5) has most species contained within except *M. pilosum,* which ties more closely to *M. longipilum* (treated as the monotypic series *Longipila*). *Melampodium nayaritense* (13) is regarded here as having stronger affinities with series *Melampodium* than with series *Sericea* as originally proposed (Stuessy 1972). Cladistic analysis (Stuessy 1979) also shows this connection and suggests even more strongly that *M. nayaritense* belongs in series *Melampodium* rather than in series *Sericea.* Series *Leucantha* (6–8), the white-rayed complex adapted to desert conditions, is a very distinct grouping. *Melampodium argophyllum* ties closest with *M. cinereum,* a position that suggests this may be the closest evolutionary tie. The flavonoid and sesquiterpene lactone chemical evidence also shows a stronger affinity in this direction (Stuessy 1971c; N. H. Fischer, pers. comm.). Stuessy (1969) treated *M. argophyllum* as a variety within *M. leucanthum*; because of its distinct morphology, it is now regarded as a recognizable species (Stuessy 1971c). Series *Cupulata* (14–19) is the most disjointed. *Melampodium cupulatum* (14) and *M. appendiculatum* (15) cluster very close to each other but are far removed from the other species (17–19) of the same series. The remaining species of the series, *M. sinuatum* (16), clusters with sect. *Rhizomaria.* Series *Sericea* (9–13) appears discrete except that *M. nayaritense* is close to series *Melampodium.*

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A NEW SUBSPECIES OF *IPOMOPSIS LONGIFLORA* (POLEMONIACEAE) FROM ARIZONA, NEW MEXICO, AND NORTHERN MEXICO

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ABSTRACT

Ipomopsis longiflora (Torr.) V. Grant subsp. **australis** Fletcher & W. L. Wagner is described from southwestern New Mexico and Arizona south and west of the Mogollon Rim. Short capsules, which do not or only slightly exceed the calyx, clearly separate subsp. *australis* from the typical subspecies, with its strongly exserted capsules.

The probable occurrence of this distinctive new species of *Ipomopsis longiflora* was first recognized by each of us during independent floristic studies in southwestern New Mexico. Recent investigations in the field and examination of available herbarium material have confirmed the existence of a new taxon, with a geographical range distinct from that of the typical form of *Ipomopsis longiflora*.

Ipomopsis longiflora (Torr.) V. Grant subsp. **australis** Fletcher & W. L. Wagner, subsp. nov.

Differt a *I. longiflora* subsp. *australis* calyce 7–9 mm longo; capsulis maturis calyce longioribus vel paulo brevioribus (6–)8–9(–10) mm longo (Fig. 1).

Much branched annual or biennial, 1.7–6 dm tall from a taproot, the stem simple, branched above, subglabrous, erect. Leaves distant, 1.5–5 cm long, pinnatifid, linear, the upper ones sometimes entire, pubescent with short, crisped hairs, these varying in density but more prominent in the axils. Flowers in open corymbose panicles, the pedicels of mature flowers slender, mostly 10–20 mm long. Calyx 7–8.5(–10) mm long, dotted with short-stalked glands, united to well above the middle, the tube scarious below the sinuses, splitting in sinuses at maturity, the lobes subulate, spinulose at the apex, the margins with short, crisped hairs. Corolla pale blue to white, often fading to pale pink, salverform, the tube (25–)35–45 mm long, narrow, the lobes (6–)9–12.5 mm long. Stamens adnate to the tube, unevenly inserted with 2 or 3 of them slightly exserted. Stigmas

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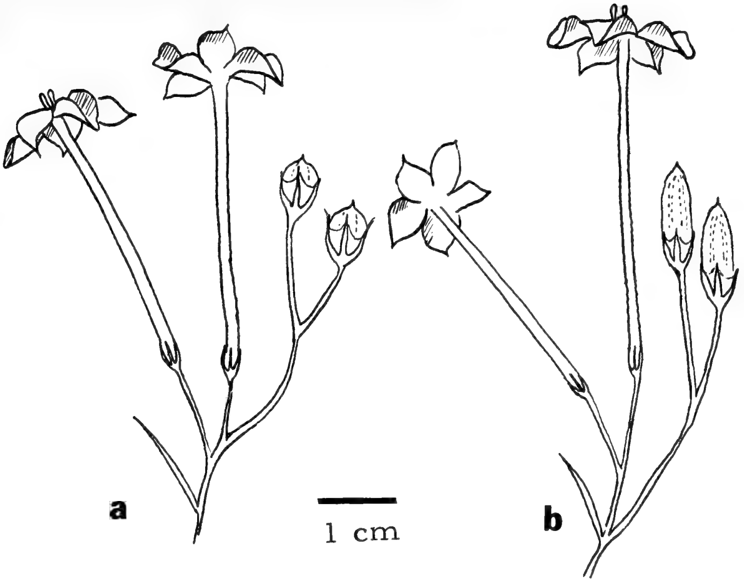

Fig. 1. Diagrammatic illustration showing the difference in capsule length between *Ipomopsis longiflora* subsp. *australis* (a) and subsp. *longiflora* (b).

somewhat exceeding the anthers. Capsule not or only slightly exceeding the calyx lobes, (6–)8–9(–10) mm long at maturity. Seeds several in each locule, angulate, viscid when wet.

Type: New Mexico, Catron Co., 0.4 km off Hwy. 180 on Rte. 519, 1.6 km s. of Pleasanton (SE¼, Sec 14, T12S, R20W), 1500 m, 10 Sep 1980, *R. Fletcher 4886* (holotype: UNM-69975; isotypes: ARIZ, ASU, MO, NMC).

Paratypes: Mexico, Sonora, 9 mi from Magdalena, *Pinkava 6485* (ASU). U.S.A., Arizona, Cochise Co., Rodeo, *Jones 25667* (MO). Gila Co., s. of Seneca, *Schmidt 34* (ARIZ). Graham Co., 20 mi e. of Safford, *Moeller 10698* (ARIZ). Greenlee Co., 5 mi s. of Clifton, *Crosswhite & Sands 808* (ASU). Maricopa Co., Mormon Flat, *Shreve 10166* (ASU). Mohave Co., 4 mi n. of Peach Springs, *Darrow 3141* (ARIZ). Pima Co., Santa Rita Mts., 1880, *Engelmann s.n.* (MO). Pinal Co., 9 mi w. of Oracle, *Wiegand & Upton 3995* (MO). Santa Cruz Co., near Elgin, *Peebles et al. 3338* (ARIZ). Yavapai Co., Montezuma Castle Nat'l. Monument, *Bomen 26* (ARIZ). New Mexico, Catron Co., 1 mi s. of Hwy. 180 at San Francisco River crossing, *Fletcher 2665* (UNM). Grant Co., near Red Rock, *Thornber 57* (NMC). Hidalgo Co., Peloncillo Mts., along Hwy. 80, 2 mi n. of the pass, *Wagner 1898* (UNM). Luna Co., w. of Hermanas, *Clark 10754* (UNM).

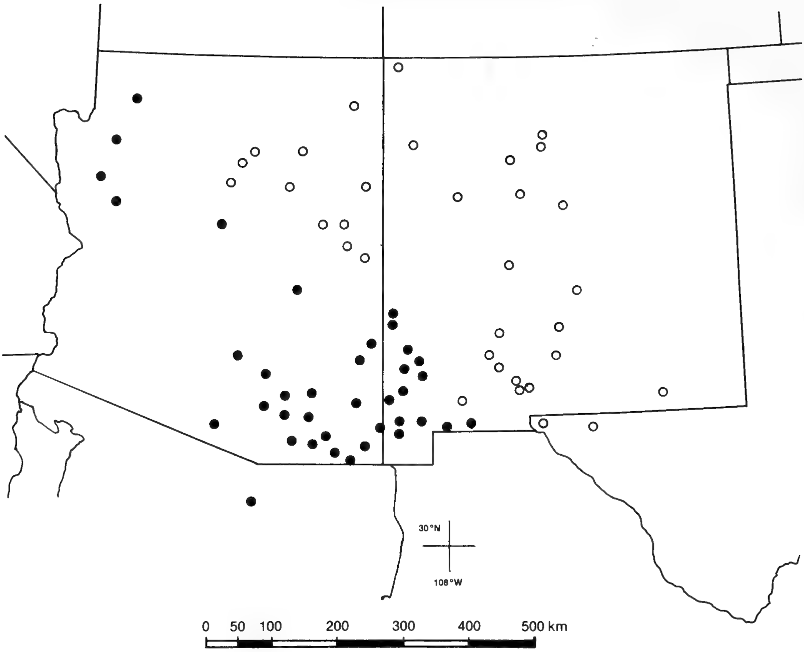

FIG. 2. Geographical distribution of *Ipomopsis longiflora* subsp. *australis* (dots) and of subsp. *longiflora* (open circles) adjacent to that of subsp. *australis*.

Distribution. In sandy soils in desert vegetation, in grasslands or in pinyon-juniper communities from Mohave Co., Arizona, south and west of the Mogollon Plateau, to southwestern New Mexico as far east as Deming, in Luna Co., and to northern Sonora and probably adjacent northern Chihuahua, Mexico, at elevations of 650–1850 m. Flowering from April to October, after rains (Fig. 2).

Plants of *Ipomopsis longiflora* subsp. *australis* are similar to those of subsp. *longiflora* in most features. They differ, however, in the length of the capsule and calyx, as well as in the degree to which the capsule is exserted beyond the calyx. In the typical subspecies, the capsule length ranges from 12–15 mm, with the calyx reaching approximately midway, whereas the capsules of subsp. *australis* are 6–9(–10) mm long and the calyx is of equal length or slightly shorter. In addition, the seeds of *Ipomopsis longiflora* subsp. *australis* are more plump than those of subsp. *longiflora.* There is also, in general, a lower density of glandular pubescence and a greater density of nonglandular hairs along the margins of the calyx in subsp. *australis* than in subsp. *longiflora.*

The ranges of the two subspecies are entirely distinct. In Arizona the two taxa occur on opposite sides of the Mogollon Plateau. Their ranges come closer together in southwestern New Mexico. Here suitable habitats are intermittent rather than completely disjunct. Based on the study of herbarium material and field work done by Fletcher, it has been determined that the two taxa grow within a few km of each other in the vicinity of Deming, Luna Co., New Mexico, but as far as we know they are never sympatric. For example, *Ipomopsis longiflora* subsp. *longiflora* was observed growing near Deming and north of Deming, whereas subsp. *australis* is known from the south, near Columbus (1952, *Castetter s.n.*; UNM). There is one collection of subsp. *australis* made in 1895 (*Mulford 1019*; MO) that is labelled as coming from Deming, however, since this is an early collection the locality may only refer to the general area of Deming. Fieldwork, however, has failed to locate any populations of subsp. *australis* from Deming.

The two subspecies obviously share the same hawkmoth pollinators, but we have no information as to whether the taxa can hybridize. We have observed no plants that could be considered to exhibit an intermediate combination of characters.

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MEETING NOTICE

The society for Economic Botany will hold its 25th annual meeting at Texas A&M University, College Station, Texas, 11–13 June, 1984. The symposium, ETHNOBOTANY OF THE GREATER SOUTHWEST, will focus on past, present, and future interactions between plants and man in the southwestern United States and northern Mexico. Symposium presentations and discussion will involve specialists from the United States and Mexico. Registration materials and information can be obtained from Dr. Hugh D. Wilson, Biology, Texas A&M University, College Station, TX 77843. Those wishing to contribute papers should contact Dr. Gregory Anderson, Biological Sciences Group, University of Connecticut, Storrs, CT 06268.

GARDEN COMPARISON OF GERMINATION AND SEEDLING GROWTH OF *YUCCA WHIPPLEI* SUBSPECIES (AGAVACEAE)

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Abstract

Subspecies of *Yucca whipplei* represent different life history modes. Subspecies *whipplei* and *parishii* are semelparous, subsp. *caespitosa* is iteroparous, subsp. *percursa* has vegetative reproduction, and subsp. *intermedia* combines both patterns of these last two taxa. Germination of all subspecies was greatly inhibited at 40°C suggesting seedling recruitment is restricted during hotter months. Brief heat treatment at 100°C prior to wetting did not enhance germination, as is the case in many chaparral shrubs commonly associated with *Yucca.* Rather, germination was reduced at this temperature, though the reduction was least for the two semelparous forms most commonly associated with chaparral. Seedling biomass after four months in a common environment showed highly significant differences among subspecies and was strongly correlated with initial seed weight. Biomass allocation patterns were significantly different among subspecies but not related to reproductive mode, seed weight or elevation or distance from the coast (of seed collection site). Leaf characteristics were associated with reproductive mode; the two semelparous subspecies had markedly higher estimated leaf areas than the other three taxa. All taxa increased allocation of biomass to corms under low moisture and high temperature "stress" conditions.

Yucca whipplei Torrey (Agavaceae) is an acaulescent, rosette-forming shrub distributed throughout semi-arid parts of southern and central California. This species has a number of distinctive floral and fruit characteristics that have led some authors to suggest its removal from the genus *Yucca* (McKelvey 1947). One characteristic unique among yuccas is *Y. whipplei*'s semelparous (monocarpic) life history; a rosette of stiff-tipped leaves grows vegetatively for some unknown number of years until a single flower stalk is produced, and then the entire plant dies within months of fruiting.

The semelparous condition is not found in all populations of *Y. whipplei.* Haines (1941) suggested five subspecies based on more or less geographically contiguous populations of differing reproduction or growth form. *Yucca whipplei* subsp. *whipplei* (subsp. *typica* of Haines) and subsp. *parishii* are the only semelparous taxa and are largely distinguished from each other by size. Subspecies *caespitosa* is an iteroparous perennial that produces multiple tightly packed

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rosettes (few to >100) from axillary buds early in development. These are all attached to a small caudex and the individual rosettes are homologous to branches that die after flowering. Subspecies *percursa* is a semelparous taxon that reproduces vegetatively by underground rhizomes that may extend several meters, often producing large dense colonies. A taxon with characteristics of subspp. *caespitosa* and *percursa* is subsp. *intermedia.* Although the subspecific designations of Haines (1941) are generally useful and are maintained in local floras, the growth form characteristics described by him for each taxon represent the most common condition throughout the regions attributed to each subspecies. Hoover (1973) pointed out that populations often consist of a mixture of reproductive modes (monocarpic, caespitose, or rhizomatous). For example, often 5% of the individuals in populations of subsp. *whipplei* actually produce more than a single rosette (J. Keeley, pers. obs.).

Subspecies of *Yucca whipplei* occupy a diversity of habitats. The semelparous subspp. *whipplei* and *parishii* are typically closely associated with chaparral, and the best developed populations are in the interior transverse and peninsular ranges. The iteroparous subsp. *caespitosa* is best developed in desert scrub vegetation bordering chaparral. The rhizomatous subsp. *percursa* commonly forms dense colonies on bare, rocky slopes and both this taxon and the coastal sage scrub subsp. *intermedia* are the most typically coastal subspecies.

The array of life history types represented in *Yucca whipplei* raises questions as to their origin and adaptive significance. Certainly seed germination and early seedling growth are critical stages that could be under different selective pressures across the *Yucca whipplei* range and may have some bearing on the different reproductive modes. The purpose of this study was to determine through garden experiments whether or not there are genetically based differences in seed germination and early seedling growth characteristics among these five taxa.

METHODS

Seeds were collected in 1978 and 1979 from five individuals in three widely separate populations of each subspecies. Air dry seed weights were taken for a sample of 100 seeds per subspecies.

Prior to germination experiments, seeds were stratified in plastic bags with a weak solution of fungicide (Dithane) and stored at 2°C for 4 weeks during early 1980. Germination was carried out on moist filter paper in plastic petri dishes maintained in the dark and scored after two weeks. Two germination experiments were performed. In the first experiment germination was compared between incubation at 25°C and 40°C for 1978 and 1979 seeds separately. Each treatment consisted of 10 petri dishes (each with 30 seeds) per population for a total of 30 dishes per subspecies. In the second experiment all seeds were incubated at 25°C, but prior to stratification and wetting, one set was heat treated in a convection oven at 110°C for 5 min and another set at 130°C for 5 min. Five dishes per population were used for a total of 15 per subspecies.

Seedling growth and biomass allocation patterns were examined as follows. Seeds were stratified as described above and planted (7 per pot) in 100 mm square pots ~10 mm below the surface of a 50/50 mix of washed sand and coarse grade perlite. Twenty pots were started for each of the three populations of each subspecies for a total of 60 pots for a control group and 60 pots for a "stressed" group as described below. Seeds were planted in early spring in an outdoor lathhouse with supplemental fluorescent lighting but covered with clear plastic to prevent moisture input from precipitation. The control group was fertilized weekly with commercial MiracleGro and maintained at field capacity soil moisture. The "stressed" group had elevated soil temperatures maintained by placing the pots 2 cm deep in sand with 37°C heating cables, fertilized monthly, and allowed to dry to the touch before rewatering. One month after planting each pot was thinned to four seedlings. After four months the largest seedling in each pot was collected and the number of leaves and length and width at the middle of the longest leaf were recorded. Leaves are linear and so leaf area was estimated by assuming each leaf approximated a rectangle. Each seedling was divided into roots, corms, and leaves, oven dried and weighed.

Data was analyzed by one-way ANOVA and Pearson product moment correlation.

RESULTS AND DISCUSSION

There was no significant difference in germination behavior between 1978 and 1979 seeds, therefore, data for both years were combined. Under nearly all conditions, subsp. *parishii* with the heaviest seeds had the highest germination (Table 1) and subsp. *percursa* with the lightest seeds had the lowest germination. All taxa showed a marked reduction in germination when incubated at 40°C (Table 1). Even though some subspecies came from desert sites and others from coastal sites, there was no significant difference in germination at 40°C. Although several of the taxa are restricted to fire-prone environments, there was no indication that heat shock provided any sort of germination cue (Table 2), as is the case in many other chaparral shrubs. This is consistent with the observation that, unlike most chaparral shrubs, *Y. whipplei* populations have an uneven age structure, with seedling recruitment in all aged stands, wherever appropriate openings in the canopy exist (J. Keeley, pers. obs.). However, the two subspecies restricted to chaparral (*whipplei* and *parishii*) showed the least reduction in germination at 110°C.

TABLE 1. PERCENT GERMINATION OF *Yucca whipplei* SUBSPECIES INCUBATED AT 25°C AND 40°C, n = 60 DISHES OF 30 SEEDS (seed weights in mg are given in parentheses).

Subspecies	Seed weight x̄ ± SD	25°C x̄ ± SD	40°C x̄ ± SD	p
whipplei	(17.6 ± 4.9)	48 ± 26	2 ± 6	<0.01
parishii	(21.3 ± 7.3)	72 ± 25	12 ± 16	<0.01
caespitosa	(18.1 ± 4.6)	57 ± 28	11 ± 14	<0.01
intermedia	(18.0 ± 3.7)	49 ± 29	6 ± 14	<0.01
percursa	(16.0 ± 4.3)	41 ± 27	8 ± 12	<0.01
p	<0.01	<0.01	NS	

Seedling biomass after four months showed highly significant differences among subspecies for all characters examined (Table 3). Sample sizes smaller than 60 reflect mortality; survival of the semelparous subsp. *whipplei* was least affected by stressed conditions, but stress greatly reduced survival of the rhizomatous subsp. *percursa.* There was a significant reduction in total biomass under stressed conditions for all subspecies. Stressed conditions did not alter the allocation of biomass to leaves for any of the subspecies, but all taxa allocated significantly more biomass to corms. Stressed conditions significantly reduced the number of leaves and thus the total estimated leaf area for all subspecies (Table 4). After four months of growth, the only seedling characteristic that was clearly associated with reproductive mode was the estimated total leaf area. Both semelparous taxa had markedly higher leaf areas than the other taxa.

Correlations of biomass characters (from Tables 3 and 4) with seed weight, elevation, and distance from the coast (of seed collection site) are shown in Table 5. Total biomass was most strongly correlated with seed weight. In addition populations from higher elevations and more interior sites tended to produce seedlings with greater biomass after four months growth. Most leaf characteristics were correlated with initial seed weight.

TABLE 2. PERCENT GERMINATION OF *Yucca whipplei* SUBSPECIES IN RESPONSE TO PREVIOUS HEAT TREATMENT OF THE SEEDS INCUBATED AT 25°C (n = 30 dishes of 30 seeds).

Subspecies	Control x̄ ± SD	110°C/5 min x̄ ± SD	130°C/5 min x̄ ± SD	p
whipplei	39 ± 24	18 ± 22	0 ± 0	<0.01
parishii	55 ± 24	31 ± 22	8 ± 18	<0.01
caespitosa	48 ± 23	14 ± 20	1 ± 2	<0.01
intermedia	32 ± 21	9 ± 14	0 ± 0	<0.01
percursa	29 ± 21	6 ± 13	0 ± 0	<0.01
p	<0.01	<0.01	<0.01	

TABLE 3. BIOMASS AND ALLOCATION PATTERNS OF FOUR-MONTH-OLD SEEDLINGS OF *Yucca whipplei* SUBSPECIES MAINTAINED UNDER WELL-WATERED AMBIENT "CONTROL" CONDITIONS AND LOW MOISTURE HIGH TEMPERATURE "STRESSED" CONDITIONS. [a]Control vs. stressed comparisons were significantly different at **$p < 0.01$, *$p < 0.05$ or $p > 0.05$ if blank.

	Biomass (mg ODW)			% Leaves		% Corms			% Roots		
Subspecies	Control x̄ ± SD (n)		Stressed x̄ ± SD (n)	Control x̄ ± SD	Stressed x̄ ± SD	Control x̄ ± SD		Stressed x̄ ± SD	Control x̄ ± SD		Stressed x̄ ± SD
whipplei	1.1 ± 0.4 (54)	**[a]	0.8 ± 0.3 (54)	46 ± 12	44 ± 9	18 ± 7	**	22 ± 8	35 ± 10		34 ± 9
parishii	0.9 ± 0.5 (60)	*	0.7 ± 0.3 (35)	55 ± 11	53 ± 9	14 ± 6	**	18 ± 7	31 ± 11		29 ± 9
caespitosa	1.0 ± 0.4 (55)	**	0.7 ± 0.3 (48)	49 ± 12	50 ± 9	14 ± 4	**	19 ± 7	37 ± 11	**	31 ± 7
intermedia	0.8 ± 0.3 (56)	**	0.5 ± 0.2 (31)	52 ± 10	52 ± 8	16 ± 6	*	19 ± 5	33 ± 9	**	28 ± 6
percursa	0.7 ± 0.3 (48)	**	0.5 ± 0.2 (23)	57 ± 8	53 ± 9	15 ± 4	**	19 ± 6	28 ± 8		28 ± 6
p	<0.01		<0.01	<0.01	<0.01	<0.01		<0.01	<0.01		<0.01

TABLE 4. LEAF CHARACTERISTICS OF FOUR-MONTH-OLD SEEDLINGS OF *Yucca whipplei* SUBSPECIES MAINTAINED UNDER WELL-WATERED AMBIENT "CONTROL" CONDITIONS AND LOW MOISTURE HIGH TEMPERATURE "STRESSED" CONDITIONS. [a]Control vs. stressed comparisons were significantly different at **$p < 0.01$, *$p < 0.05$, or $p > 0.05$ if blank. [b]Leaf area was estimated by assuming each leaf approximated a rectangle and multiplying by the total number of leaves/plant.

	Leaf width (mm)			Leaf length (mm)			No. of leaves			Estimated total leaf area (cm^2)[b]		
Subspecies	Control x̄ ± SD		Stressed x̄ ± SD	Control x̄ ± SD		Stressed x̄ ± SD	Control x̄ ± SD		Stressed x̄ ± SD	Control x̄ ± SD		Stressed x̄ ± SD
whipplei	2.4 ± 0.5	**[a]	2.1 ± 0.7	14.0 ± 1.8		14.6 ± 1.9	4.4 ± 0.7	*	4.1 ± 0.7	14.5 ± 4.3	**	12.6 ± 5.8
parishii	2.6 ± 0.5	**	2.2 ± 0.7	13.5 ± 2.3		13.6 ± 2.3	3.9 ± 0.6	**	3.4 ± 0.6	14.1 ± 4.7	**	11.0 ± 6.4
caespitosa	2.3 ± 0.5		2.3 ± 0.9	13.2 ± 2.1		12.3 ± 1.8	3.9 ± 0.5	**	3.4 ± 0.5	12.1 ± 3.5	*	10.1 ± 5.9
intermedia	2.1 ± 0.6		2.1 ± 0.6	13.7 ± 1.8	*	14.6 ± 2.3	3.9 ± 0.7	**	3.3 ± 0.5	11.6 ± 3.3	**	9.5 ± 3.6
percursa	2.2 ± 0.5		1.9 ± 0.5	11.8 ± 2.0		12.6 ± 1.7	4.1 ± 0.1	**	3.4 ± 0.7	10.5 ± 3.5	*	8.3 ± 3.6
p	<0.01		<0.01	<0.01		<0.01	<0.01		<0.01	<0.01		<0.01

TABLE 5. CORRELATION OF SEED WEIGHT, ELEVATION AND DISTANCE FROM THE COAST OF SEED COLLECTION SITE WITH GROWTH CHARACTERISTICS OF FOUR-MONTH-OLD *Yucca whipplei* SUBSPECIES COMBINED (n = 273 for controls and n = 191 for stressed plants). *p < 0.05, **p < 0.01, dash indicates no significant correlation.

	Seed weight		Elevation		Distance from coast	
	Control	Stressed	Control	Stressed	Control	Stressed
Total biomass	0.46**	0.41**	0.14**	0.22**	0.18**	0.19**
Percent leaves	—	—	—	—	—	—
Percent corms	—	—	—	—	−0.17*	—
Percent roots	—	—	0.15*	0.15*	—	—
Leaf width	0.39**	0.36**	—	0.25**	0.30**	0.22**
Leaf length	0.21**	0.25**	—	—	—	—
Number of leaves	—	0.23**	—	—	—	—

In summary, *Yucca whipplei* exhibits significant ecotypic differentiation in seed germination and early seedling growth characteristics. Although there were highly significant differences among subspecies in biomass allocation patterns, these were not related to reproductive mode, elevation, or distance from the coast. It is unknown whether these population differences were selected by localized environmental differences or reflect genetic drift in populations that are often isolated from one another by considerable distances. Some patterns were similar among all taxa and undoubtedly reflect similar selective influences. For example all subspecies responded to low moisture and high temperature stress conditions in allocating more biomass to corms, possibly reflecting the fact that all are distributed in habitats or microhabitats subject to unpredictable droughts. Total biomass of seedlings after four months was also unrelated to reproductive mode. It tended to increase with elevation and distance from the coast and appears to be controlled by seed weight. The only clear association between reproductive mode and any of the other characters examined is in leaf characteristics. The two semelparous subspecies (*whipplei* and *parishii*), after four months growth in a common environment, had markedly higher total leaf areas than the other three taxa. Of the five *Yucca whipplei* subspecies, these two semelparous taxa are the ones most closely associated with the fire-prone chaparral. Larger leaf areas may allow for more rapid growth rates in subsequent years, a characteristic of selective value in habitats subject to frequent fires.

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THE PHYTOGEOGRAPHICAL SIGNIFICANCE OF SNOW MOUNTAIN, NORTH COAST RANGES, CALIFORNIA

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Abstract

Snow Mountain (2152 m), on the Lake-Colusa-Glenn tricounty boundary in northwestern California, is the southernmost peak of the North Coast Ranges to exceed 1900 m. A quarter (128 spp.) of its known flora above 1500 m is at a margin of range there. For 126 of these, Snow Mt. is essentially the southernmost Coast Range locality and, of these 105 are of Sierran affinity. These 128 species are listed, with estimates of numerical importance and summaries of known ranges in California. Distribution patterns and geologic history of montane northern California suggest that many of these species entered the North Coast Ranges from the Klamath Ranges about as early as they occupied the Sierra Nevada and are not necessarily of Sierra Nevadan origin. The small number of Coast Range endemic taxa probably originated in situ from Klamath Region stocks and are now essentially relictual.

In 1893, Katharine Brandegee published a list of 95 taxa characteristic of the Sierra Nevada that had to that date been found in isolated occurrences in the North Coast Ranges. Of these taxa, 84 were reported from the vicinity of Snow Mountain, though most of these records do not appear to be documented by specimens. They resulted from two trips: one by T. S. Brandegee in 1891, the other by K. Brandegee in 1892. Since then there has been almost continuous interest among collectors in the flora of Snow Mt., but no compilation of that flora. The massif is centered nearly on the Lake-Colusa-Glenn tricounty boundary. At lat. 39°23′N (long. 122°45′W) it is the southernmost peak of the North Coast Ranges that exceeds 1900 m (the East Peak reaches 2152 m; the West Peak, 2147 m). To the south, maximum elevations drop off rapidly.

Portions of Snow Mt. have been proposed for Federal Wilderness status for many years, but action is currently at a standstill. The area is one of diverse natural values but most important is its flora. One of us (LRH) first visited Snow Mt. in 1956. Since 1979 we have collaborated on compilation of a florula of the mountain massif above 1500 m, an area of approximately 55 km^2 encompassing an elevational range of 650 m. To date, more than 500 taxa of vascular plants are known from this area, more than a quarter of which are at an extreme margin of their known geographical ranges. The great majority of these are predominantly Sierra Nevadan (abbreviated SN below) or Cascade (C) taxa in California that range west into the

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Klamath Ranges (KR) and thence south, normally spottily and only at higher elevation, through the North Coast Ranges (NCR) to Snow Mt. They may or may not also occur in the Transverse (T) or Peninsular (P) Ranges of southern California. Some have isolated occurrences in the South Coast Ranges (SCR), especially the San Benito and Santa Lucia Ranges. Two taxa are at their northern limit of known distribution on Snow Mt. and a few others are endemic to NCR. Most of those in the last category were described from Snow Mt. material.

This paper reports the phytogeographically interesting taxa known so far from Snow Mt., summarizes their ranges in California, and attempts to assess the vegetational history of the high NCR and the significance of the region for California phytogeography. A paper covering the entire flora is being prepared. In it we present habitat information for all taxa and outline community types.

Perhaps 200,000 specimens from California have been added to herbaria since the completion of Munz' Supplement (1968). Neither Jepson (1925) nor especially Munz (1959, 1968) was able to encompass even the herbarium material available in California when they compiled range descriptions. Range descriptions in floras are not satisfactory for determining currently documented limits of range. To decide whether our Snow Mt. records represent known range limits, we supplemented monographic and floristic literature with examination of about 50,000 herbarium specimens in AHUC, CAS, DAV, DS, JEPS, POM, RSA, and UC. Furthermore, we were given access to the floristic computer files (SLID) at Pacific Union College (PUA) and to data compiled at CHSC and HSC. In several instances the aid of current monographers was enlisted. The list below is not one of "range extensions," but rather of the taxa that make Snow Mt. phytogeographically important. Some of these occurrences have been known and published since the last century, but most are not accounted for by the range descriptions of Jepson (1925) or Munz (1959, 1968).

The North Coast Ranges (NCR) can be distinguished from the more ancient Klamath Ranges (KR) on the basis of geology and topography, and to a lesser extent vegetationally. The predominant substrate of NCR is the Jurassic-Cretaceous Franciscan Complex of sediments and metasediments that have been thrust under continental rocks, the peaks of the range achieving near-current prominence by Miocene. Some peaks of NCR, including Snow Mt., St. John Mt., and the North Yolla Bolly massif, are composed primarily of volcanics and metavolcanics, also of Mesozoic age. By contrast, KR consist of Mesozoic plutonic rocks—igneous and highly metamorphosed substrates including granites and marbles, with a higher proportion of ultrabasic rocks such as serpentine (Jennings 1977). These ranges (KR) make up the oldest continuous land surfaces in

California, having been uplifted by the end of the Mesozoic. The North Coast Range Thrust Fault (South Fork Mountain Fault) divides the two geologic regions. Topographically, this fault essentially follows the valleys of the lower Klamath River and the South Fork of the Trinity River (just east of South Fork Mt.) in the north, arcs east through Stuart Gap just north of the North Yolla Bolly massif, then trends southward, separating the Central Valley from NCR. The narrow band of schistose rocks of South Fork Mountain and adjacent areas are problematical in regional assignment, but now seem most closely allied to NCR rocks (Irwin 1966, Jennings 1977).

Vegetationally, the montane forests of KR differ from those of NCR by the importance in KR of *Tsuga mertensiana* and a more pronounced habitat segregation of *Pinus ponderosa* from *Pseudotsuga menziesii* than occurs in NCR. At lower elevations, mixed evergreen forest in KR characteristically includes *Chrysolepis chrysophylla,* but *Rhododendron macrophyllum* replaces it in equivalent forests in NCR (Küchler 1977).

Few studies of flora or vegetation patterns in higher NCR have been published; Ferlatte's (1974) treatment of the Trinity Alps (KR) is the closest regional flora. Clark (1937) presents a general discussion of vegetation types. Hemphill (1952 Ph.D. diss., Oregon State Univ.) and Keeler-Wolf and Keeler-Wolf (1974 Senior Thesis, Univ. California, Santa Cruz) have completed extensive natural history studies that are not published. Except for Küchler's map (1977), NCR higher montane vegetation is not discussed in Barbour and Major's tome (1977) on the terrestrial vegetation of the state. Snow Mt. is at the southern end of Küchler's (1977) Coast Range Montane Forest, which is approximately equivalent to the Yellow Pine and Red Fir Forests of Munz (1959), the White fir-mixed conifer and Red fir Forests of the Sierra Nevada (Rundel et al. 1977), and the *Abies concolor* and *Abies magnifica* zones of the Klamath Mountains (Sawyer and Thornburgh 1977). Most Snow Mt. taxa are found predominantly or exclusively in the wide diversity of non-forest habitats that occur within these zones. Such habitats include forest openings, serpentine barrens and grasslands, outcrops, screes, rocky flats, and wet meadows.

Geographical subdivisions of the higher NCR are not standardized. Some workers, apparently following Clark (1937), have applied the term Yolla Bolly Mountains to the entire higher NCR but local place names suggest this is inappropriate. We present our scheme in Fig. 1 and summarize it below. Insofar as possible, we have followed names on recent and old maps and have tried to make subdivisions follow natural topographic lines that might reflect habitat barriers to migration.

The northern North Coast Ranges (nNCR: n. and w. of North Yolla Bolly Mts.) are generally too low to support red fir forest or

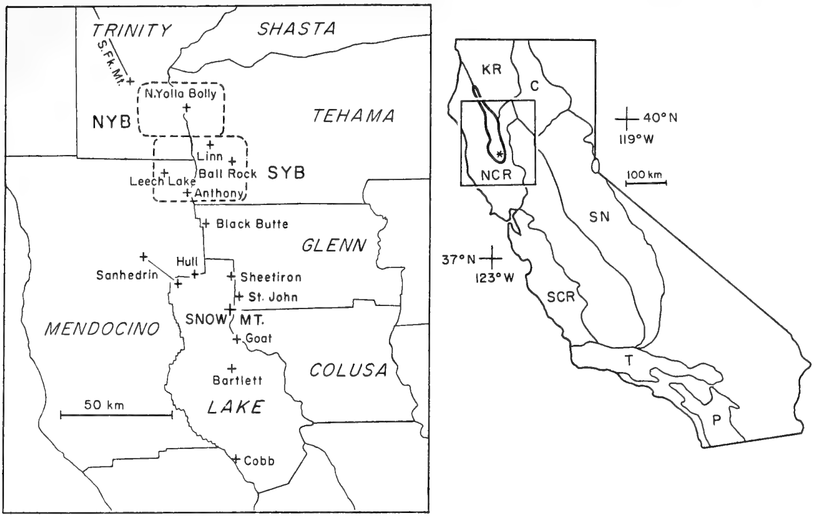

FIG. 1. California mountains and mountain ranges referred to in this paper. C = Cascade Range; KR = Klamath Ranges; NCR = North Coast Ranges (the high NCR are more heavily outlined; "*" indicates the position of Snow Mt.); P = Peninsular Ranges; SCR = South Coast Ranges; SN = Sierra Nevada; T = Transverse Ranges. The enlarged area on the left shows details of the high NCR and lower NCR south of Snow Mt. NYB = North Yolla Bolly Mts.; SYB = South Yolla Bolly Mts.

other upper montane communities, to which the taxa listed here are mostly restricted on Snow Mt. The long ridge of South Fork Mt. encompasses the highest point in nNCR (1850 m); otherwise only the Lassic massif exceeds 1600 m. Both support some high montane communities, but most northwestern California localities from north of the North Yolla Bolly Mts. for these taxa are in KR rather than nNCR.

For our purposes, the North Yolla Bolly Mts. (NYB) include the North Yolla Bolly massif proper (NYB Peak and Black Rock Mt.), Lazyman Butte, and Devil's Hole Ridge south to The Knob. The South Yolla Bolly Mts. (SYB) include Sugarloaf Mt., the SYB massif proper (Harvey Peak, Mt. Linn, Square Lake, Boswell Ridge, and Ovenlid), Ball Rock, Whitlock Camp (Round Mt.), Solomon Peak (the "South Yollo Bolly" of Jepson), Soldier Ridge, Hammerhorn Mt., Buck Rock, Castle Peak, Leech Lake Mt., Government Flat, and Anthony Peak and its southern ridge south to Mendocino Pass at the Tehama-Glenn-Mendocino tricounty boundary.

There are several historically and phytogeographically important collecting localities between SYB and Snow Mt. that will be specified individually in the following treatments. They are more or less isolated from one another and have no inclusive regional name. Progressively farther south from SYB, they are: Black Butte (2272 m max. elev., Glenn Co., including Keller Lake, Snow Basin, and Plaskett Meadows); Hull (2096 m, including Spruce Grove, Monkey Rock, Windy Gap, Hull Mt. proper, and Boardman Ridge); Sanhedrin (a long ridge including Impassable Rock and Mt. Sanhedrin, Mendocino Co. and Sanhedrin Lookout, Lake Co.); Sheetiron Mt. (1983 m, Lake-Glenn Co. boundary); and St. John Mt. (2057 m, Glenn Co.).

Several peaks south of Snow Mt. in Lake Co. also harbor a few of the taxa considered here and are phytogeographically important in their own rights. We consider that Goat Mt. (1867 m, ca. 13 km south of Snow Mt. on the Lake-Colusa Co. boundary and separated from it by a 1300-m divide) is, in historical/phytogeographical terms, part of the Snow Mt. massif, though we have not studied it as thoroughly and mention occurrences there separately. Farther south in Lake County are Elk Mt. (1206 m), Bartlett Mt. (1476 m), and Cobb Mt. (1440 m). Single known occurrences on these peaks are cited individually below, but two or more documented occurrences from farther south than Goat Mt. served to remove taxa from the select group considered here.

In the list below we give an estimate of numerical importance *on Snow Mt.* for each taxon, using the four relative terms "abundant," "common," "occasional," and "rare." Only taxa that dominate numerically within their general life-form (e.g., trees or small annuals) over a range of habitats were considered "abundant"; "rare" was reserved for taxa known from only one or two populations. Elevational range on Snow Mt. is given, but habitats are mentioned only for plants that are ecologically restricted. The modifier "local" follows numerical importance estimates for taxa with strikingly patchy distributions but little ecological restriction. These data are followed by NCR localities south of Snow Mt. (if any), and then throughout California progressively distant from Snow Mt., using the names and regional abbreviations given above and in Fig. 1. Asterisks indicate taxa listed for Snow Mt. by Brandegee (1893); unless noted, we have confirmed their presence. Nomenclature follows Munz (1959, 1968) except where authorities are cited.

PHYTOGEOGRAPHICALLY IMPORTANT SNOW MT. PLANTS

**Abies concolor.* Common, above 1550 m, but rarely a strong forest dominant. Also on Goat Mt. and Cobb Mt. Pine Mt. (Lake Co.), St. John Mt., Sheetiron Mt., Sanhedrin, Hull, SYB, NYB, nNCR, KR, C, SN, T, P.

**Abies magnifica* var. *shastensis.* Abundant, the dominant tree above ca. 1800 m, often in mature, even-aged stands. About 10% of cone scales have non-exserted bracts, a key character for var. *magnifica.* St. John Mt., Sanhedrin, Hull, Black Butte, SYB, NYB, nNCR, KR (where it intergrades with *A. procera*), C, SN.

Achillea lanulosa subsp. *lanulosa.* Common, above 1500 m. Sanhedrin, Hull, SYB, NYB, nNCR, KR, C, SN, T, P. Our plants key to *A. millefolium* var. *pacifica* (Rydb.) Jones (Nobs, in Abrams and Ferris, 1960), but have the chromosome number of Nobs' *A. m.* var. *californica* (Poll.) Jeps. ($n = 27$, count courtesy of F. M. Chuang). This offers some support for the preference of some authors (e.g., Tyrl, 1975) to recognize only one taxon of western North American *Achillea.*

Aconitum columbianum. Occasional, 1650–2050 m. Black Butte, SYB, KR, C, SN.

Agrostis thurberiana. Rare, 1900–2000 m. SYB, KR, C, SN, T.

Agrostis variabilis. Rare, 1900–2000 m. Black Butte, SYB, NYB, nNCR, KR, C, SN.

Allium campanulatum. Occasional, scree, 1450–2135 m. Also on Cobb Mt. (*Baker 2222b*), St. John Mt. ("John's Pk.," *Mackie s.n.,* 1902), Hull, Black Butte, SYB, NYB, KR, C, SN, T, P. Disjunct in SCR of Monterey Co.

Alnus incana (L.) Moench subsp. *tenuifolia* (Nutt.) Breitung (=*A. tenuifolia* Nutt.). Occasional, streamsides, 1550–1900 m. Hull, Black Butte, SYB, NYB, KR, C, SN.

**Antennaria argentea.* One collection without elevation (*Brandegee s.n.,* 24 Jun 1891). Reported from Elk Mt. (Brandegee, 1893). Black Butte, SYB, nNCR, KR, C, SN.

Antennaria geyeri. Occasional, scree, above 2000 m. SYB, KR, C, SN.

**Arabis platysperma.* Common, above 1650 m. Hull, Black Butte, SYB, NYB, KR, C, SN, T, P.

Arabis aff. *repanda.* Common, above 1500 m. Black Butte, SYB, KR. True *A. repanda* is known from Nevada Co. s. in (and e. of) SN and in T and P. The undescribed NCR/KR taxon is morphologically distinct and geographically disjunct from it.

Arceuthobium abietinum Engelm. ex Munz f. sp. *concoloris.* Rare, at 1600 m. Above Alder Springs, Black Butte, KR, C, SN, T. Also at Van Damme State Park, coastal Mendocino Co.

Arceuthobium californicum Hawksworth and Wiens. Rare, on *Pinus lambertiana,* 1640 m. Southwest of Lake Pillsbury, Brush Camp Ridge, Bear Wallow Ridge (reported in Hawksworth and Wiens, 1972), nNCR, KR (reports), C, SN, T, P.

Arctostaphylos nevadensis. Common, near red fir, above 1900 m. Hull, Black Butte, SYB, NYB, nNCR, KR, C, SN.

Arctostaphylos patula subsp. *patula.* Occasional, 1600–1900 m. Also on Goat Mt. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, KR, C, SN.

Arenaria congesta var. *congesta.* Occasional, 1700–2135 m. Also on Goat Mt. Hull, Black Butte, SYB, KR, C, SN. Some NCR plants could be considered var. *crassula,* but we believe that var. does not merit recognition.

**Arenaria nuttallii* subsp. *gregaria.* Common, widespread, above 1800 m. Also on Goat Mt. St. John Mt., Sanhedrin, Hull, ne. Mendocino Co., SYB, KR.

**Arnica longifolia* subsp. *myriadenia.* Occasional, wet meadows, above 1950 m. SYB, KR, C, SN. Confused with *A. mollis* in NCR; further taxonomic study of this group is needed.

Aster occidentalis. Occasional, wet meadows, above 1800 m. NYB, nNCR, KR, C, SN.

Astragalus purshii. Rare, 1640 and 1900 m. SYB, KR, C, SN, T. Subspecific limits in this complex species are still not clear. Barneby (1964) considered all NCR plants (and SCR plants, from San Benito Co.) to be var. *tinctus.* To be conservative, our range summary includes the arguably separable var. *lectulus* and var. *longilobus* as well as var. *tinctus.*

Botrychium crenulatum Wagner. Rare, shaded seep, 1680 m (*Howard 2,* JEPS). Recently described (Wagner and Wagner, 1981), this inconspicuous fern is now known from California (Modoc Co. s. through SN to Los Angeles Co.), Oregon, Montana, Utah, and Nevada. This is the first collection from the California Coast Ranges, but it is to be expected wherever appropriate habitats are found (W. H. Wagner, pers. comm. 1982).

**Brickellia greenei.* Common, above 1800 m. Black Butte, SYB, nNCR, KR, C, SN.

Carex aurea. Occasional, 1650–2050 m. Black Butte, SYB, KR, C, SN, T, P.

Carex fracta. Occasional, 1375–2050 m. Also on Bartlett Mt. (*Howell 21013*). Sanhedrin, SYB, NYB, KR, C, SN, T, P.

Carex hoodii. Occasional, 1375–1900 m. Black Butte, SYB, nNCR, KR, C, SN, T, P.

Carex jonesii. Common, wet meadows, above 1925 m. Black Butte, SYB, KR, C, SN, T.

Carex pachystachya. Common, wet meadows, 1600–2000 m. Black Butte, SYB, nNCR, KR, C. Immature material is readily confused with *C. festivella.* One collection of apparently good *C. pachystachya* is known from Sonoma County (*Hoover 5081*).

Carex paucicostata. Occasional, 1650–2050 m. SYB, NYB, KR, C, SN.

Castilleja applegatei var. *fragilis* (Zeile) N. Holmgren. Common, above 1500 m. Sanhedrin, Hull, Sheetiron, SYB, NYB, nNCR, KR, C, SN. Not clearly differentiated from *C. martinii* of the Coast Ranges.

**Ceanothus cordulatus.* Abundant, above 1800 m. Also on Goat Mt. Sanhedrin, Hull, above Alder Springs, SYB, KR, C, SN, T, P.

**Cercocarpus ledifolius.* Occasional, 1525–2050 m, some individuals old and gnarled. St. John Mt., Dicks Butte (ne. Mendocino Co.), KR, C, SN, T, P.

**Chaenactis douglasii* var. *rubricaulis.* Occasional, above 2000 m. Also on Goat Mt. St. John Mt., Sanhedrin, Hull, SYB, KR, C, SN.

Chenopodium incognitum. Rare, ca. 2150 m. Black Butte, SYB, KR, C, SN. *Twisselman 1440* from San Luis Obispo Co. is morphologically distinct but undescribed (fide Wahl annotation, 1955).

Chimaphila umbellata var. *occidentalis.* Occasional, ca. 1600 m. Also on Elk Mt. (*Tracy 2336*). Sanhedrin, Red Mt. (nw. Mendocino Co.), nNCR, KR, C, SN, T, P.

Claytonia chamissoi Ledebour. Occasional, shallow water, 1900–2000 m. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, KR, C, SN, T, P.

Claytonia lanceolata. Rare, collected once (Baker, 1954). Hull, nNCR, KR, C, SN.

Claytonia saxosa Brandegee. Type locality. Occasional, local, above 1650 m. Also on Goat Mt. Sanhedrin, SYB, nNCR, KR.

**Collinsia torreyi.* Occasional, open red fir forest, above 1600 m. Hull, Dicks Butte (ne. Mendocino Co.), Black Butte, SYB, NYB, KR, C. Because of the variability in leaf shape in our plants from lance-ovate to linear-lanceolate we do not recognize var. *latifolia.*

Collinsia wrightii. Occasional, local, 1800–2100 m. Black Butte, SYB, nNCR, KR, C, SN, T.

Cordylanthus viscidus. Rare, yellow pine forest, below 1600 m. SYB, NYB, nNCR, KR, C, SN.

Cornus stolonifera. Occasional, above 1500 m. Black Butte, NYB, KR, C, SN. Taxonomic treatment of Munz (1959) is followed here but *C. stolonifera* and *C. occidentalis* (the latter mostly at lower elevations) are not easily distinguished.

Cryptantha affinis. Common, above 1500 m. Also on Cobb Mt. (*Lummi s.n.,* 1893). Sheetiron Mt., Sanhedrin, Black Butte, SYB, KR, C, SN, T, P.

Cynoglossum occidentale. Occasional, above 1500 m. Also on Cobb Mt. (*Dearing et al. s.n.,* 11 Jun 1968). Sanhedrin, Hull, above Alder Springs, SYB, KR, C, SN.

Danthonia unispicata. Occasional, above 1900 m. Black Butte, SYB, KR, C, SN.

Dicentra uniflora. Occasional, ca. 1950 m. Black Butte, nNCR, KR, C, SN.

Dodecatheon jeffreyi subsp. *jeffreyi.* Rare, 1800–1900 m. Black Butte, SYB, NYB, KR, C, SN.

Epilobium ciliatum Raf. subsp. *glandulosum* (Lehm.) Hoch and Raven. Common, above 1800 m. Sanhedrin, Black Butte, SYB, NYB, KR, C, SN, T, P.

Epilobium glaberrimum subsp. *glaberrimum.* Occasional, above 1800 m. Sanhedrin, Black Butte, nNCR, KR, C, SN, T, P.

Epilobium nivium. Type locality. Occasional, rock outcrops, above 1600 m. Also on Goat Mt. St. John Mt., Sheetiron Mt., Castle Peak (SYB of n. Mendocino Co.).

**Eriogonum lobbii.* Occasional, above 1550 m. St. John Mt., Hull, SYB, KR, C, SN.

**Eriogonum spergulinum* var. *reddingianum.* Common, above 1900 m. Hull, Black Butte, SYB, KR, C, SN, T. Disjunct in Santa Lucia Mts., Monterey Co.

**Eriogonum strictum* subsp. *proliferum.* Occasional, 1550–2050 m. Northeast Mendocino Co., SYB, KR, C. Collections of subsp. *proliferum* from the Yolla Bolly Mts. and south have been annotated by Reveal as three separate varieties and as intermediates between these. We see little to be gained from recognizing the varieties created by Reveal (1978), but we suspect the dwarfed serpentine form from NCR and Klamath Mts. deserves taxonomic recognition.

Eriogonum nervulosum (Stokes) Reveal. Type locality. Occasional, above 1975 m. Otherwise known only from: Colusa Co., Frenzl Cr. Botanical Area, fide G. L. Stebbins; Lake Co., Complexion Canyon, *Stebbins 6687*; Cobb Mt. vicinity (Lake-Sonoma Co. line), *Patterson s.n.,* in 1979.

**Eupatorium occidentale.* Occasional, rock outcrops, above 1900 m. Black Butte, SYB, NYB, KR, C, SN.

Fritillaria glauca. Occasional, scree, above 1950 m. Also on Goat Mt. Hull, Black Butte, SYB, nNCR, KR, C (of Oregon).

Galium bifolium. Occasional, moist meadow margins, above 1500 m. Hull, Black Butte, SYB, nNCR, KR, C, SN, T.

**Galium grayanum* Ehrend. Occasional, scree, mostly above 2000 m. Also on Goat Mt. St. John Mt., Hull, Black Butte, SYB, KR, C, SN. Two varieties were recognized by Dempster and Ehrendorfer (1965). Because of their mixed geographic ranges and, on Snow Mt., mixed populations (perhaps even mixed clones), we concur with Dempster and Ehrendorfer (1965, p. 321–322) that their var. *nanum* either is a set of dwarfed forms derived independently from typical *G. grayanum* or is induced by severe environmental conditions. Accordingly, we do not differentiate the two varieties taxonomically.

Galium sparsiflorum subsp. *glabrius* Demp. & Steb. Occasional, 1500–1900 m. Also on Trough Spring Ridge, se. of Snow Mt. (*Chisaki 1166A*). St. John Mt., above Alder Springs, KR, C.

**Gayophytum diffusum* subsp. *parviflorum.* Abundant, above 1500 m. Sheetiron Mt., Hull, above Alder Springs, Black Butte, SYB, NYB, nNCR, KR, C, SN, T, P. Some populations have petal and anther size within the range of the outbreeding subsp. *diffusum* as defined by Lewis and Szweykowski (1964) but the stigma is like that of subsp. *parviflorum.*

Gayophytum heterozygum. Rare, ca. 1900 m. Sanhedrin, above Alder Springs, SYB, nNCR, KR, C, SN, T, P. Also disjunct in Monterey and San Luis Obispo Cos.

Hackelia amethystina. Common, above 1500 m. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, NYB, nNCR, KR, C, SN.

**Haplopappus greenei.* Occasional, mostly above 1900 m. Hull, Bald Mt. (ne. Mendocino Co.), Black Butte, SYB, nNCR, KR, C.

Hazardia whitneyi (Gray) Greene var. *discoideus* (Howell) Clark (*Haplopappus w.* var. *d.* Howell). Occasional, above 1600 m. Hull, Black Butte, SYB, nNCR, KR, C.

Hieracium greenei. Rare, open red fir forest, 1850 m. St. John Mt., Hull, SYB, NYB, nNCR, KR, C, SN, T, P.

**Holodiscus boursieri.* Abundant, a subdominant shrub above 1550 m. Also on Goat Mt. Sanhedrin, Black Butte, Red Mt. (nw. Mendocino Co.), SYB, NYB, nNCR, KR, C, SN, T, P. The montane intermediates between coastal *H. discolor* and alpine *H. microphyllus* are taxonomically confused. We follow nomenclature of Munz (1959) for lack of a better alternative. Snow Mt. is the southernmost Coast Range locality for any of the montane intermediate forms.

**Horkelia tridentata* subsp. *flavescens.* Rare, ca. 1900 m. Sheetiron Mt., Sanhedrin, Hull, nw. Mendocino Co., SYB, NYB, KR, C, SN.

**Ipomopsis aggregata.* Rare, dry yellow pine forest, 1550 m. Black Butte, SYB, KR, C, SN.

**Ivesia gordonii.* Rare, scree, 2100 m. SYB, NYB, KR, C, SN.

Juncus howellii. Rare, wet meadow, 2010 m. Black Butte, SYB, KR, C, SN.

Kelloggia galioides. Occasional, above 1800 m. Reported from Cobb Mt. (Neilson, 1981). Sanhedrin, Hull, Black Butte, NYB, nNCR, KR, C, SN, T, P.

Lathyrus pauciflorus Fernald. Rare, 1750–1950 m. Sanhedrin, SYB, KR, C, SN.

**Leptodactylon pungens* subsp. *pulchriflorum.* Occasional, above 2000 m. St. John Mt., nNCR, KR, C, SN, T.

**Lesquerella occidentalis* subsp. *occidentalis.* Occasional, above 2100 m. Also on Goat Mt. Hull, SYB, NYB, KR, C, SN.

Lewisia nevadensis. Occasional, moist rocky flats, ca. 1950 m. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, KR, C, SN, T.

Lewisia triphylla. Occasional, moist rocky flats, 1950–2050 m. Hull, Black Butte, SYB, KR, C, SN.

**Linanthus harknessii* var. *harknessii.* Reported by Brandegee (1893); no specimens nor living plants have been found. Black Butte (Plaskett Mdws. is the type locality of var. *condensatus*), SYB, KR, C, SN.

Linanthus rattanii. Type locality imprecise, possibly Snow Mt. Common, 1500–1600 m. Sanhedrin, Hull, Long Valley and Red Mt. (nw. Mendocino Co.), Black Butte, SYB.

Linum lewisii Pursh. Occasional, above 1850 m. Black Butte, SYB, NYB, KR, C, SN, T, P, north. Also in SCR, but at lower elevations. [*Jepson 13538,* cited by Jepson (Fl. Calif. 2:397) from Alameda Co., is *L. angustifolium.*]

Listera convallarioides. Rare, shaded seep, 1680 m. Sanhedrin, Black Butte, SYB, KR, C, SN, T, P.

Lithophragma glabra. Occasional, ca. 1950 m. Hull, Black Butte, NYB, KR, C, SN, T.

Lomatium ciliolatum var. *ciliolatum.* Common, above 1900 m. Also on Goat Mt. Sheetiron Mt., Hull, Black Butte, SYB, NYB, nNCR. Specimens from 1250 m and below in the Mt. Hamilton Range (SCR), annotated as this variety by Mathias and Constance, differ in their less compact compound leaves with narrower lobes; they lack the additional clusters of leaflets at the juncture of the opposite primary divisions that are especially conspicuous in NCR plants.

**Machaeranthera shastensis* var. *eradiata.* Occasional, above 1900 m. Hull, Black Butte, SYB, KR, C.

Melica bulbosa var. *bulbosa.* Rare, open red fir forest, 2090 m. Above Alder Springs, Black Butte, KR, C, SN. Variety *inflata* (=*M. bella* Piper) is quite distinct and occurs at lower elevations from Yolo to San Benito Cos. and in the Sierra Nevada.

Melica stricta. Rare, sheltered outcrops, 2075 m. Hull, Black Butte, SYB, NYB, KR, C, SN, T.

Microseris nutans. Occasional, above 1900 m. Longvale (nw. Mendocino Co.), nNCR, KR, C, SN.

**Mimulus breweri.* Common, wet meadow margins, above 1850 m. Sanhedrin, Hull, above Alder Springs, Black Butte, SYB, KR, C, SN, T, P.

Mimulus nanus. Occasional, above 2000 m. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, KR, C, SN.

**Mimulus pilosellus* Greene (*M. primuloides* var. *p.*). Common, wet meadows, above 1850 m. Hull, Black Butte, SYB, NYB, KR, C, SN.

Monotropa hypopithys. Rare, oak-pine woods, 1350 m. Also at Pilot Grove Campground, 1200 m, 15 km sw. of Snow Mt. (*Hamann et al. s.n.,* in 1969). Sanhedrin, above Alder Springs, KR, C.

Muhlenbergia filiformis. Occasional, above 1900 m. SYB, NYB, KR, C, SN, T, P.

Osmorhiza occidentalis. Occasional, above 1700 m. Black Butte, SYB, KR, C, SN. *Purpus s.n.* (April 1898) from "Potter Valley, Mendocino Co." is likely from a higher elevation on Sanhedrin.

**Pedicularis semibarbata.* Common, above 1550 m, becoming abundant under red fir above 1900 m. Also on Cobb Mt. (*Baker 2179a*); reported from Bartlett Mt. (Brandegee, 1893) but not found by Howell (1946). Sanhedrin, Hull, Black Butte, nNCR, KR, C, SN, T, P.

Pellaea brachyptera. Occasional, outcrops and screes, above 1550 m. St. John Mt., Sanhedrin, Hull, nw. Mendocino Co., SYB, KR, C.

Penstemon purpusii. Type locality. Common, above 1700 m. Also on Goat Mt. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, NYB, nNCR, KR.

Phacelia mutabilis. Occasional, open red fir forest, above 1900 m. Also on Goat Mt. and Cow Mt. [Sonoma Co. plants (*Heckard T-133*; see Heckard, 1960) are highly atypical and are more closely related to *P. nemoralis* Greene.] Sanhedrin, Black Butte, SYB, nNCR, KR, C, SN, P.

Phacelia procera. Rare, streamsides, above 1800 m. Hell's Half Acre (n. of Hull), Black Butte, SYB, KR, C, SN.

Phlox diffusa subsp. *diffusa.* Occasional, rocky flats, above 1950 m. Hull, Black Butte, SYB, KR, C, SN, T.

**Pinus jeffreyi.* Occasional, local, above 1550 m, sometimes in mixed stands with *P. ponderosa.* Many trees are unusually old and stunted. Hull, nw. Mendocino Co., SYB, NYB, nNCR, KR, C, SN, T, P. Also disjunct in se. San Benito Co.

Poa bolanderi. Rare, scree, 1950 m. Black Butte, SYB, KR, C, SN, T, P.

**Polygonum davisiae.* Rare, snowbed scree, 2135 m. Hull, SYB, KR, C, SN.

Polygonum kelloggii. Common, wet meadow margins, above 1900 m. Black Butte, SYB, NYB, KR, C, SN, T, P. Intergrading and confused with *P. confertiflorum,* which is widespread at lower elevations (including s. Lake Co.).

Polygonum minimum. Occasional, meadow margins, above 1850 m. SYB, NYB, KR, C, SN.

Polystichum scopulinum. Occasional, outcrops, 2075 m. Black Butte, SYB, NYB, KR, C, SN, T, P.

Potentilla drummondii. Rare, 1920 m. SYB, NYB, KR, C, SN.

Potentilla glandulosa subsp. *nevadensis.* Common, above 1800 m. Also on Goat Mt. Hull, above Alder Springs, Black Butte, SYB, NYB, nNCR, KR, C, SN, T, P.

**Purshia tridentata.* Occasional, as patches of old, gnarled, low and spreading shrubs, above 1950 m. Hull, KR, C, SN.

**Pyrola picta* var. *picta.* Occasional, above 1500 m. Also on Elk Mt. (*Tracy 2331*). Sanhedrin, Black Butte, SYB, KR, C, SN, T, P.

**Pyrrocoma apargioides* (Gray) Greene (*Haplopappus a.* Gray). Reported by Brandegee (1893); no specimen has been found. Only report for NCR: SN (Plumas Co. south) and adj. Nevada.

**Quercus vaccinifolia.* Occasional, dominant of shrubby thickets, 1950–2100 m. Sanhedrin, Hull, Black Butte, nw. Mendocino Co., SYB, nNCR, KR, C, SN.

**Raillardella scabrida* Eastwood. Type locality. Occasional, above 1950 m. Sanhedrin, Hull, SYB, NYB, nNCR.

**Ranunculus alismaefolius.* Occasional, moist rocky flats, 1950 m. KR, C, SN.

Ribes binominatum. Occasional, above 1800 m. Also on Goat Mt. Hull, Black Butte, SYB, NYB, nNCR, KR, C.

**Ribes lobbii.* Abundant, a subdominant shrub at 1850–2150 m. Sheetiron Mt., Sanhedrin, Hull, Black Butte, SYB, nNCR, KR, C.

Ribes nevadense. Rare, streamside under yellow pine, 1555 m. Sanhedrin, above Alder Springs, Black Butte, KR, C, SN, T, P.

Rorippa truncata (Jeps.) Stuckey. Occasional, wet meadows, 1830–1950 m. In California otherwise known from the shores of Clear L., Lake Co.; Lake Chabot, Solano Co.; and the San Gabriel and San Bernardino Mts.; widely but uncommonly distributed from the northern Rocky Mts. through the major river valleys of the central and western U.S. (Stuckey, 1972).

Sagina saginoides. Occasional, wet meadows, 1900–2050 m. Sheetiron Mt., Black Butte, SYB, NYB, KR, C, SN, T, P.

**Sedum obtusatum* subsp. *retusum.* Occasional, rocky places, 1500–1950 m. Also on Goat Mt. Sanhedrin (type locality), Black Butte, SYB, NYB, KR. Intergrades with subspp. *obtusatum* and *paradisum* Denton in KR.

Senecio triangularis. Occasional, above 1500 m. Sanhedrin, Black Butte, SYB, NYB, nNCR, KR, C, SN, T, P.

Sphenosciadium capitellatum. Occasional, 1575–1950 m. Reported from Cobb Mt. vicinity (Neilson, 1981). Black Butte, KR, C, SN, T, P.

Stephanomeria lactucina. Occasional, below 1600 m. Sanhedrin, Black Butte, SYB, KR, C, SN.

Stipa californica. Occasional, above 1800 m. Species limits in the difficult *S. occidentalis* lineage, of which this is a member, are currently under study by M. Barkworth (UTC). In California, the entire lineage is predominantly Sierran, extending west to KR; otherwise known from NCR by single collections from Black Butte and SYB.

Thlaspi montanum L. var. *montanum.* Occasional, ca. 1750 m. Hull, Eden Valley (ne. Mendocino Co.), NYB, KR, C, SN.

Trifolium longipes. Occasional, 1550–1950 m. Sanhedrin, Hull, Sherwood Valley (ne. Mendocino Co.), Black Butte, SYB, KR, C, SN.

**Veratrum californicum.* Common, wet meadows, above 1750 m. Sanhedrin, Hull, nc. and ne. Mendocino Co., Black Butte, SYB, KR, C, SN, T, P.

Veronica serpyllifolia var. *humifusa.* Occasional, wet meadows, above 1500 m. Sheetiron Mt., Hull, Black Butte, SYB, KR, C, SN, T, P.

**Viola macloskeyi.* Occasional, wet meadows, above 1800 m. Hull, Black Butte, NYB, KR, C, SN, T, P.

**Viola purpurea* subsp. *integrifolia.* Common, above 1500 m; variable and not clearly separable from var. *purpurea* or from *V. quercetorum.* Also on Goat Mt. Sanhedrin, above Alder Springs, Black Butte, SYB, KR, C, SN. Baker (1949) cites Snow Mt. for both subsp. *purpurea* and subsp. *integrifolia,* the latter at its southern limit.

DISCUSSION

Of the 128 taxa considered here to be at a margin of range, 43 were cited by Brandegee (1893) as basically Sierran (seven of these are now considered to belong to taxa not represented in SN). We have documented an additional 62 taxa that are characteristic of the Sierra Nevada, though their distributional centers are in some cases in the Klamath Mountains. Thus, 82% of the taxa listed are of Sierran affinity. Many, but not all, of these grow farther south in the Sierra Nevada than in the Coast Ranges.

Twenty-one other taxa are at the absolute southern margin of their ranges and are not found in the Sierra Nevada. Twelve of these are found spottily in the North Coast Ranges, are centered in the Klamath Mountains, extend east and usually north in the Cascades (sometimes as far south in the Cascades as n. Butte Co.). They are *Carex pachystachya, Collinsia torreyi* var. *latifolia, Eriogonum strictum* subsp. *proliferum, Fritillaria glauca, Galium sparsiflorum* subsp. *glabrius, Haplopappus greenei, Hazardia whitneyi* var. *discoideus, Machaeranthera shastensis* var. *eradiata, Monotropa hypopithys, Pellaea brachyptera, Ribes binominatum,* and *Ribes lobbii.* Five taxa (*Arabis* aff. *repanda, Arenaria nuttallii* subsp. *gregaria, Claytonia saxosa, Penstemon purpusii,* and *Sedum obtusatum* subsp. *retusum*) have been found only in the NCR and KR, and four are endemic to the North Coast Ranges (*Epilobium nivium, Linanthus rattanii, Lomatium ciliolatum* var. *ciliolatum,* and *Raillardella scabrida*).

Two taxa are at the northernmost margin of California ranges on Snow Mt.: *Eriogonum nervulosum* (which is also endemic to the southern North Coast Ranges but is closely related to *E. ursinum* of KR, C, and SN) and *Rorippa truncata,* which has an unusually scattered distribution in North America east to the Mississippi River (Stuckey 1972).

Since Brandegee's (1893) initial documentation of "Sierra Nevada plants" in the high North Coast Ranges, the prevailing notion (e.g., Hulse-Stephens 1982) has been that members of these taxa have migrated north through the Sierra, west through the Cascade and Klamath Ranges, and south in the Coast Ranges to their current localities. We suspect that this explanation is based to some extent on a confusion between centers of population density and centers of origin.

There is considerable evidence that development of floras in California has been a coastward phenomenon, particularly regarding the forests. The general history of the middle and late Tertiary is one of increasingly continental and arid inland climates, with which successive waves of vegetation moved westward (Axelrod 1976, 1977; Raven and Axelrod 1978; Stebbins 1982). The direct evidence for these changes comes from fossil floras in which trees vastly predominate. Apparently, no such floras exist for northwestern California, including the entire Klamath Region. Hypotheses involving non-forest herbs and shrubs from that part of California, therefore, must rely on indirect evidence of other kinds.

Countering the general trend of coastward development of floras is evidence from the relative ages of the Klamath Region, the North Coast Ranges, and the Sierra Nevada. The Klamath Region, though derived from the same Nevadan (Late Jurassic) pluton as the Sierra Nevada, is the oldest continuously available land in the state, having been uplands of varying height (with several periods of uplift followed by erosion) throughout the Tertiary. Whittaker (1961) concluded that, because of its age and geological (including substrate) complexity, the Klamath Ranges are a floristic and vegetational center for the forests of much of the western United States. They are an important center for relictual endemic taxa (Stebbins and Major 1965), and no doubt have also provided stocks for outward migration and evolution, particularly during the climatic changes of the Tertiary. Both the North Coast Ranges and the Sierra Nevada are considerably younger as montane environments. The high NCR has apparently provided montane habitats since the end of the Miocene (Christensen 1966, Oakeshott 1971) but the Sierra Nevada was too low until Late Pliocene (ca. 12 million years ago) to produce a strong rain shadow in western Nevada. Axelrod (1977, p. 149) calculated that the Mt. Reba flora in the Sierra Nevada has been uplifted about 1850 m since it was deposited in the Pliocene. Both NCR and SN had considerable mountain-building activity from Late Pliocene to mid-Pleistocene (Bateman and Wahrhaftig 1966, Christensen 1966, Oakeshott 1971). Thus, the order of appearance of montane habitats in these three major regions is Klamath Ranges, North Coast Ranges, and finally Sierra Nevada. For the plants of Klamath stock that currently occupy NCR and SN (probably the majority of taxa on our list), it seems reasonable to assume that populations have persisted in NCR for at least as long as in SN.

More work is needed to establish the relative magnitudes of these two countervailing effects, and we assume that both will prove to be important. Yet it is necessary to realize that many of these "Sierra Nevada plants" are likely to be relative latecomers to SN, regardless of their current relative population densities.

It is likely that the NCR endemics listed above arose mostly from Klamath Range stocks during the last half of the Tertiary under the influence of slowly changing climates. The small and interrupted ranges of some of them may indicate that extant populations are essentially relictual, having survived the more rapid fluctuations of the Late Pliocene and Pleistocene in localized pockets.

For most of the species at a margin of range on Snow Mt., it is no doubt the rapid decline in maximum elevation to the south that makes Snow Mt. their southern limit. Occurrence of many of these taxa in the mountains (including SN) of southern California is evidence that latitudinally determined climatic change is much less important than more local phenomena such as rain shadows and elevation. Because of the diversity of habitats occupied by the phytogeographically interesting taxa on Snow Mt., there is no single, precise answer to the question of why these taxa are never or rarely found farther south. Yet loss of appropriate habitats with declining maximum elevations is clearly the most general answer that can be posed.

Both the number (128) and the proportion (25%) of Snow Mt. plants at a margin of range are quite high (perhaps uniquely so) for such a small area. We know of no comparable data for regions in which the prevailing habitat type (general montane in this case) continues but a large proportion of the flora stops. However, under some circumstances (e.g., where mountains give way to desert), a similar or even larger proportion of the flora could be at a margin of range. Regardless of whether our use of superlatives is accurate, the flora of Snow Mt. is unique and will continue to instruct those who study it about the history and distribution patterns of California plants.

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STIPA LEMMONII (VASEY) SCRIBNER (POACEAE): A TAXONOMIC AND DISTRIBUTIONAL STUDY

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ABSTRACT

Stipa lemmonii (Vasey) Scribner is sometimes treated as comprising three varieties: var. *lemmonii*, var. *jonesii*, and var. *pubescens*. Morphological and distributional data obtained from over 300 specimens representing the geographic range of the species do not support recognition of these infraspecific taxa. The known range of the species is extended to include Nevada and Utah.

Stipa lemmonii (Vasey) Scribner is a native grass of western North America. Two varieties have been described: *S. lemmonii* var. *jonesii* Scribner and *S. lemmonii* var. *pubescens* Crampton. These, together with var. *lemmonii*, are the subject of this study. Scribner (1901) described var. *jonesii* as "a small form of the species with rather more slender culms and panicles, and spikelets with the outer glumes 7–8 mm long and flowering glumes about 6 mm long." He cited five specimens but did not suggest any geographic or ecologic peculiarities for the variety. *Stipa lemmonii* var. *pubescens* was described (Crampton 1955) as being similar to the species, differing in "having the blades and sheaths entirely pubescent." Crampton cited two specimens, one of which (the holotype) had been growing in serpentine soil.

Taxonomists have varied in their treatment of these two varieties. Abrams (1923), Hitchcock (1925, 1935, 1951) and Munz (1959) accepted var. *jonesii*, but Peck (1961) and Hitchcock et al. (1969) did not. Munz (1959) also recognized var. *pubescens*, the only one of these authors to do so. In this work, the validity of these two varieties is analyzed by examination of a large number of herbarium specimens representing the full morphologic and geographic range of the species.

MATERIALS AND METHODS

More than 300 herbarium specimens from several herbaria (see acknowledgments) were examined. Of these, 199 were selected for use in the numerical analyses. These included all specimens with pubescent sheaths and up to five additional specimens per county.

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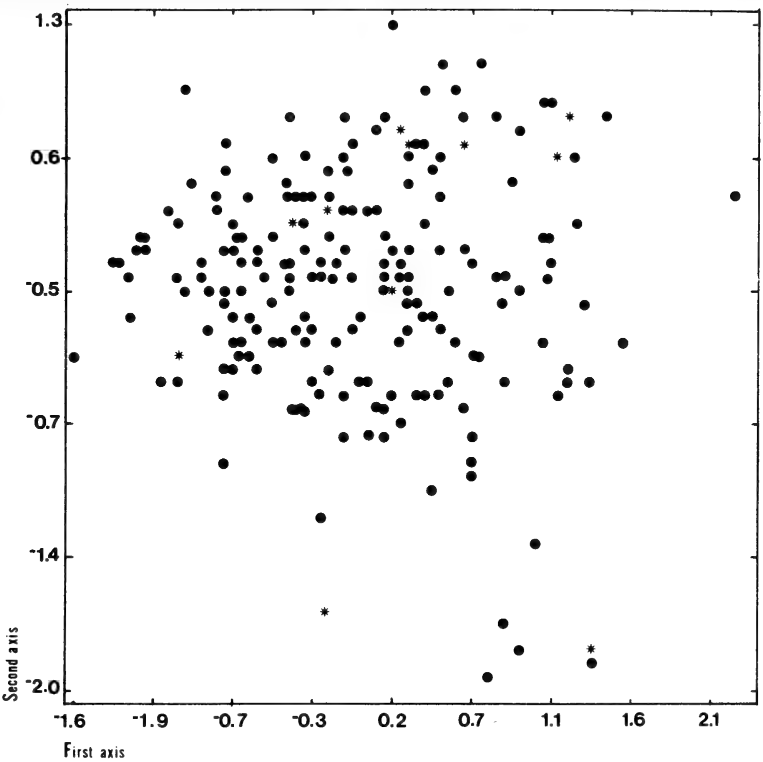

FIG. 1. Projection of the OTUs onto the first two principal axes. The first axis accounts for 50% of the variance, the second for 30%. The weights associated with each character on the two axes are (character first axis, second axis): Culm 0.663, −0.577; inflorescence 0.686, −0.560; glume 0.775, 0.465; floret 0.710, 0.571. Stars = pubescent specimens; dots = glabrous specimens.

These specimens all came from the U.S. Information on the morphological variation and distribution of the species in Canada was obtained from a previous study (Barkworth, unpubl. ms.).

Five morphological characters, reputed to distinguish the varieties, were scored on each of the specimens used in the numerical analyses: culm length, inflorescence length, lower glume length, lemma length (including the callus) and presence or absence of pubescence on the lower leaf sheaths. The geographic and ecological data on the label were also recorded. Soil type was scored as serpentine, non-serpentine, or, unless specifically stated otherwise, unknown.

To determine whether the species could be divided into distinct groups of small ("var. *jonesii*") and large ("var. *lemmonii*") plants, principal component analysis (PCOMP) was run on the four quan-

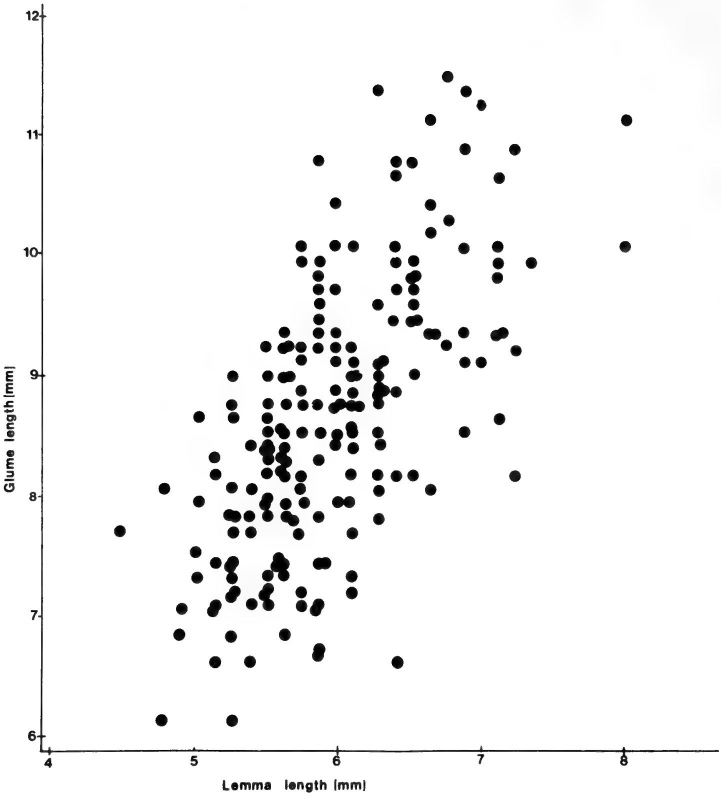

FIG. 2. Scattergram of glume length versus lemma length. The regression equation is: glume length = 1.525 + 1.194 (lemma length).

titative characters. In addition, glume length was plotted against lemma length because these two characters were specifically cited by Scribner in his description of var. *jonesii.*

To investigate the status of var. *pubescens,* we examined the degree of association between pubescence and serpentine soils. The chi-

TABLE 1. SUMMARY OF THE MORPHOLOGICAL DATA FOR *Stipa lemmonii* (n = 199).

Character	Minimum	Maximum	Mean	SD
Culm length (cm)	15.8	89.5	44.3	14.1
Inflorescence length (cm)	7.7	21.0	10.2	2.6
Lower glume length (mm)	6.1	11.5	8.6	1.1
Floret length (mm)	4.5	8.0	6.0	0.6

square statistic, as modified by Yates for use with 2 × 2 tables (Steel and Torrie 1960, Nie et al. 1975) was used to assess the statistical significance of the association between pubescence and serpentine soil. The programs used were NTSYS (Rolf et al. 1976) and SPSS (Nie et al. 1975). They were run on a VAX 11/780.

RESULTS

The PCOMP analysis (Fig. 1) provides no support for the recognition of any infraspecific taxa. Glume and floret length contribute most to the first axis (weights of 0.775 and 0.710 respectively) but the others were also positive (culm length 0.663; inflorescence length 0.686). On the second axis, culm and inflorescence length had negative coefficients (−0.577 and −0.560 respectively) although glume and floret length had positive coefficients (0.465 and 0.571 respectively). The distribution of the OTUs on the first two axes of the PCOMP plot (which account for 80% of the total variance) appears to be random. The same is true of the third axis. Similarly, the scattergram of glume length versus culm length (Fig. 2) does not suggest any easy division of the OTUs into "small" and "large" specimens. Thus our data provide no support for the recognition of *S. lemmonii* var. *jonesii* as a distinct taxon. Table 1 presents a synopsis of the quantitative data.

Positive information on soil type was available for only 42 specimens. Of these, 39 were among those used in the rest of the study. We added three "specimens" to represent the pubescent specimens collected on serpentine soils by Dibble and Griggs (1979). Only five of the 42 specimens were pubescent. Four (including the Dibble and Griggs specimens) were from serpentine soil, the other from sandy soil. There were 18 other specimens from serpentine soil, but all these had glabrous leaf sheaths. The corrected value of chi-square was 0.70; thus the association between pubescence and serpentine soils is not statistically significant.

On seven pubescent specimens the soil type was not specifically stated but the habitat descriptions on the labels do not suggest serpentine soils (e.g., blue oak woodland; open sagebrush slope; grassy slope with ponderosa pine; open woods). Pubescent plants do not appear to be geographically limited in their distribution: collections have been made at scattered locations in Washington, Oregon, and California (Fig. 3). Since no other morphological or ecological characteristic appears to be associated with the presence of pubescence on the leaf sheaths we suggest that var. *pubescens* does not merit formal recognition.

This taxonomic decision is of interest to more than the botanical community because *Stipa lemmonii* var. *pubescens* has been nominated for endangered plant status (U.S. Fish and Wildlife Service

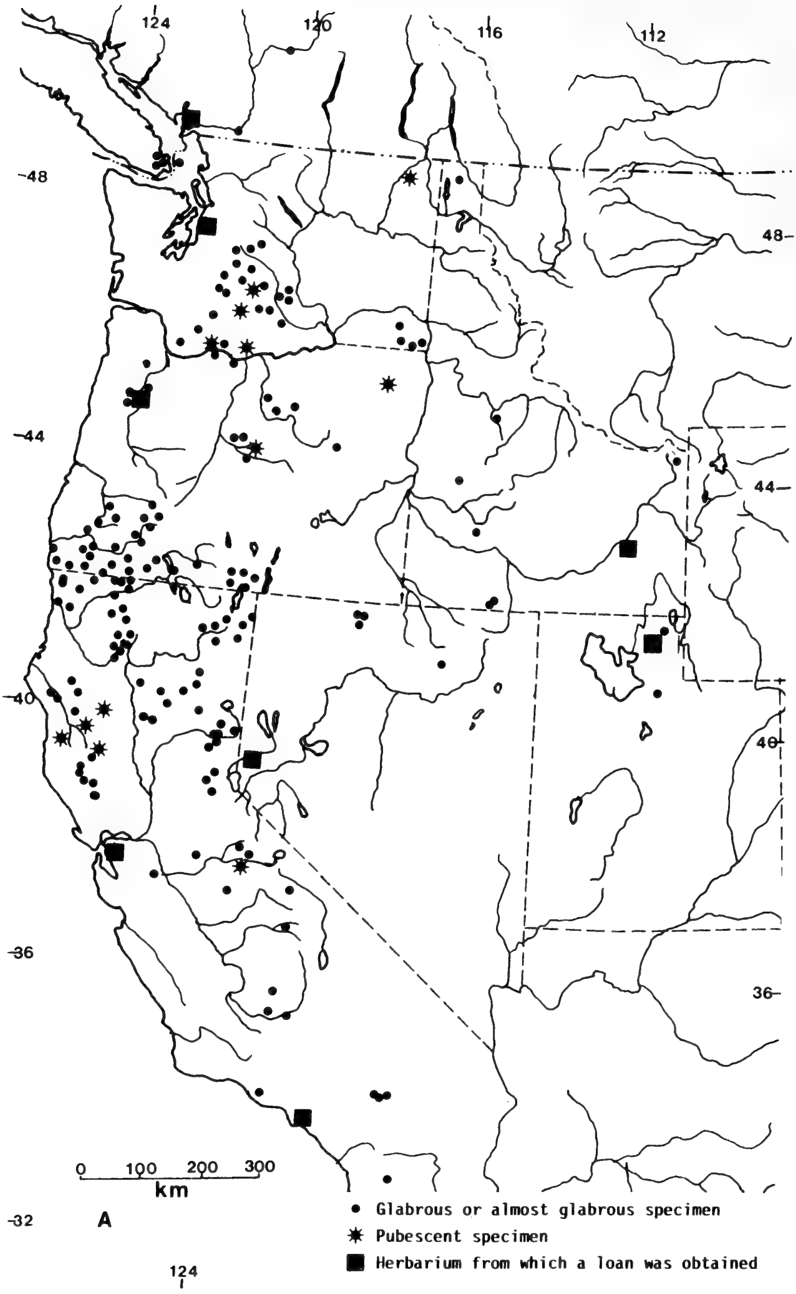

FIG. 3. Distribution of *Stipa lemmonii.*

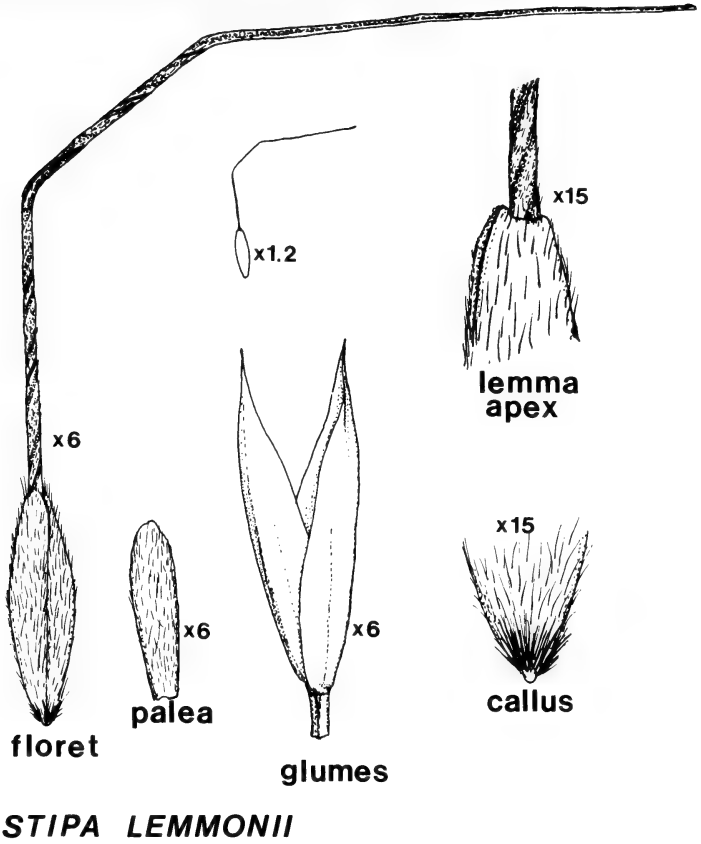

FIG. 4. Spikelet of *Stipa lemmonii.*

1976). Dibble and Griggs (1979) state that it is associated with serpentine chaparral communities. Moreover, they state that their field observations suggest that the most pubescent plants grow on red, decomposed serpentine; less pubescent plants, on green, undecomposed serpentine; and glabrous plants, on the surrounding, non-serpentine soil. Their observations were, however, limited to three serpentine locations in Lake and Tehama Counties, California. Further observations are needed at other sites.

We suggest that the presence or absence of copious pubescence may be determined by a very small number of genes, possibly only one or two, for which the character state "copiously pubescent" represents the recessive allele. If this is true, pubescent plants can be expected to occur, albeit at low frequency, wherever the necessary

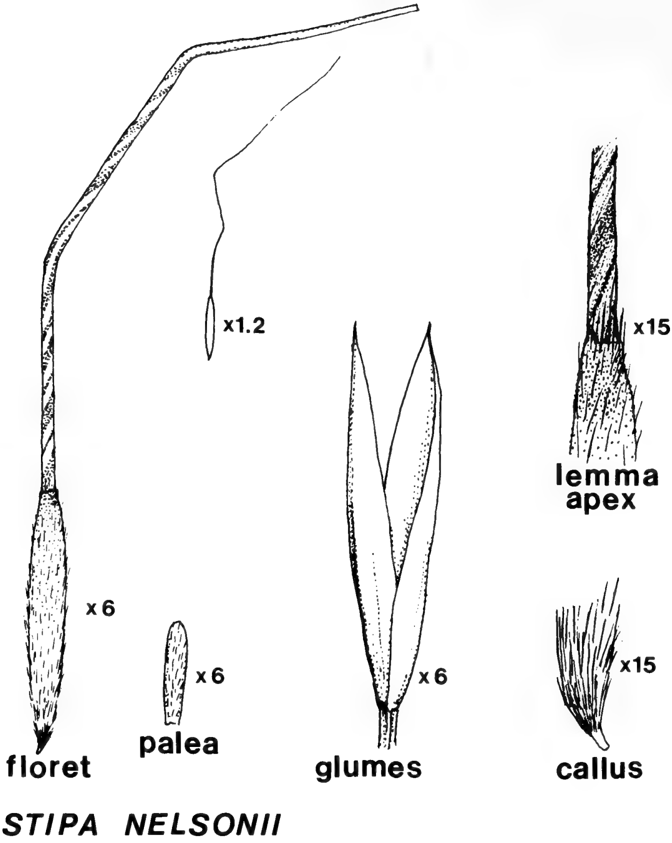

FIG. 5. Spikelet of *Stipa nelsonii.*

alleles are present. At some locations the genes for pubescence may be linked to those for serpentine tolerance. This would account for the tolerance gradient observed by Dibble and Griggs. Variation in the degree of pubescence between duplicate herbarium specimens (e.g., *Opeck 1055, Rogers 422, Hitchcock and Muhlick 22382*) indicate that the degree of pubescence is variable within a population. Dibble and Griggs also noted that the two forms sometimes grow together. The frequency of pubescent plants should be expected to vary from one locality to another, depending on the genotypes present in the founding members and linkage to other traits.

The distribution map of *S. lemmonii* (Fig. 3) shows some additions to the reported range of the species. Holmgren and Holmgren (1977) described the species as "approaching [the Intermountain

Region] on the west and possibly entering it." The following specimens confirm that it is present in Nevada: HUMBOLDT CO.: *J. L. Gentry, Jr. and G. Davidse 1573.* Santa Rosa Range, T42N R38E S25, 19 Jun 1967; *A. Tiehm and M. Williams 1200.* Santa Rosa Range, Hinkey Summit, 28 Jun 1975. Its presence in Utah is documented by: CACHE CO.: *M. Barkworth, J. Maze and R. J. Shaw 4233.* Jardine Juniper Trail, 12 mi e. of Logan, 19 Jun 1983; *M. Barkworth, J. Maze and R. J. Shaw 4234.* Cottonwood Canyon trail, 14 mi e. of Logan, 19 Jun 1983; *M. Barkworth 4240.* Temple Fork turnoff from Canyon Road, 17 mi e. of Logan, 26 Jun 1983; *M. E. Jones s.n.,* Wasatch Mountains, July 1880. [Dr. S. Welsh (Brigham Young University) informed us that Jones collected in City Creek and American Fork Canyons near Salt Lake City towards the end of that month.]

The Nevadan specimens were misidentified as *S. columbiana* sensu A. S. Hitchcock, i.e., *S. nelsonii* Scribner (Barkworth and Maze 1979, 1982; Barkworth et al. 1979). These two species are frequently confused, but *Stipa lemmonii* (Fig. 4) has a "hump" at the apex of the lemma and a palea that is subequal to the lemma. *Stipa nelsonii* (Fig. 5) often has apical lemma lobes but they are membranous, not thick and humplike, and its palea is only about half the length of the lemma. Jones had identified his specimen as *S. viridula,* a species that differs from *S. lemmonii* in having a very short, glabrous, palea.

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NOTES AND NEWS

The Yolla Bolly Mountains of California: New Records and Phytogeographical Notes.—The authors spent three summers in the Yolla Bolly Mts. collecting information for a report on the natural values of the area (Keeler-Wolf and Keeler-Wolf, A contribution to the natural history of the Yolla Bolly Mountains of California, senior thesis, Univ. California, Santa Cruz, 1974). During this period, and more sporadically in the past several years, a large number of new distribution records of vascular plants were accumulated for the area.

The Yolla Bolly Mts. comprise the northern half of the high (1500 m+) Inner North Coast Range (INCR) of California. They extend south ca. 46 km from the region of Black Rock Mt. and the North Yolla Bolly Mts. in northwestern Tehama and Southeastern Trinity Counties to Mendocino Pass (1525 m) along the Mendocino-Tehama County border. The southern INCR has no generally accepted inclusive name (Heckard and Hickman, Madroño 31:30–47, 1984). Both the north and south halves are similar geologically and are primarily composed of metamorphic and sedimentary rocks of the Franciscan Assemblage (Bailey et al., Bull. Calif. Div. Mines Geol. 183:1–177, 1964). The INCR is largely geologically distinct from the adjacent Klamath Province except for the belt of South Fork Mt. Schist, which forms the ridge between Black Rock, N. Yolla Bolly, and Tomhead Mts. and is considered to be a gradational series between the rocks of the metamorphosed Franciscan belt and the W. Klamath Province (Irwin, Bull. Calif. Div. Mines Geol. 190:17–37, 1966). To the north, the Yolla Bolly Mts. are separated from the Trinity Alps by ca. 60 km of lower (largely under 1500 m) mountains.

Both halves of the INCR are floristically closely related and share an extensive cover of mixed conifer forest on slopes between ca. 1100 and 1800 m. Below this forest belt are large tracts of northern oak woodland interspersed with patches of natural grassland with affinity to the coastal prairie community. Douglas fir forest occurs in the mesic low elevation canyons. There are large areas of serpentine and non-serpentine chaparral on the lower slopes of the eastern side of the INCR.

The Yolla Bolly Mts. are higher in elevation than the southern half of the INCR. Ten peaks rise to over 2135 m, compared to only three in the southern INCR. The montane area (above 1500 m, as defined here) is larger and less fragmented by intervening deep canyons than in the southern INCR. Plant communities such as red fir forest, montane meadows, and riparian thickets are characteristically more extensive and richer in species than corresponding communities in the southern INCR. The two highest mountain masses, the North and South Yolla Bolly Mts. (2395 and 2466 m) support small areas of subalpine forest dominated by *Pinus balfouriana.* Subalpine forest is not represented in the southern INCR.

In addition to having a more extensive and diverse montane zone than the southern INCR, the Yolla Bolly Mts. also have higher mean annual precipitation (ca. 2050 mm max. vs. ca. 1780 mm for southern INCR; Karhl, The California water atlas, 1979), and are closer to the large montane area of the Klamath Province, which must have acted as a source for recolonization of many higher elevation taxa in the Pleistocene.

The above factors are principally responsible for the large number of vascular plants reaching their southern range limits in the Yolla Bolly Mts. Currently, 105 taxa are known to occur no farther south in the California coast ranges. This is nearly as many taxa (123) as reach their southern range limits in the vicinity of Snow Mt., the southernmost 2100-m peak in the INCR (Heckard and Hickman, op. cit.). Many of these taxa are typical, widely occurring montane species such as *Antennaria alpina* subsp. *media, Luetkea pectinata, Oxyria digyna, Pinus monticola, Populus tremuloides,* and *Tsuga mertensiana* and have been previously reported for the area (Jepson, Res. Pap. PSW-82, 1972). However, the highest elevations (over 2134 m) are roadless A manual of the flowering plants of California, 1925; Munz, A California flora, 1959; Griffin and Critchfield, The distribution of forest trees in California, USDA For. Serv.

and have been little visited by collectors (though both Jepson and Munz made brief visits). Most (70%) of the 70 new records we report represent southern range extensions of ca. 72–100 km from known locations in the Trinity Alps and other high Klamath Province mountains and were generally found around the higher peaks in the range.

We found ten taxa that represent newly defined northern range limits. Most of these plants occur in the extensive serpentine and non-serpentine chaparral on the eastern side of the Yolla Bolly Mts. The new records extend the known ranges of these plants 50–80 km from low elevation INCR locations in Lake, Colusa, and Mendocino Counties.

Two lowland taxa from Humboldt and Del Norte Counties, *Lathyrus delnorticus* and *Holodiscus discolor* var. *delnortensis,* were found to reach new southern limits in the Douglas fir forests on the western side of the Yolla Bolly Mts. Five typically lowland coastal taxa were also found well above their listed elevational limits, probably as a result of the close proximity of high elevation forest communities to relatively mesic lowland coastal forest in these mountains.

Perhaps the most interesting of the following categories of range extensions are the six species known from the Cascade-Sierra Cordillera, but which are apparently absent from the intervening mountains of the Klamath Province. This discrepancy may be due to insufficient collecting in the Klamaths. However, one conspicuous taxon, *Juniperus occidentalis* subsp. *australis* is already known to follow this pattern (Griffin and Critchfield 1972). It seems more likely that these species have found their present refugia in these relatively xeric mountains following the Xerothermic Period, when the Klamath Province mountains may have become unsuitably mesic.

In the following list all taxonomy, unless otherwise noted, is in accordance with Munz (A California flora, 1959; Supplement to California flora, 1968). All cited collection numbers represent material of the authors deposited at JEPS. An asterisk signifies a taxon that we feel was positively identified in the field, but is not yet represented by voucher material.

I. Plants reaching newly defined southern limits of distribution:

A. Montane taxa (typically occurring above 1500 m in nw. Calif.) with nearest known stations in the Trinity Alps (Ferlatte, A flora of the Trinity Alps of northern California, 1974).

Acer glabrum var. *torreyi 650.*
Arabis holboellii var. *retrofracta 189.*
Arnica mollis 543. (Most individuals fit this description well, but a few showed affinities with *A. longifolia* subsp. *myriadenia.*)
Aster alpigenus subsp. *andersonii 399.*
*Calamagrostis purpurascens.**
*Caltha howellii.**
*Carex spectabilis.**
Cryptogramma acrostichoides 357.
Eriophyllum lanatum var. *lanceolatum 363.*
Erythronium grandiflorum var. *pallidum 170.*
Habenaria sparsiflora 398.
Juncus mertensianus 503.
Lupinus albicaulis 26.
Mitella pentandra 392.
Mitella trifida 286.
Poa pringlei 666.
*Poa canbyi.**
Polemonium pulcherrimum 365.
Pyrola asarifolia var. *purpurea 540.*
Pyrola secunda 297.
Ribes lacustre 573.
Salix jepsonii 670.
Salix commutata 382.
Sanguisorba annua 580.
*Scirpus congdonii.**
Sidalcea oregana subsp. *spicata 373.*
Stipa occidentalis 667.
Valeriana capitata subsp. *californica.**

B. Montane species previously known from other mountain ranges in the Klamath Province (Munz, A California flora, 1959; Lewis, The plant communities of the Marble Mountain Wilderness Area, California, M.S. thesis, Pacific Union College, 1966; Muth, A flora of the Marble Valley, Siskiyou County, California, M.S. thesis, Pacific Union College, 1967; Sawyer and

Thornburgh, The ecology of relict conifers of the Klamath region, in-house report for U.S. For. Serv. PSW, Berkeley, Calif.).

Aster occidentalis var. *intermedius.**
*Berberis aquifolium.**
Botrychium simplex 651.
*Calamagrostis breweri.**
Cardamine breweri 482.
*Carex ormantha.**
Carex straminiformis 668.
Dentaria tenella var. *palmata 197.*
*Deschampsia caespitosa.**
Montia cordifolia 352.
Montia sibirica var. *heterophylla 156.*
*Polemonium californicum.**
Polystichum lonchitis 575.
Potentilla drummondii 492.
Smilacina racemosa var. *glabra 2.*

C. Montane species previously known from the Sierra Nevada or Cascade Range but unknown from the Klamath Province (nearest known stations adjacent to Klamath Province generally in Modoc or E. Siskiyou Co., Munz op. cit.).

Eriogonum ovalifolium var. *nivale 662.*
Erigeron compositus var. *glabratus 661.*
Haplopappus uniflorus 538. (Some individuals resemble *H. apargioides* and may be responsible for Brandegee's report of this species in the INCR; Zoe 4:168–176, 1893.)
Lonicera involucrata var. *flavescens 216.* (This taxon may also be known from Russian Pk. in the Klamath Mts., Sawyer and Thornburgh op. cit.)
*Ribes montigenum.**

D. Plants with previous southern limits known from low elevation mesic coastal forests in Del Norte and Humboldt Counties.

Holodiscus discolor var. *delnortensis.**
Lathyrus delnorticus 268.

II. Plants reaching newly defined northern limits of distribution:

A. Chaparral species generally restricted to serpentine, with nearest known stations in Lake or Glenn Counties.

Astragalus clevelandii 516.
Ceanothus jepsonii var. *albiflorus 657.*
*Madia hallii.**
Streptanthus breweri 584.
*Zigadenus fontanus.**

B. Chaparral or low montane species with nearest known stations in Lake or Mendocino Counties.

*Cirsium coulteri.**
*Dicentra chrysantha.**
Juncus mexicanus 656.
Salvia columbariae 672.
Senecio douglasii 658.

III. Plants reaching newly defined high elevation limits:

A. From adjacent mesic coastal forests.

Anemone quinquefolia var. *grayi 186.* (to 1828 m and north from Sonoma Co.)
Fritillaria lanceolata 181. (to 1875 m)
Fritillaria mutica Lindl. *180.* (to 1828 m)
Trillium chloropetalum 90. (to 2012 m)
Trillium ovatum 574. (to 1920 m)

B. From adjacent chaparral or lower montane habitats.

Erythronium californicum 177. (to 1676 m)
Lessingia nemaclada 369. (to 2012 m)

C. From lower elevation moist habitats.

Eryngium articulatum 549. (to 1067 m)
Petasites palmatus 144. (to 1280 m)

We would particularly like to thank L. Heckard and J. Hickman for checking the determination and ranges of a number of these specimens and sharing their knowledge of the flora of the North Coast Range. J. T. Howell and L. Constance also aided in the determination of several specimens. We thank W. Ferlatte for reviewing a copy of the MS and G. Lester for sharing his collection records from North Yolla Bolly

with us.—T. KEELER-WOLF and V. KEELER-WOLF, 943 Aquarius Way, Oakland, CA 94611. (Received 10 Nov 82; accepted 6 Sep 83.)

CHROMOSOME NUMBERS AND CYTOGEOGRAPHIC PATTERNS IN *Claytonia perfoliata* AND *C. parviflora* (PORTULACACEAE).—Previous studies reported a euploid series from diploid to decaploid in the *Claytonia perfoliata* complex (Miller, Syst. Bot. 3:322–341, 1978). The purpose of this note is to report hitherto cytologically unknown populations of *C. perfoliata* Willd. and *C. parviflora* Hook. These chromosome numbers expand the known ranges of diploids, tetraploids, hexaploids, and decaploids and, in addition, provide interesting insight into phytogeographic patterns of the group. Vouchers for the following chromosome counts are deposited in OSC:

Claytonia perfoliata Willd. $2n = 12$ (as 6 bivalents): Mexico, Estado Baja California, Isla Guadalupe, *Moran 25837-*S_1; Estado Queretaro, Cerro Zamorano *Ornduff 8583-*S_1. U.S.A., Graham Co., AZ, Pinaleño Mts., Frye Canyon, *Miller 802*; Maricopa Co., AZ, Apache Trail at Fish Creek Canyon, *Miller 878*. $2n = 24$ (as 12 bivalents): Pinal Co., AZ, Santa Catalina Mts., Nugget Canyon e. of Oracle Ridge *Reeder & Reeder 6842-*S_1. $2n = 36$ (as 18 bivalents): Gila Co., AZ, Fossil Creek Canyon, *Miller 870*; Maricopa Co., AZ, Roosevelt Dam, *Miller 800*. $2n = 60$ (as 30 bivalents): Guatemala, Departamento Totonicapán, Sierra Madre near San Cristobal Totonicapán, *Miller 759, 760*.

Claytonia parviflora Hook. $2n = 12$ (as 6 bivalents): U.S.A., Fresno Co., CA, ne. of Trimmer, *Miller 767-*S_1. $2n = 36$ (as 18 bivalents): Eldorado Co., CA, Middle Fork American River Canyon near Auburn, *Miller 737*.

The discovery of additional stations for diploid *C. perfoliata* in the mountains of southeastern Arizona, Guadalupe Island, and Queretaro was predictable on the basis of morphology. These collections possessed deltoid and mucronate mature basal leaves, a feature characteristic of diploids reported in earlier work. On the other hand, the existence of one population of decaploids in the Guatemalan Highlands is surprising in view of its phytogeographic position at the southern limit of the species. Other populations of *C. perfoliata* are known from Guatemala including those indigenous to the limestone Cordillera de los Cuchumatanes and volcanic Sierra Madre (Standley and Steyermark, Fieldiana (Botany) 24:209–210, 1945), although the chromosome number of these populations is unknown. Both Guatemalan collections and one from Volcan Tacaná, Chiapas, exhibited typical diploid basal leaf morphology. Decaploids referable to *C. perfoliata* have been reported from central Oregon and the Columbia River Gorge (Miller, Syst. Bot. 1:20–34, 1976). Long distance dispersal of seed from Oregon to the Guatemalan Highlands is unlikely. A more plausible hypothesis would be thousands of years of self-fertilization in the Guatemalan plants incorporating fusion of unreduced gametes.

Diploids and putative autopolyploids of *C. perfoliata* may now be viewed as constituting a series of disjunct populations spanning the west American cordillera from the California Coast, Transverse, and Peninsular Ranges (including the Channel Islands), through isolated pockets in the mountains of the Sonoran Desert, to the Sierra Madre Occidental, Trans Mexican Volcanic Belt, and Guatemalan Highlands. This phytogeographic pattern is consistent with a hypothetical Pliocene or early Pleistocene occurrence of continuous diploid populations that fluctuated in size during alternating arid and fluvial climates. This view does not explain the distribution of diploid *C. perfoliata* on the volcanic, oceanic Isla Guadalupe. Unlike the Channel Islands of California, Guadalupe Island was probably not connected to the mainland of Mexico. Therefore seed of diploid *C. perfoliata* was probably dispersed to the island by birds or man. I thank Reid Moran, Robert Ornduff, and John and Charlotte Reeder for collecting seed and the American Philosophical Society for financing a collecting trip to Guatemala. The National Science Foundation (DEB 76-06048) provided additional travel money that made this project feasible.—John M. Miller, Department of Biology, Sul Ross State University, Alpine, TX 79832. (Received 17 Sep 82; accepted 16 Feb 83.)

Notes on the Mentor Effect and Male Sterility in *Malacothrix* (Asteraceae).—During biosystematic studies in *Malacothrix* (Lactuceae) plants resulting from interspecific crosses have been grown in cultivation, and most of them have been judged to be hybrid because they have had intermediate morphology, abnormalities in meiosis, and low percentages of stainable pollen. In a few such crosses plants were produced that were morphologically like the female parent rather than hybrid in appearance, even in cases where the female parent had been found to be self-incompatible. Apparently, the presence of foreign compatible pollen had allowed the self-incompatibility mechanism to be bypassed, a phenomenon known as the mentor effect (D. de Nettancourt, *Incompatibility in Angiosperms,* p. 70, 1977). This effect has been found in a variety of angiosperm families, including Asteraceae, and I have observed it in four self-incompatible species of *Malacothrix.* One interesting case concerns the bringing together of recessive male sterility alleles by the mentor effect, the first report of such alleles in *Malacothrix.* Crosses between plants of *M. floccifera* (DC.) Blake and *M. phaeocarpa* Davis (ined.) were involved. The former is a small, white-flowered annual that is widely distributed within the California Floristic Province, and the latter is a rarely collected, white-flowered, annual species that is presently known from only 16 populations in the southwestern portion of the range of *M. floccifera.* Twenty-four plants of *M. floccifera* representing three natural populations were grown in cultivation and all were self-incompatible. Ten plants of *M. phaeocarpa* from one population were grown in cultivation and all were autogamous and strongly self-pollinating, as evidenced from fruit set in undisturbed heads. Crosses between the two species with *M. floccifera* as the female parent were generally unsuccessful, but six hybrid plants were produced and all had stainable pollen of less than 5% and meiotic irregularities including a ring of four chromosomes. A seventh plant, which is assumed to have resulted from self-fertilization, had the morphology of *M. floccifera* and was found to have no pollen. A few stained protoplasts without nuclei were found after 24 hr of staining with 1% cotton blue-lactophenol and spore wall development had not taken place. Meiosis in the plant was visibly normal and seven bivalents were present at diakinesis. Regular first and second division segregation occurred and four, normal-appearing, nucleated cells enclosed within the PMC wall were produced. Gametophytic breakdown apparently occurred beyond this stage.

The male sterile plant was used as the female parent in the crosses indicated below, which also include the original P-1 crosses (garden numbers for individual plants are given in parentheses; the female parent is on the left in each cross).

P-1	*M. floccifera* × *M. phaeocarpa*		*M. floccifera* × *M. floccifera*
	(515-3) ↓ (592-3)		(515-1) ↓ (515-3)
F-1	Male Sterile	×	*M. floccifera*
	(618-1B)	↓	(665-1)
F-2	Male fertile (723-1A) 98% stainable pollen Male sterile (723-1B) No pollen Male sterile (723-1C) No pollen		

Male fertile (723-2A) 95% stainable pollen
Male sterile (723-2B) No pollen
Male sterile (723-2C) No pollen
Male sterile (723-1C) × Male fertile (723-2A)
↓
F-3 3 Male fertile; 2 Male sterile

All of the male sterile plants had normal-appearing meiotic patterns through telophase II. The ratios of 4 male sterile: 2 male fertile in the F-2 and 3 male fertile: 2 male sterile in the F-3 are not significantly different from the ratios expected on the basis of an exact test based on the binomial distribution using the appropriate values for probability and sample size.

In another self-incompatible species, *M. californica* DC., the mentor effect has disclosed other apparently recessive genes that are lethal or have an effect on fitness. Twenty-three plants resulting from crosses involving four other species of *Malacothrix* as the male parent were grown in cultivation. All had the morphology of *M. californica* and those that flowered had over 90% stainable pollen and normal meiosis. Six of the plants lacked green pigment and died before reaching maturity and one plant displayed a phenotype in which flower heads remained almost completely closed at maturity.—W. S. DAVIS, Department of Biology, University of Louisville, Louisville, KY 40292. (Received 4 May 83; accepted 20 Sep 83.)

NOTEWORTHY COLLECTIONS

NEW MEXICO

ASTRAGALUS HUMILLIMUS Gray ex. Brand (FABACEAE).—San Juan Co., ca. 2 km sw. of Waterflow, on the e. side of 'The Hogback' at (T29N R16W S16) on small pockets of sandy soil on ledges and in cracks on a tannish-white sandstone of the Mesa Verde series, at 1615–1645 m. Localized population of ca. 500 plants. 4 Jul 1980, *Kramp s.n.,* 18 May 1981, *Knight 1389* (UNM, NY). Verified by R. C. Barneby. Collected on the southern portion of 'The Hogback' ca. 3 km sw. of Waterflow, at (T29N R16W S21) on a tannish-white sandstone of the Mesa Verde series at 1630 m, a localized population of perhaps 200 plants; 18 May 1981, *Knight 1891* (UNM).

Significance. The species is a candidate for federal listing in Colorado. These collections represent the first since its discovery 105 years ago (by Brandegee in sw. CO). It is a new record for NM, located approximately 55 km s. of the presumed type locality. The 1981 collections represent the first flowering specimens ever seen. The species appears to be specific to a narrow geological subunit of the Mesa Verde sandstone series, a trait explaining its rarity and its 105-year disappearance.

ASTRAGALUS NATURITENSIS Payson (FABACEAE).—San Juan Co. ca. 4 km sw. of Waterflow, on the e. side of 'The Hogback,' at (T28N R16W S4), on sandy pockets and in cracks of a coarse white Cretaceous sandstone in the Mesa Verde series at 1600 m; 25 Apr 1982, *Knight 1891* (UNM). Verified by R. C. Barneby.

Significance. This species is a candidate for federal listing in Colorado. This collection represents a new record for NM, ca. 80 km south of the southern-most Colorado records. All known populations are very localized.

PHACELIA SPLENDENS Eastwood (HYDROPHYLLACEAE).—San Juan Co., ca. 3 km n. of Waterflow, at (T30N R15W S31) on barren knolls of Fruitland clay at 1630 m; 26 Apr 1981, *Knight 1357* (UNM).

Significance. First record for New Mexico, approximately 50 km s. of the nearest locale in sw. CO. Also known from se. UT.—PAUL J. KNIGHT, New Mexico Department of Natural Resources, Villagra Building, Santa Fe, NM 87503.

APACHERIA CHIRICAHUENSIS Mason (CROSSOSOMATACEAE).—Socorro Co., San Mateo Mountains, e. slope, in East Red Canyon at (T7S R5W S4), on a n.-facing cliff of rhyolite at 1905 m, rare; 4 Sep 1981, *Wahl s.n.*; 23 Sep 1981, *Knight and Fletcher 1789* (UNM). San Mateo Mountains e. slope, in Hidden Springs Canyon at (T7S R6W S36), abundant on e.- and w.-facing rhyolite cliffs at 2060 m, with *Silene wrightii, Draba mogollonica, Penstemon pinifolius, Erigeron scopulinus* and *Brickellia californica*; 23 Sep 1981, *Knight and Fletcher 1791* (UNM). San Mateo Mountains e. slope, in 'The Gorge,' at (T8S R5W S11) on rhyolite cliffs and bluffs at 1970 m, abundant and extensive; 6 Jun 1982, *Fletcher 6149* (UNM). San Mateo Mountains e. slope, in Indian Cr. Canyon at (T8S R5W S21) on w.-facing cliffs of rhyolite at 2030 m, scattered, and (T8S R5W S16) on all exposures of rhyolite cliffs at 2155 m, abundant and extensive; 8 Jun 1982, *Knight, Fletcher and Whal 2183* (UNM).

Significance. This taxon is at present a candidate for federal listing. These collections represent the first records in NM, and the first records out of the Chiricahua Mts. of AZ, representing a disjunction of 280 km ne. Many of the associates that occur with this species were hitherto known only from the mountains of sw. NM and s. AZ, indicating strong floristic affinities between the San Mateo Mountains and the more southwestern ranges of New Mexico.—PAUL J. KNIGHT and CHARLES R. WAHL, New Mexico Department of Natural Resources, Villagra Building, Santa Fe, NM 87503; REGGIE FLETCHER, USDA-Forest Service, 517 Gold Street, Albuquerque, NM 87102.

ANNOUNCEMENT

Reorganization of membership in the International Organization of Plant Biosystematists (IOPB). The IOPB was founded in 1960 to promote international cooperation in the study of biosystematics. The IOPB is open to all persons working or interested in the field of biosystematics. The history and past activities of IOPB have been given in Taxon, 31:386–387, 1982. Membership fee for 1983–1987 is only $25.00. Send payment to: Dr. Liv Borgen, Secretary-Treasurer, IOPB, Botanical Garden and Museum, Trondheimsveien 23B, Oslo 5, Norway. Membership in IOPB is for the period between each International Botanical Congress (next in Berlin in 1987).

The IOPB Newsletter is being reestablished and will be sent to all members who join the reorganized IOPB beginning in 1983. The Newsletter has been a useful source of information on biosystematists and biosystematic research being carried on throughout the world. Send items on current research, publications, requests for research materials, etc. to: Dr. Krystyna Urbanska, Editor, IOPB Newsletter, Geobotanisches Institut, E.T.H., Zürichbergstrasse 38, CH-8044, Zürich, Switzerland.

ANNOUNCEMENT

SHRUB RESEARCH CONSORTIUM FORMED

The Forest Service's Intermountain Forest and Range Experiment Station, the Utah Division of Wildlife Resources, Brigham Young University, and Utah State University announce the formation of a Shrub Research Consortium. Formed to promote, support, and coordinate programs of research and associated graduate education, the Consortium will be located at the Shrub Sciences Laboratory, 735 North 500 East, Provo, UT 84601. Activities will relate to: (1) improvement and development of shrub plant materials; (2) methods of seeding, planting, culture, and management of shrubs in natural settings; and (3) assisting where feasible with publishing and disseminating research results.

Specific goals of the Consortium are:

1. Develop a program consisting of statements of research needs and priorities and current studies aimed at meeting those needs. The Consortium may determine and set objectives, priorities, and guidelines for studies, based on interpretation of need, available funds, capabilities of institutions and personnel, and other work under way within or outside the Consortium. Principal areas of shrub research will include, but will not be limited to: ecology, genetics, pathology, entomology, soils, hydrology, wildlife habitat, and livestock grazing.
2. Encourage proposals to conduct research from both member and nonmember institutions desiring to participate and capable of contributing appropriately to solving problems selected for study.
3. Arrange for printing and distribution of publications and reports.
4. Sponsor seminars, conferences, symposia, and other meetings to coordinate research on wildland shrubs and to disseminate research results.

Applications for membership from organizations involved in wildland shrub research are encouraged.

For further information contact:
Dr. Arthur R. Tiedemann, Chairman SRC
Shrub Sciences Laboratory
Intermountain Forest and Range Experiment Station
735 N. 500 E.
Provo, UT 84601.

ANNOUNCEMENT

The Society of Wetland Scientists will hold its fifth annual national meeting in San Francisco, California, on 23–25 May 1984, at the Westin Miyako Hotel. Field trips to unique wetland areas in the San Francisco Bay area will occupy one day of the meeting. The plenary session will consist of formal presentations on wetland biology, wetland management, and wetland regulations. Proceedings of the meeting will be published in *Wetlands, Journal of the Society of Wetland Scientists.* Group discussions and poster sessions will also be an integral part of the meeting. Deadline for abstracts is 31 Jan 1984. For more information write to Marc Boulé, Meeting Coordinator, Shapiro and Associates, Inc., 1812 Smith Tower, Seattle, WA 98104.

ANNOUNCEMENT

CALIFORNIA BOTANICAL SOCIETY GRADUATE STUDENT MEETINGS

The 9th California Botanical Society Graduate Student Meetings will be held at California State University, Chico, 7–8 April, 1984. Short research papers and reports on work in progress will be presented by graduate students in botany and related fields.

A banquet is scheduled for Saturday evening and will be followed by a talk by Dr. Jack Major, Professor Emeritus, UC Davis. A field trip to Table Mountain is planned for Sunday morning. Members and non-members of the Society are invited to participate.

For further information regarding registration for the Meetings, and due date for abstracts, please contact Sandra Morey, Department of Biological Science, California State University, 1st & Normal Streets, Chico, California 95929; or leave messages at (916)895-5063 or (916)895-5356.

The Botanical Society recognizes the following individuals awarded for outstanding presentations at the October 1982 Graduate Student Meetings at UCLA:

Cindy Walker, Occidental College (completed project): Crassulacean acid metabolism in *Isoetes bolanderi* in high elevation oligotrophic lakes.

Chuck Wimpee, UCLA (research in progress): RuBP carboxylase pseudogene cluster?

Kathy Griffin, UCLA (research proposal): Phytoplankton physiology as a means of explaining extinctions in the fossil record: A thesis proposal.

The Society also acknowledges and thanks the graduate students of the Department of Biology at UCLA as well as the staff and faculty for their work in preparing and hosting the 1982 Meetings.

REVIEWS

Plants of Wet to Moist Habitats in and Around Eugene, Oregon. By GEORGIA MASON. Privately published, Eugene. 1983. Obtainable from the author for $6.00; P.O. Box 3440, Eugene, OR 97403.

This book is a meritorious example of simplicity in book production. The 200+ page book is quick-copied from typescript and has a plastic spiral binding, which accounts for the very low price. Such a process is highly appropriate for a work that deals with such a specialized and restricted flora. The size of the book, 6″ × 8.5″, makes it convenient for carrying in the field, and the spiral binding allows the book to lie flat on the work table.

The book follows the format of Hitchcock and Cronquist's *Flora of the Pacific Northwest* in that it consists almost wholly of identification keys. The keys are frequently rather bulky because considerable descriptive material is incorporated therein, much more than in the *Flora.* Users will probably be happy to find that words are not abbreviated in Mason's book, as they are in the *Flora.* Line drawings occur occasionally in the margins and are sometimes a bit crude but mostly effective. The bulky keys and paucity of illustrations will keep the book from being readily used by anyone but those with good botanical backgrounds. Although the introduction states that conscious effort was made to keep the vocabulary simple, technical accuracy has not been sacrificed for the sake of simplicity. A terse glossary follows the main text; an index is included. Except for genus names and well-known plants, common names are mostly not given.

The publication of a "florula" such as this is a most welcome addition to botanical references of Oregon. Mason is the author of another valuable regional flora, *Plants of the Wallowa Mountains of Northeastern Oregon.* (Incidentally, this earlier work was reprinted, with corrections and additions, in 1980 and is available for $7.95 + $1.00 postage from Museum of Natural History, University of Oregon, Eugene, OR 97403.) In particular, people working with wetland plants will appreciate Mason's new work. The species chosen for inclusion may seem puzzling at times, since "moist" means areas close to water. Many species are included that are not true wetland plants. Also, a few surprises (in terms of presumed occurrence around Eugene) will be found here, such as *Gentiana sceptrum,* a plant of the coastal wetlands, and *Selaginella douglasii,* of the Columbia River Gorge. There are inevitable gaps to be filled in, too; for example, *Salix fluviatilis* and *Alnus rhombifolia* are both common along the Willamette River in Eugene and the grass genera *Agrostis, Bromus* and *Poa* are not represented in the book at all. We may expect future editions to be more finely tuned to the restriction implied in the title of the book. For now, I think that botanists working anywhere in the southern end of the Willamette Valley will be remiss if they do not add this to their working collection of botanical books.—D. H. WAGNER, Biology Dept., University of Oregon, Eugene, OR 97403.

Wildflower Genetics. By ANTHONY J. F. GRIFFITHS and FRED R. GANDERS. Flight Press, Vancouver, B.C., Canada. 1983. $9.95 (paper). ISBN 0-919843-00-X.

From time to time a field botanist is bound to run across sports and genetic anomalies in natural populations of plants. Discovery of these is usually regarded as no great matter, and taxonomists are apparently supposed to ignore them in their descriptions. Why, then, have the authors compiled an entire book on these simple deviations?

First, they want to promote awareness of natural genetic phenomena at a level that interested students and natural historians can appreciate; and second, they want to stimulate a variety of research projects on the causes of genetic variation. This delightful book succeeds, or will succeed, at both levels.

This is a tantalizing subject, of course, and the contents of the book are based almost exclusively on the authors' eight years of field experience in the Pacific Northwest. Information is listed under broad categories of variation, e.g., fruit color mutations, flower form mutants, etc., and the stories of some species are told in much greater detail than others, for instance, *Collinsia parviflora* and *Plectritis congesta—P. brachystemon.* All too often, however, nothing whatsoever is known about the inheritance patterns of some very common variations. I would like to know more about the jumping genes in *Hesperis matronalis,* and though allusion is made to a similar phenomenon in the snapdragon, no reference is cited so that I might look further. This is a weakness in the book that might limit its usefulness—there are no references to other work at all, e.g., Ornduff's studies on Pacific Northwest *Impatiens.*

Many of the species studied, and nearly all the genera, are found throughout the Western and Rocky Mt. states, so the examples chosen will be relevant to classwork in these areas. And because genetic variation can be found almost anywhere, the wide audience that this book may benefit should have little trouble finding its own regional examples.

There is a short glossary, a very brief list of suggested reading, and a helpful index.—C. DAVIDSON, Idaho Botanical Garden, Box 2140, Boise, ID 83701.

Gardening with Native Plants of the Pacific Northwest. By A. R. KRUCKEBERG. University of Washington Press, Seattle. 1982. $24.95. ISBN 0-295-95893-6.

Gardeners wanting to grow native plants in the Pacific Northwest have till now faced a serious shortage of literature to guide them. One might propose that lack of diversity in a north temperate flora might be part of the reason for the lack of an adequate horticultural manual; perhaps there are not enough plants to make one worthwhile. Arthur Kruckeberg has dealt a death blow to such a theory by including in this book some 250 species of ornamental value, including 50 conifers and broadleaved trees, 75 species of shrubs and ground cover, and 125 herbaceous perennials. Designed for all types of gardeners, the main benefit of this book will be felt west of the Cascades in Oregon and Washington, and in northern California; but people farther east, e.g., in Idaho, will also profit richly from the information here. Among the herbaceous perennials, most of the genera and many species mentioned grow wild in the mountains of Idaho, and about half of them are in, or in the immediate vicinity of, our garden in west central Idaho. I found the information interesting, and certainly engagingly written, even when I thought there was little chance I would be able to establish a particular plant. On the other hand, a gardener knows that each introduction is an experiment and that no guide will tell him everything he needs to know. Some plants that should grow perfectly well in the places chosen drop dead immediately; others that obviously have no chance of survival thrive for years. One always appreciates a pragmatic guide, and *Gardening with Native Plants of the Pacific Northwest* is certain to become a sine qua non for gardeners in this area. Included are general information on planting and propagation, advice on collecting plants in the wild, a guide to native plants for particular settings, sources of information on natives, a glossary, and a list of references.

One omission, perhaps not a very important one, is a discussion of ecological fine-tuning and ecotypic differentiation of native populations. These processes can present difficulties to those wishing to transplant or sow seeds from one region into another. Apparently, the closer the source is to the garden, the easier the establishment, at least for some plants.—C. DAVIDSON, Idaho Botanical Garden, Boise, ID 83701.

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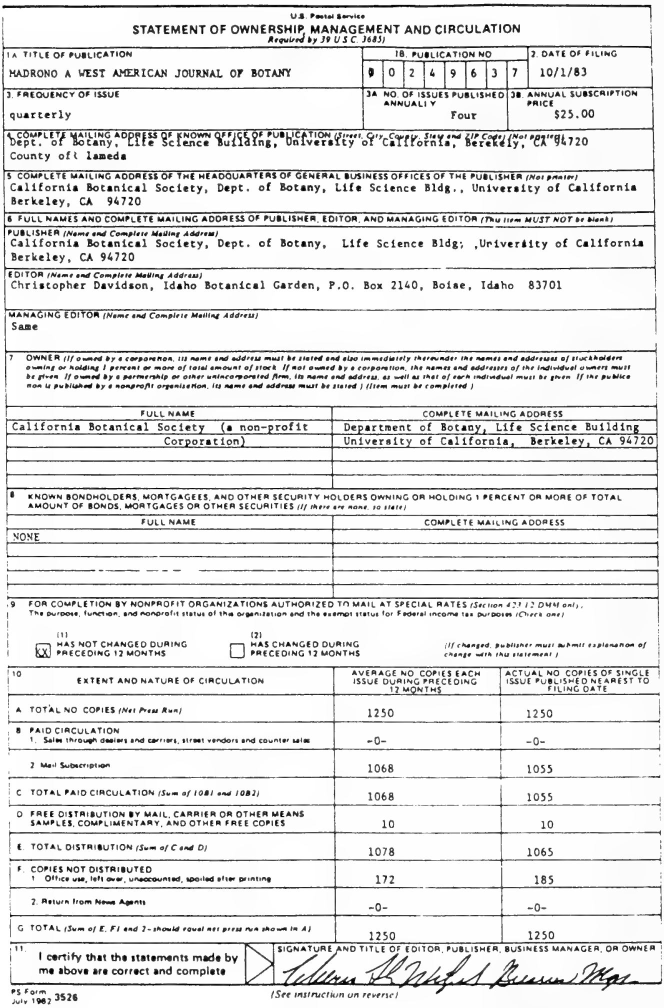
You will note with dismay that the page charges for pages exceeding the 8-free-page allotment per two year period have increased from $40.00 to $60.00. The increase in costs to the California Botanical Society actually occurred some time ago, but it has not till now been passed on to authors. We regret the necessity of this increase. It will apply to all papers submitted after 1 Jan 1984.

The delay in publication from time of acceptance to time of appearance, on the other hand, has decreased to ca. six months, or two journal issues. We hope this benefit will compensate for the added costs.—ED.



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REALIGNMENTS IN NORTHERN CALIFORNIA *ANGELICA* (UMBELLIFERAE)

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Botany Department, University of California,
Davis 95616

ABSTRACT

Angelica breweri and *A. hendersonii* are reduced to varietal status under *A. arguta* and *A. tomentosa,* respectively, based on their morphological similarities. A key to northern California *Angelica,* expanded descriptions, and distribution maps are provided.

Angelica in California consists of stout perennial herbs distinguished from other umbelliferous genera by their large well defined leaflets on each of several compound leaves. In addition, each dorsally flattened schizocarp consists of two mericarps, each with five well developed ribs; the lateral two are generally broadly winged.

With its 80 species, all in the northern hemisphere, *Angelica* is the largest genus in subtribe Angelicinae. The greatest number of species is found in Japan, with 23 (Heywood 1971), and North America, with 22 (Kartesz and Kartesz 1980, DiTomaso 1981). Fourteen of the North American taxa occur in the Pacific Northwest (Munz 1959, Cronquist 1961, Mathias and Constance 1977, DiTomaso 1981). Munz (1959) recognized eight species of *Angelica* in California. Recently, *A. callii* Math. & Const. was described from the southern Sierra Nevada (Mathias and Constance 1977) and I reestablished *A. californica* Jepson from central and northern California (DiTomaso 1981). Therefore, I recognize ten California taxa of *Angelica,* seven of which occur north of the San Francisco Bay region.

Several northern California angelicas have been a source of confusion since their discovery. For example, the variability within *A. tomentosa* has led to its confusion with both *A. hendersonii* Coult. & Rose and *A. arguta* Nutt. ex Torrey & Gray. Joseph Tracy noted on his specimens of *A. hendersonii* [*15155* and *15205* (JEPS)] that similar specimens from Alton (*6560*) and Eureka (*6902*), California, had been cited previously as *A. tomentosa* by Jepson (1936). Furthermore, the more inland form of *A. tomentosa* is cited as *A. arguta* by Ferlatte (1974), but he states that "the scabrous petals and ovaries of this material resemble some forms of *A. tomentosa.*"

Observations were made of numerous specimens and several populations of *A. arguta, A. breweri, A. tomentosa,* and *A. hendersonii*

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in northern California, all belonging to sect. *Angelica* of the subgenus *Angelicastrum* (Drude 1898).

Realignments are here proposed, descriptions and distributions are expanded, and relationships among species are discussed. A revised key to the taxa of northern California *Angelica* is offered.

TAXONOMY

ANGELICA ARGUTA Nutt. ex Torr. & Gray var. ARGUTA, Fl. N. Am. 1:620. 1840.—TYPE: Washington, "Wappatoo and near Fort Vancouver in the Lower Columbia River Basin," *Nuttall s.n.,* 1840 (Holotype: no longer at NY). Columbia River, *Nuttall s.n.* (Lectotype: BM).

Angelica lyallii S. Wats., Proc. Am. Acad. 17:374. 1882.—TYPE: Washington, "Galton and Cascade Mountains, near the British boundary," 1859 and 1861, *Lyall s.n.* (Holotype: K; photo: POM!).

Angelica piperi Rydb., Fl. Rocky Mts. 631. 1922.—TYPE: Washington, Walla Walla Co., Blue Mts., 15 Jul 1896. *Piper 2336* (Holotype: NY).

Plants stout, 1–2 m tall, the foliage and stem glabrous, strongly scented, the inflorescence glabrous, rarely sparsely pubescent; leaves deltoid, to 1 m long and broad, 2 to 3 times ternately pinnate, the leaflets lanceolate to elliptic, (3–)6–9(–13) cm long, 1–5(–7) cm broad, attenuate to acute, the larger petiolulate and with 1 or 2 lobes or leaflets at base, the others sessile, leaflet length/width ratio 2:1 to 5:1 excluding petiolule, serrate, the teeth acuminate to obtusely tipped, ± regularly spaced, the abaxial and adaxial surfaces glabrous, green; petiole stout, 1–5 dm long, sheathing at base; cauline leaves reduced upward, pinnate, the uppermost sheaths bladeless; involucre absent; rays 20–60 (rarely to 75), 2–10 cm long, glabrous, rarely sparsely pubescent, spreading to ascending, unequal, webbed; umbels flat-topped to spherical; involucel bractlets usually absent, occasionally few, filiform, inconspicuous; pedicels 1–11 mm long, spreading, unequal, glabrous, webbed; flowers white, occasionally pink, the petals oval to obovate, glabrous; styles slender, much longer than the conical stylopodium; ovaries glabrous; fruit green to purple, oval to oblong, 8–9 mm long, 6–7 mm broad, the dorsal ribs low, rounded, the lateral broader but narrower than to equaling the body; vittae 6, 1 under each interval, 2 on the commissure; $n = 11$ (Bell and Constance 1960); flowers July to September.

Locally common on dry, moist or wet soils in mixed evergreen, yellow pine and red fir forests; Del Norte, and Siskiyou Counties, California, east to Utah, north to British Columbia, Alberta, and Wyoming (Fig. 1); 200–2200 m.

FIG. 1. Distribution of *Angelica arguta* var. *breweri* (●), and the southwestern distribution of *A. arguta* var. *arguta* (★).

Problems with the determination of the holotype and its locality date from at least 1888, when Coulter and Rose noted that *A. arguta* had not been collected again until it was discovered by Thomas Howell in 1882 at the base of Mt. Adams, Washington. This specimen, however, was distributed as *A. genuflexa* Nutt. ex Torrey & Gray. An 1884 collection by Henderson (*382*), from Hood River, Oregon, was also distributed as *A. genuflexa,* although it is now determined as *A. arguta.* In addition, Henderson visited Wappatoo Island on several occasions but failed to relocate *A. arguta* (Coulter and Rose 1900). In 1887, Macoun led an exploration to Wappatoo Island but also failed to find *A. arguta* at its original location. However, he did discover an abundance of *A. genuflexa* (Coulter and Rose 1888). Since then, Constance (pers. comm., 20 Aug 1980) has visited this area several times but has been unable to find any *Angelica.*

According to the records of the Torrey Herbarium at the New York Botanical Garden, the holotype specimen of *A. arguta* was lost many years ago while on loan. However, an additional type specimen exists at BM, although the label states simply, "Columbia River." Whether this specimen was collected from Wappatoo Island or elsewhere along the Columbia River is unknown. I suspect, as does Constance (pers. comm., 20 Aug 1980), that Nuttall may have erroneously recorded the location of his 1840 collection of *A. arguta.* He probably did not collect it on Wappatoo Island, but rather on the Columbia River east of Fort Vancouver.

Angelica arguta var. **breweri** (Gray) DiTomaso, stat. nov.—*Angelica breweri* Gray, Proc. Am. Acad. 7:348. 1868.—TYPE: California, Alpine Co., Sierra Nevada, near Ebbetts Pass, *Brewer 2011,* 1863 (Holotype: GH!).

Foliage and stem glabrous to villose, the inflorescence pubescent; leaflets lanceolate, (3–)6–10(–13) cm long, 1–3(–5) cm broad, acuminate, leaflet length/width ratio 3:1 to 5:1 (rarely to 8:1) excluding petiolule, the teeth acuminate, both abaxial and adaxial surfaces glabrous, or occasionally the abaxial surface pubescent along veins; rays 20–50, 2–10 cm long, usually glabrous or pubescent towards base or apex; pedicels pubescent or occasionally glabrous; petals pubescent to villose; ovaries thinly pubescent to occasionally tomentose; fruit 8–12 mm long, 5–8 mm broad; vittae usually 6 (rarely 8), 1 (rarely 2) under each interval, 2 (rarely 4) on the commissure; $n = 33$ (Bell and Constance 1957); flowers June to September.

Locally common on dry and open wooded slopes in yellow pine, lodgepole pine, and fir forests; northern and central Sierra Nevada, California, and adjacent Nevada from Mariposa County north to Shasta County, rarely in Siskiyou County (Fig. 1); 1000–3000 m.

ANGELICA TOMENTOSA S. Wats. var. TOMENTOSA, Proc. Am. Acad. 11: 141. 1876.–TYPE: California, San Mateo Co., Crystal Springs, *Bolander s.n.,* 1873 (Holotype: GH!). The holotype represents a morphological intermediate between *A. tomentosa* var. *tomentosa* and the coastal bluff *A. tomentosa* var. *hendersonii.* The type location is the most coastal site of *A. tomentosa* var. *tomentosa* yet observed.

Angelica tomentosa var. *elata* Jepson, Fl. W. Mid. Calif. 356. 1901.—TYPE: California, Napa Co., upper Napa Valley, near Calistoga, *Jepson 13484*, 30 Aug 1895 (Holotype: JEPS!).

Plants stout, 7–20 dm tall, the foliage and stem glabrous to pubescent, occasionally tomentose, strongly scented, the inflorescence glabrous to pubescent; leaves deltoid, to 1 m long and broad, 2 to 3 times ternately pinnate, the leaflets lanceolate to ovate, 2–12 cm long, 1–7 cm broad, acute to acuminate, the larger petiolulate and with 1 or 2 narrow lobes or leaflets at base, the others sessile, leaflet length/width ratio 2:1 to 4:1 excluding petiolule, serrate to entire, the teeth acute to acuminate, regular to irregularly spaced, both abaxial and adaxial surfaces (or at least the lower) glaucous, abaxial surface pubescent to sparsely scaberulous, adaxial surface glabrous to scaberulous; petiole stout, 1–4 dm long, sheathing at base; cauline leaves reduced upward, pinnate, the uppermost sheaths bladeless; involucre absent (rarely 1 or more inconspicuous bracts present); rays 20–60, 2–11 cm long, usually glabrous, occasionally scabrous to pubescent, spreading in flower and fruit, unequal, webbed; umbels flat-topped in bud, becoming more nearly spherical with age; involucel absent (rarely 1–3 bractlets present), glabrous to villose, filiform, inconspicuous; pedicels 1–10 mm long, spreading to ascending, unequal, pubescent to tomentose, rarely glabrous, occasionally webbed; flowers white, occasionally pink, the petals oval to obovate, glabrous to villose; styles slender, much longer than the conical stylopodium; ovaries glabrous to tomentose; fruit green to purple, oval to oblong, 6–10 mm long, 4–6 mm broad, glabrous to sparsely villose, the dorsal ribs low, rounded, the lateral ribs broader but narrower than to equaling the body; vittae usually 6 or occasionally 8 (rarely to 13), usually 1 or occasionally 2 (rarely 3) under each interval, 2 or occasionally 4 (rarely 6) on the commissure; n = 11 (Bell and Constance 1960); flowers July to September.

Dry slopes and meadows to moist, shaded areas; chaparral and yellow pine forest in mountains of southern California; from Riverside County north to Del Norte and Siskiyou Counties, California (Fig. 2); 660–2400 m.

Angelica tomentosa var. **hendersonii** (Coult. & Rose) DiTomaso, stat. nov.—*Angelica hendersonii* Coult. & Rose, Bot. Gaz. 13:

FIG. 2. Distribution of *Angelica tomentosa* var. *tomentosa* (●) and *A. tomentosa* var. *hendersonii* (★).

80. 1888.—TYPE: Washington, Pacific Co., Long Beach, Ilwaco, *Henderson 2158,* 5 Aug 1885 (Holotype: F!; isotypes: CAS! WTU!). The type specimen represents the northernmost locality for *A. tomentosa* var. *hendersonii.*

Inflorescence pubescent to tomentose; leaves to 6 dm long and 10 dm broad, the leaflets lanceolate to ovate or oval, the blades often folded upward along midvein, (2–)5–10(–15) cm long, (1–)3–6(–12) cm broad, acute to obtuse, leaflet length/width ratio 1:1 to 2:1 excluding petiolule, doubly serrate to serrate or crenate, the teeth obtuse to acute, irregularly spaced, the abaxial surface pubescent to tomentose, occasionally appearing glaucous, the adaxial surface glabrous or occasionally sparsely pubescent, dark green; petiole 1–6 dm long; rays 20–65, 2–8(–12) cm long, pubescent to tomentose (rarely glabrous), occasionally ascending; involucel absent or occasionally 1–several inconspicuous bractlets present, pubescent to tomentose; flowers usually white, often pinkish in bud, the petals villose to tomentose; ovaries pubescent to tomentose; fruit 6–9 mm long, 5–8 mm broad; $n = 11$ (Bell and Constance 1960); flowers June to August.

Maritime bluffs and flats, largely north coast shrub; coastal strand from Monterey County, California, to Pacific County, Washington (Fig. 2); sea level–100 m.

DISCUSSION

Confusion in distinguishing *A. arguta* and *A. tomentosa* in northern California is a result of the importance assigned to ovary pubescence by Munz (1959) and other workers. The problem arises because the glabrous or sparsely scabrous ovary of Klamath Mountains *A. tomentosa* resembles the glabrous ovary of *A. arguta.* Northern California populations of the two taxa can be distinguished more easily by leaflet characters: the glaucous, sparsely scabrous leaflets of *A. arguta.* The pubescence of the fruit and leaves in *A. arguta* var. *breweri* constitutes the only significant morphological difference observed between this and typical *A. arguta.* The geographical distribution of *A. arguta* may have been continuous at one time, but apparently has become disrupted more recently by volcanic activity and climatic change in northeastern California (Harris 1976). The presence of trichomes on the ovary may have been a variable feature before the isolation of *A. arguta* var. *breweri,* as seen by the occasional occurrence of pubescent ovaries in specimens from Siskiyou County, California (Fig. 1). However, with the exception of these rare instances, *A. arguta* var. *breweri* remains distinct from populations of *A. arguta* var. *arguta,* even as far north as British Columbia. I have chosen, therefore, to regard *A. arguta* var. *breweri* as a

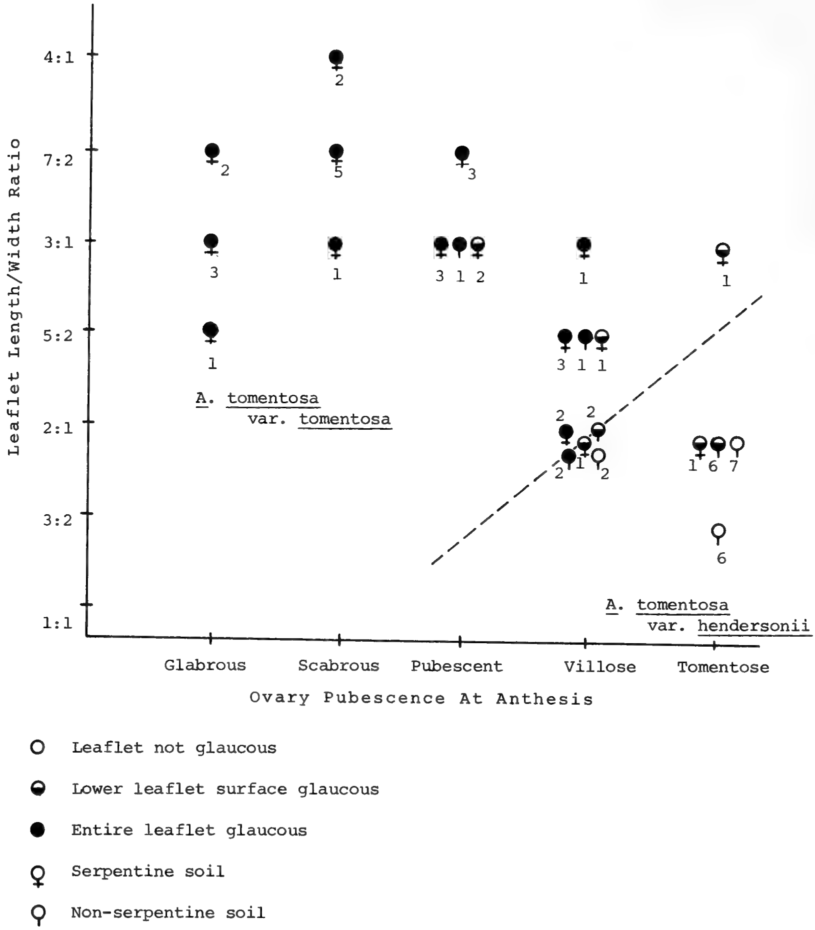

FIG. 3. Variation in a number of features in the *Angelica tomentosa* complex. Populations intersecting dashed line are distinguished as either var. *tomentosa* or var. *hendersonii* based on other characters described in the key. Numerals indicate number of populations observed.

variety characterized by ovary pubescence and by its geographical isolation.

The *A. tomentosa* complex is extremely variable in a number of morphological characters and varies clinally in two directions, north-south and east-west. Along the north-south cline, pubescence varies apparently with soil substrate. Along the east-west cline, variations occur in pubescence, soil adaptability, leaflet glaucousness, and leaflet length/width ratio (Fig. 3).

Populations of *A. tomentosa* from Santa Clara County to Riverside County are pubescent to tomentose throughout and occur on various soil types. From Santa Clara County to mid-Trinity County, *A. tomentosa* is morphologically similar to southern California specimens but occurs exclusively on serpentine soil. From northern Trinity County to southern Siskiyou County, the species is very abundant both on and off serpentine soils, but lacks the pubescence of the southern populations. Both fruit and leaflets are sparsely scabrous to glabrous, thus leading to confusion with *A. arguta.*

In addition to the north-south cline, there is considerable morphological disparity between coastal bluff *A. hendersonii* and *A. tomentosa* in the Klamath Mountains. Variation from the coastal form to the inland mountains is shown in Fig. 3. Inland specimens have narrower and flatter leaflets, are less pubescent, have glaucous leaflet surfaces, and are abundant on serpentine soils. In contrast, the more coastal, sandstone form tends to have wider, folded leaflets that are more pubescent and less glaucous.

Variation patterns between adjacent populations become subtle as one moves further inland. Jepson (1936) noted that "*Angelica hendersonii* seems as if it were, phylogenetically, a littoral adaptation of the inland *Angelica tomentosa.*" Developmental evidence also suggests a close relationship between the two taxa. Of the seven taxa of northern California *Angelica* examined, only *A. tomentosa* and *A. hendersonii* developed a simple first leaf.

It is presumed that many taxa in California, including *Angelica,* were clearly derived from genera with wider distributions in the temperate regions of Eurasia and North America (Raven and Axelrod 1978). Considering the marked northward extension of *A. hendersonii* as contrasted with the southward extension of *A. tomentosa* (Fig. 2), I believe the coastal form may have given rise to the present-day inland form. The lack of *A. tomentosa* at upper elevation and on serpentine soils of the coastal ranges and Cascades of Oregon and Washington, as well as the Sierra Nevada, supports this argument.

Although there is a morphological continuum between the extremes, I feel it useful to distinguish the coastal and inland phases, especially in view of the obvious morphological differences at their extremes.

Key to Northern California *Angelica*

Mature fruit 3–4 mm long; leaves genuflexed at joints of leaflets and branches; leaf rachis often purple; involucel bractlets several, filiform, ca. 7–10 mm long, not reflexed; swampy areas. .... *A. genuflexa*

Mature fruit 5–12 mm long; leaves not genuflexed; leaf rachis green; involucel bractlets inconspicuous, or if conspicuous, then reflexed, moist or dry areas.
- Fruit ribs equal; involucel bractlets conspicuous, reflexed; pedicels ca. 10–15 mm long; coastal. .... *A. lucida*
- Fruit ribs unequal, the lateral larger than the dorsal and intermediate; involucel bractlets inconspicuous; pedicels unequal, 2–13 mm long; coastal and inland.
  - Ovary glabrous (*A. californica* rarely pubescent in Tehama County).
    - Leaflets glabrous, never scabrous, green to dark green; northern Siskiyou and Del Norte Counties. .... *A. arguta* var. *arguta*
    - Leaflets scabrous, sparsely scabrous or scaberulous, glaucous or light green.
      - Leaflets glaucous; rays spreading in fruit; leaflet length/width ratio 2:1 to 4:1; flowering July to September. .... *A. tomentosa* var. *tomentosa*
      - Leaflets not glaucous, darker green above, light green below; rays often ascending in fruit; leaflet length/width ratio 2:1 or less; flowering May to July; Shasta to Contra Costa County. .... *A. californica*
  - Ovary scabrous to tomentose.
    - Leaflet length/width ratio averaging 2:1 to less (excluding petiolule); tertiary and minor veins on lower surface raised, villose to tomentose; immediate coastal bluffs and terraces. (Occasional intermediates with *A. tomentosa* var. *tomentosa* may be found.) .... *A. tomentosa* var. *hendersonii*
    - Leaflet length/width ratio averaging 2:1 to 5:1 (excluding petiolule); tertiary and minor veins on lower surface never raised, glabrous to villose; inland.
      - Leaves glaucous to pale green; ovary scabrous to tomentose; Klamath Mts. to Peninsular Ranges of southern California. .... *A. tomentosa* var. *tomentosa*
      - Leaves green; ovary villose; Sierra Nevada to eastern Shasta County. .... *A. arguta* var. *breweri*

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NOTES ON THE FLORA OF LESLIE GULCH, MALHEUR COUNTY, OREGON

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ABSTRACT

Several endemics occur on certain substrates in the Owyhee Region of Malheur County, Oregon where normal vegetation is excluded. It has been hypothesized that chemical features of the substrates account for the endemism and exclusion of normal vegetation. Chemical and mineralogical test results presented here lead to the conclusion that physical rather than chemical characteristics account for plant distribution.

Leslie Gulch is a drainage of about 90 km^2 that empties into Owyhee Reservoir, Malheur County, Oregon. The gulch lies on the west side of the Sucker Creek Formation of the Owyhee Region of Kittleman et al. (1965). The original spelling Succor Creek was changed to Sucker Creek in the first revision of the Mitchell Butte Quadrangle in 1921 (Axelrod 1964). Kittleman et al. (1965) named the Sucker Creek Formation from the spelling on this map. Currently the Board of Geographic Names lists the correct spelling as Succor Creek. However, the name of a stratigraphic formation cannot be changed. The entire region has a complicated stratigraphy of volcanic rocks and volcanic sediments. Leslie Gulch itself cuts through a very isolated geologic deposit and is the center of an area with a large number of rare and interesting plant species. The ash-tuff typical of the gulch is composed of sparse phenoclasts of quartz and sanidine in a vitroclastic matrix and has been named the Leslie Gulch Ash-Flow Tuff Member of the Sucker Creek Formation (Kittleman et al. 1965).

Within Leslie Gulch eight rare plant species are known to occur. Three of them, *Astragalus sterilis* Barneby, *Eriogonum novonudum* Peck, and *Trifolium owyheense* Gilkey, are endemic to the Owyhee Region, where they grow almost exclusively on outcrops of volcanic material. *Ivesia rhypara* Ertter & Reveal is known from two locations in Leslie Gulch and one in Nevada. *Artemisia packardiae* Grimes & Ertter grows on dikes of Jump Creek Rhyolite in Leslie Gulch and on cliff faces of similar rhyolites along the Owyhee River to the south. *Senecio ertterae* Barkley, *Mentzelia packardiae* Glad, and *Phacelia lutea* var. *mackenziorum* Grimes & Packard grow only on

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talus slopes of a greenish-yellow ash-tuff in lower Leslie Gulch and Spring Creek Gulch immediately adjacent southward. These slopes are quite distinct from the Leslie Gulch Ash-Flow Tuff Member exposed in upper Leslie Gulch. Kittleman et al. (1965) made no mention of the greenish-yellow ash-tuff in their description of the Leslie Gulch Ash-Flow Tuff Member. I refer to it as talus-tuff because it tends to form extensive talus slopes.

It is well known that features of edaphic habitats may inhibit plant growth yet support rare or endemic plant species. Glad (1976) stated that both *Mentzelia packardiae* and *M. mollis* Peck grow on green or grey montmorillonite derived from the Sucker Creek Formation. Her tests showed extremely high concentrations of potassium, and she therefore concluded that the potassium content of the 'soil' excluded normal vegetation and accounted for the apparent edaphic endemism of the mentzelias. Tests were performed to evaluate the hypothesis that the chemical features of the Leslie Gulch Ash-Flow Tuff restricted plant distribution.

METHODS

Three study sites were chosen on the basis of elevational differences and the presence of large populations of endemic species. The first site is at the head of Leslie Gulch and supports the largest known population of *Ivesia rhypara.* The other two sites support large populations of *Senecio ertterae, Mentzelia packardiae,* and *Phacelia lutea* var. *mackenziorum,* the first near Mud Spring (1200 m) and another 0.9 km above Owyhee Reservoir (900 m).

Emission spectrography tests on the substrates were performed at the Utah Engineering Experiment Station at the University of Utah to determine if any unusual ions were present, or if any ions were present in unusual amounts. Samples of some of the endemic plants were also tested to see if they were accumulating any of these ions.

Cation exchange capacity (CEC) determinations were done at the Soil, Plant and Water Analysis Laboratory at Utah State University to determine the quantity of exchangeable ions in the substrates. Percent nitrogen was also checked as an indication of the amount of organic matter. The CEC of some soil at the bottom of the Mud Spring talus slope was also determined, after a zeolite was discovered, to see if the zeolite was accumulating in normal soil.

Gravimetric water content was tested to get a relative idea of the amount of water available to the plants. Samples were screened to get particle size distribution, and individual fragments were examined microscopically. Anatomical sections were made of the roots of *Mentzelia packardiae,* which at times have noticeably mucilaginous sheaths, to check for anatomical adaptations.

RESULTS AND DISCUSSION

The results of the chemical and mineralogical tests gave no indication of any chemical feature that would limit or restrict plant growth in either the talus-tuff or the Leslie Gulch Ash-Flow Tuff. It is more likely that the distribution of the endemics in Leslie Gulch is determined by physical rather than chemical factors.

The results of the emission spectrography tests showed that there are no elements present in unusual amounts, and that no unusual ions are present. Likewise, ions are not accumulating in any of the plants. Tests performed by Richard Halse in his study of *Phacelia* sect. *Miltitzia* (Halse, unpubl. data) also did not show unusual amounts of potassium. The results of the X-ray diffraction showed that at least one zeolite, heulandite, is present in the talus-tuff. The talus-tuff had a very high CEC, 60–100 meq/100 g, while that of the Ash-Flow Tuff was very low, 3–6 meq/100 g. The CEC of the soil below the talus slope showed no evidence that the zeolite was being accumulated in the soil. The presence of the zeolite is in some respects unusual. However, if other edaphic factors, such as the amount of organic matter and the physical characteristics of the substrate, were more suitable, the zeolite might have a beneficial rather than a limiting effect on plant growth. Alternatively, the heulandite might play a role in restricting plant growth if the ions available are not present in proportions that are suitable for plants.

None of the samples tested had greater than 0.03% N.

Gravimetric determinations showed that water accounted for 13–19% of the weight of the talus-tuff during the growing season. Water content of the Ash-Flow Tuff was almost negligible. Although measurements of gravimetric water content in the talus-tuff indicate that the absolute amount of water is probably not a limiting factor, they give no indication of how the water is distributed within the talus-tuff, nor how much of it is available to the plants.

Most of the talus-tuff will not pass through a #10 screen, indicating a very porous environment for the roots. Microscopic examination of individual fragments of talus-tuff showed them to be very porous; much of the water in the samples had apparently soaked into these fragments. When roots of the *Mentzelia, Senecio,* or *Phacelia* come into contact with pieces of talus or bedrock the roots branch into innumerable rootlets that cling to or penetrate large pores in the talus fragments. The water supply within the fragments might be much higher in volume than the water vapor present in the pores among the fragments. The distribution of water in such talus slopes is very different from that of water in substrates with smaller pores, such as loam.

The frequent shifting of the talus slopes also has an impact, both directly and indirectly on the establishment of plants. First of all, the frequent movement of the substrate almost entirely precludes the establishment of an organic layer and hence of distinct soil horizons. Second, the shifting talus presents problems for seed germination and seedling survival. Early spring, when water relations are most favorable for germination and establishment of propagules, is the season when increased moisture content makes the slopes least stable. It is interesting to note that the *Mentzelia, Senecio,* and *Phacelia* all germinate in later spring to early summer. *Senecio ertterae, Mentzelia packardiae,* and *Phacelia lutea* var. *mackenziorum* show several adaptations to these talus slopes. The roots of all three are quite fleshy, and at least those of the *Mentzelia* are at times mucilaginous. Cross sections of roots of *M. packardiae* showed no anatomical adaptations, but the mucilaginous sheath was evident. Fleshy organ development is a typical response to arid habitats, and the mucilaginous sheath may be an adaptation to help protect the roots from desiccation.

The root systems of the annuals are also quite extensive, the lateral growth much exceeding the vertical. The plants often grow in dense stands, and hundreds of intertwining root systems materially stabilize the talus.

The outcrops of the Leslie Gulch Ash-Flow Tuff also offer a harsh physical environment to which several plants have adapted. The results of the CEC and percent-N tests show that these outcrops are edaphically even more sterile than the talus-tuff. Although the absolute amounts of essential elements are about the same, the Ash-Flow Tuff does not have a zeolite with a correspondingly high CEC. On these exposed outcrops wind and water prevent the accumulation of organic matter, nitrogen build-up, and soil formation. The rubble layer that does develop is very shallow (seldom more than 4 or 5 cm). *Ivesia rhypara, Astragalus sterilis, Eriogonum novonudum,* and *Trifolium owyheense* all show adaptations of their root systems that maximize the use of available resources. *Ivesia rhypara* has very long extensively branching roots that creep over the surface of the bedrock under any rubble that may accumulate. In Leslie Gulch plants are generally found along cracks into which the tough woody roots apparently penetrate quite deeply. At the Nevada locality the substrate appears to be a combination of alluvium with much unsorted material, as well as ash or tuff deposits similar to those found in Leslie Gulch, but nothing is known about its chemistry (for a discussion of this species, see Ertter 1983). *Astragalus sterilis* and *Trifolium owyheense* have large fleshy or woody roots that also penetrate deeply into cracks. At the bedrock-rubble interface several stems issue from the roots and grow through the rubble layer. *Eriogonum novonudum* also sends large woody roots into cracks in the bedrock, but its caudex is lifted above the rubble layer. Deep roots from which stems emerge through a rubble layer are a common feature of plants of talus and bedrock outcrops throughout the area (pers. obs.), including *Trifolium leibergii* Nels. & Macbr. and *Arenaria nuttallii* var. *fragilis* Mag. & Holmgren.

Artemisia packardiae Grimes & Ertter is another Owyhee Region endemic that has a unique edaphic relationship and distribution. This species was not found until field work had been completed. Consequently no chemical or mineralogical tests were performed on its substrate. Since its initial discovery at Three Forks of the Owyhee River and in Leslie Gulch, it has been found to grow extensively on rhyolitic cliffs near Three Forks, and along the Owyhee River between Rome and Owyhee Reservoir. There is another population on cliff faces in Succor Creek State Park some 16 km northeast of Leslie Gulch. These rhyolitic cliffs are apparently remnants of more extensive rhyolitic formations that covered much of the Owyhee Region during the moister parts of the Miocene and Pliocene. Again, physical features of the habitat probably account for the distribution of *A. packardiae* today. Grimes and Ertter (1979) suggested that *A. packardiae* is a relict species that evolved from populations of *A. michauxiana* Bess. subsequent to the Pleistocene glaciations. It is likely that immediately after the glaciations, while *A. packardiae* is hypothesized to have been evolving, the area was moister than today. Danin and co-workers (Danin 1972, Danin et al. 1975) have found that plants growing on cliff faces may receive more moisture than those growing on adjacent flats and slopes. Raven and Axelrod (1978) suggest that plants confined to limestone cliffs in California may also be relicts of a Pleistocene flora. *A. packardiae* then might also be restricted by physical features of a diminishing habitat.

CONCLUSIONS

The rare and endemic species of the Owyhee Region are probably not so much adapted to chemical features of the substrates as to the harsh physical features of the outcrops, talus slopes, and cliff faces on which they grow. The species all show morphological adaptations to their environment. It is likely that these species are pioneers adapted to recently exposed habitats and that they might be competitively excluded from more normal substrates (i.e., soil). Other workers (Gankin and Major 1964, Kruckeberg 1954) have demonstrated that endemics may be restricted to edaphic sites by low competitive ability. Observations on the Owyhee Region endemics growing on ecotonal areas support this idea. All of the species will grow on ecotonal areas where edaphic conditions are less harsh. However, as density of other species increases the density of the endemics decreases. Glad (pers. comm.) tried without success to germinate seeds of *Mentzelia mollis* and *M. packardiae* to test this hypothesis.

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PUBLICATION ANNOUNCEMENT

The Kingston Range of California: A Resource Survey. Natural and Cultural Values of Kingston Range, Eastern Mojave Desert, California. Rising over 7000 feet from the desert floor of the Mojave, the Kingston Range harbors on its slopes and peaks a remarkable array of plants, animals, geological formations, and archaeological sites. Little was known of the area's natural and cultural resources until a team of nine UC Santa Cruz undergraduates set out to compile a record of what Environmental Field Program director Dr. Ken Norris calls these ". . . high islands, surrounded by a sea of inhospitable desert."

The Kingston Range of California: A Resource Survey documents the results of the team's study. This 393-page book contains separate chapters describing the area's geology, vegetation and flora, vertebrate fauna, archaeology, and history, as well as a section on land-use policy and analysis. The comprehensive descriptions should provide a valuable reference for land-use planners, policy makers, or anyone interested in the unique mountain ranges of the Mojave.

The Kingston Range of California: A Resource Survey is bound in paper and illustrated with black-and-white photographs, drawings, and maps. Copies are available for $14.00 each (Please make checks payable to the UC Regents), plus $2.00 for postage and handling, from: Environmental Field Program, 231 Kerr Hall, University of California, Santa Cruz, CA 95064.

NEW AND RECONSIDERED MEXICAN ACANTHACEAE

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ABSTRACT

Pseuderanthemum pihuamoense, distinguished by a broad, nontapering wing on the petioles and relatively long bracts, and **Henrya tuberculosperma**, distinguished by a relatively long, pubescent capsule and large, tuberculate seeds, are described from west-central Mexico. The new combination **Holographis peloria** is made based on *Stenandrium pelorium* Leonard, and a new name, **Louteridium rzedowskii**, is proposed for *L. brevicalyx* Rzedowski. Keys are provided to contrast each taxon with its relatives.

Studies of Acanthaceae from west-central Mexico have resulted in the discovery of several new taxa (Daniel 1980, 1981) and many range extensions of previously described taxa. During the preparation of a treatment of the family for McVaugh's *Flora Novo-Galiciana,* additional new species have been found and several taxonomic alterations and nomenclatural modifications have become necessary. In this report two species are newly described from west-central Mexico, a new combination is made in *Holographis,* and a new name is proposed for *Louteridium brevicalyx* Rzedowski.

Pseuderanthemum pihuamoense T. F. Daniel, sp. nov.

Planta suffruticosa usque ad 6 dm alta. Folia ovata vel elliptica, 50–200 mm longa, 20–70 mm lata, basi late (7–27 mm lata) alata. Bracteae lanceolatae vel subulatae, 3–15 mm longae. Bracteolae subulatae, 1.5–4.0 mm longae. Calyx 4–6 mm longus, glandulosus. Corolla non vidi. Capsula 14–17 mm longa, glandulosa. Semina 3.0–3.5 mm longa. Fig. 1.

Erect subshrubs to 6 dm tall; stems subquadrate, sparsely pubescent with retrorse or antrorse trichomes, 0.2–0.3 mm long, or glabrous above, glabrate below; leaves ovate to elliptic, 50–200 mm long, 20–70 mm wide, mostly 2.5–3.5 times longer than wide, the blades tapering to a broad, nontapering (7–27 mm wide) wing extending to the node, the wing truncate to subcordate at base, the leaf apex acuminate to subfalcate, the surfaces sparsely pubescent; flowers borne in opposite, sessile to subsessile dichasia (these usually reduced to one flower) from upper leaf axils or in an inflorescence of axillary or terminal spikes, the spike axis densely pubescent with stiff, flexuose to antrorse, mostly eglandular trichomes; bracts lan-

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FIG. 1. Holotype of *Pseuderanthemum pihuamoense* T. F. Daniel.
FIG. 2. Holotype of *Henrya tuberculosperma* T. F. Daniel.

ceolate to subulate, 3–15 mm long, 0.5–3.0 mm wide, pubescent like the inflorescence axes; bractlets subulate, 1.5–4.0 mm long, 0.3–0.7 mm wide, pubescent like the inflorescence axes; calyx 5-lobed, 4–6 mm long, glandular (the glands often inconspicuous), the lobes subulate, 3.5–4.5 mm long; corolla not seen; capsule 14–17 mm long, sparsely glandular on outer surface; seeds plano-convex, 3.0–3.5 mm long, 3 mm wide, covered with irregular ridges largely composed of tubercules bearing minute barbs.

TYPE: Mexico, Jalisco, ca. 12–13 km sw. of Pihuamo [ca. 19°15′N, 103°25′W], 19 Nov 1970, *McVaugh 24459* (Holotype: MICH!).

PARATYPE: Mexico, Jalisco, 12.8 km sw. of Pihuamo, 6 Dec 1959, *McVaugh & Koelz 1500* (MICH).

Habitat. Steep rocky (limestone) hillsides in dense forest dominated by *Brosimum* at an elevation of about 550 m.

Although the two collections of this species cited above lack corollas, this species appears to belong to *Pseuderanthemum.* It closely resembles other species of this genus in features of the capsule and seed. *Pseuderanthemum pihuamoense* is distinctive among Mexican and Central American species of the genus by the broad, nontapering petiolar wing that is subcordate to truncate at its base. This species can be distinguished from other species occurring in western Mexico by the following key:

1. Leaf blades forming a conspicuous wing along the petiole, the wing 7–27 mm wide (from edge to edge), not tapering towards the node, truncate to subcordate at base; bracts 3–15 mm long. .... *P. pihuamoense*
1. Leaf blades merely decurrent along the petiole (sometimes scarcely so), a wing, if present, 1–6 mm wide, tapering towards the node, long-attenuate to acute at base; bracts 0.7–4.0 mm long.
    2. Calyx 5.5–8.5 (–12.0) mm long; thecae 2.5–3.0 mm long; leaves often absent at anthesis, the petioles to 5 mm long, the blade only slightly decurrent along the petiole, if at all. .... *P. praecox*
    2. Calyx 2.0–4.5 mm long; thecae 1.0–2.2 mm long; leaves present at anthesis, the petioles 5–150 mm long, the blade decurrent almost to the node.
        3. Corolla 10–14 mm long; bracts 1.8–3.0 mm long; bractlets subulate, 1.0–2.5 mm long; calyx 3.5–4.5 mm long; seeds 2.5–3.5 mm long. .... *P. standleyi*
        3. Corolla 27–36 mm long; bracts 0.7–1.5 mm long; bractlets triangular, 0.5–0.8 mm long, calyx 2–3 mm long; seeds 2.0–2.5 mm long. .... *P. alatum*

Henrya tuberculosperma T. F. Daniel, sp. nov.

Frutex usque ad 1 m altus. Caules subquadrati glandulosi. Folia petiolata, laminae ovatae, 25–80 mm longae, 10–55 mm latae. Inflorescentia spicata densa. Bracteae lanceolatae vel oblanceolatae, 5–7 mm longae, glandulosae. Bracteolae oblanceolatae, 9–14 mm longae, glandulosae. Corolla luteola vel albida, 14–19 mm longa. Capsula 8–11 mm longa, pubescens. Semina 2.5–3.5 mm longa, glabra, tuberculata. Fig. 2.

Shrubs to 1 m tall; stems subquadrate, evenly pubescent with a mixture of eglandular and glandular trichomes 0.1–0.5 mm long near apex, sparsely pubescent (often in opposite, vertical lines) to glabrate below; leaves petiolate, the petioles to 20 mm long, the blades ovate, 25–80 mm long, 10–55 mm wide, rounded to acute to truncate at base, acute to acuminate at apex, the surfaces sparsely pubescent; flowers borne in dense, axillary or terminal, erect or ascending spikes to 10 cm long, the spike axis glandular; bracts lanceolate to oblanceolate, 5–7 mm long, 1–2 mm wide, glandular; bractlets oblanceolate, 9–14 mm long, glandular, mucronate at apex, the mucro 0.2–0.8 mm long; calyx 2.5–3.0 mm long, the lobes lance-subulate, glandular, subequal, the four primary lobes 2.0–2.5 mm long, the reduced lobe 0.5–1.0 mm long; corolla pale yellow or whitish with purple, yellow and reddish markings on the upper lip, 14–19 mm long; thecae 1.9–2.2 mm long; capsule 8–11 mm long, pubescent over entire outer surface; seeds 2.5–3.5 mm long, glabrous, plano-convex, the convex surface covered with conical tubercules bearing erect or retrorse barbs, the flat surface smooth to papillose or tuberculate.

TYPE: Mexico, Jalisco, 24–28.8 km sw. of Autlán, 9 Apr 1951, *McVaugh 11946* (Holotype: MICH!; isotype: US!).

PARATYPES: Mexico, Sinaloa, 24 km ne. of Concordia, 25 Mar 1976, *Marin M76-79* (ARIZ). Jalisco, 37.92 km ne. of La Huerta, s. of Autlán, 20 Mar 1982, *Daniel 2123* (ASU, ENCB); 21.2 km al sw. de Atenquique, *Lott et al. 978* (ASU).

Habitat. Rocky slopes in deciduous forest at about 800 m.

Happ (1937) placed considerable emphasis on the relative position of the mucro in defining taxa of *Henrya* in his revision of the genus, resulting in numerous poorly defined species. Although Gibson (1974) generally followed Happ's taxonomy in her treatment of the Guatemalan species of *Henrya,* she noted that many of the taxa probably represented only forms of *H. scorpioides* Nees in DC.

I became interested in the distinctions between *H. scorpioides* and the type species of *Henrya, H. insularis* Nees in Benth., during my study of the genus in western Mexico. In his key, Happ (1937) separated these species with similar ranges only by the position and stance of the mucro. Additional differences between the species involving density of the inflorescence, bract shape and length, and capsule length and pubescence were provided in Happ's descriptions. With the addition to herbaria of more material of *Henrya* from Mexico since the time of Happ's revision, the distinctions used by him are no longer valid. There appear to be no significant characteristics to distinguish between the two species.

For these reasons, I believe specimens treated by Happ as *H. insularis* and *H. scorpioides* are part of the same variable species. When these taxa are combined, *H. insularis* (1846) has priority over *H. scorpioides* (1847). *Henrya grandifolia* Fernald, *H. mephitica* Happ, *H. ortegana* Happ, and *H. brevifolia* Happ are also indistinguishable from this species. *Henrya rupicola* Happ and *H. barclayana* Nees in Benth. differ from typical specimens of Happ's *H. scorpioides* only by the mucro's being situated up to 1 mm below the apex. *Henrya pilosa* Happ has pilose-glandular stems, bracts, and bractlets but is otherwise indistinguishable from *H. insularis* in this broad sense.

A thorough monograph of *Henrya* is necessary in order to understand completely this large complex and to assess some of the other dubious species recognized by Happ. Specimens of the species newly described above were unknown to Happ, all of them having been collected during recent explorations of the Nueva Galicia region. *Henrya tuberculosperma* is rather closely related to the *H. insularis* assemblage with which it is sympatric. It consistently differs from the wide-ranging and variable *H. insularis,* however, in characters of the capsule and seed. The two species can be distinguished by the following key:

1. Inflorescence lax, spreading; capsule 5–8 mm long, glabrous or pubescent above the middle (rarely entirely pubescent); seeds 1.5–2.0 mm long, the convex surface with flexuose-spreading or flexuose-appressed, slender, hair-like projections lacking barbs. . . . . *H. insularis*
1. Inflorescence dense, erect or ascending; capsule 8–11 mm long, usually pubescent over entire outer surface; seeds 2.5–3.5 mm long, the convex surface covered with stout, conical tubercules bearing barbs. .... *H. tuberculosperma*

A collection (*Palmer 75*) from Durango, treated by Happ as *Henrya flava* (Eastwood) Happ, appears equally similar to the two species discussed above. Fruits are not known from this collection, however, and its disposition must await further collections and study.

Holographis peloria (Leonard) T. F. Daniel, *comb. nov.—Stenandrium pelorium* Leonard, Wrightia 2:83. 1960. TYPE: Mexico, Durango, Santiago Papasquiaro [25°03′N, 105°26′W], Aug 1896. *Palmer 392* (Holotype: US!; isotype: K!).

After initial uncertainty about its generic position, Leonard (1960) described this species in *Stenandrium.* Although the generic distinctions between *Stenandrium* and *Holographis* are subtle at best, this species appears to be more closely related to species of the latter genus. It resembles certain other species of *Holographis* by its caulescent habit (caulescent or acaulescent in *Stenandrium*), slightly exserted stamens (included in *Stenandrium*), linear to oblanceolate, mucronate calyx lobes (lance-subulate, emucronate in *Stenandrium*), zygomorphic corolla (subactinomorphic or rarely zygomorphic in *Stenandrium*), and bilobed stigma (asymmetrically funnelform in *Stenandrium*). Only one Mexican species of *Stenandrium, S. subcordatum* Standley, has a strongly zygomorphic corolla. The zygomorphic corolla of *H. peloria* differs from the corolla of that species by its ovate to elliptic rather than obovate lobes of the upper lip.

Following the key in my recent monograph of *Holographis* (Daniel 1983), *H. peloria* is allied to the group of species with whorled, nonorbicular-spinose leaves and a long (10–18 mm) corolla lacking glands on the outer surface, i.e., *H. pallida* Leonard & Gentry, *H. pueblensis* T. F. Daniel, and *H. ehrenbergiana* Nees. These four species can be distinguished by the following key:

1. Stems lacking retrorse trichomes, the cauline trichomes straight to ascendant-appressed, 0.1–0.7 mm long; laminar margin revolute; bracts triangular to lance-subulate to subulate, emucronate; flowers vertically oriented to anthesis; stamens 9–11 mm long. (See distinctions between *H. pueblensis* and *H. ehrenbergiana* in Daniel, 1983.)
1. Stems with some trichomes retrorse, 0.05–0.3 mm long (sometimes with longer, flexuose trichomes as well); laminar margin flat; bracts lanceolate to ovate to obovate, often mucronate; flowers horizontally oriented at anthesis; stamens 3–4 mm long.
   2. Leaves 1.8–2.5 times longer than wide; bracts 6.5–13 mm long, 3.5–5 mm wide; bractlets 6–10.5 mm long; corolla red, 12–16 mm long; capsule glabrous. .... *H. peloria*
   2. Leaves 2.5–4 times longer than wide; bracts 3–5 mm long, 1–1.8 mm wide; bractlets 3–4 mm long; corolla white to lavender, 10–12 mm long; capsule pubescent. ..... *H. pallida.*

Louteridium rzedowskii T. F. Daniel, nom. nov.—*Louteridium brevicalyx* Rzedowski, Ciencia (México) 28:53. 1973 (not *L. brevicalyx* A. Richardson, Tulane Stud. Zool. and Bot. 17: 66. 1972).

Unfortunately most species of *Louteridium* are known from few collections. *Louteridium brevicalyx* A. Richardson is represented by only two collections from western Michoacán, and *L. rzedowskii* is known only from the type collection from central Guerrero. Examination of the paratype of *L. brevicalyx* A. Richardson and an isotype of *L. rzedowskii* reveals that these species are very similar morphologically. They can be distinguished by the characters in the following key:

1. Calyx 10–14 mm long, 3-lobed or 5-lobed with 3 large lobes and 2 reduced lobes, the large lobes lanceolate to ovate, 8–11 mm long; capsule with straight, eglandular trichomes 0.2–0.5 mm long. .... *L. brevicalyx*
1. Calyx 5–8.5 mm long, 3-lobed (reduced lobes absent), the lobes broadly triangular, 3.5–6.5 mm long; capsule glandular, lacking straight, eglandular trichomes. .... *L. rzedowskii*

Continued exploration in western Mexico should resolve whether or not these plants are indeed separate species or variants of one.

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INTERACTION BETWEEN A SHRUB, *BACCHARIS PILULARIS* SUBSP. *CONSANGUINEA* (ASTERACEAE), AND AN ANNUAL GRASS, *BROMUS MOLLIS* (POACEAE), IN COASTAL CALIFORNIA

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ABSTRACT

Current theory in plant ecology attempts to explain which environmental factors and plant characteristics are particularly important in determining plant distribution. In central coastal California, an introduced grass species and a native shrub species exploit similar disturbed habitats. However, investigation showed that seedlings of the shrub, *Baccharis pilularis* subsp. *consanguinea* (DC) C. B. Wolf, suffered from interference with seedlings of the grass, *Bromus mollis* L., and that the effects of the interference increased under dry conditions. Furthermore, these results seem to be related to characteristics of the seeds of the two species. This information is useful in explaining grassland-brushland relationships in a particularly complex vegetation pattern.

INTRODUCTION

It is widely recognized that patterns of plant distribution are dynamic. Present patterns are the result of past changes and are continuing to change. Recent theories have successfully elucidated important elements of these processes, including temporal and spatial scale.

Many large-scale differences in plant distribution may be explained by consideration of relatively few factors and responses producing changes over long periods of time (Harper 1982). Grime (1977) considered two categories of external environmental factors, stress and disturbance, and postulated that major strategies of plant adaptations arose in response to these impulses. His theory appears to have wide application.

Grime's theory cannot explain many smaller-scale variations. Harper (1977), using a different approach, described in detail changes that occur more quickly. By analyzing demographic responses of specific plant populations, he was able to show how many environmental factors, including some operating on a very small scale, can contribute to population growth and shrinkage.

The approaches of Grime and Harper concentrate on different levels of description of vegetation properties. Use of both theories

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together may be especially rewarding in explaining patterns of vegetation that until now have eluded comprehension.

A complex vegetational pattern occurs in coastal California where there is a mosaic of forest, shrubland, and grassland vegetation types in which native and introduced species are both important. The spatial and temporal complexity of this mixture has produced problems in vegetation classification that are difficult to ignore. One common shrubland type, often called coastal prairie-scrub mosaic, coastal scrub or coastal sage scrub, exemplifies this complexity (Heady et al. 1977, Mooney 1977).

Axelrod (1978) has attempted to describe the origin of coastal scrub. He states that it is a pioneer type of vegetation that has recently expanded its range in response to increased disturbances of other vegetation types. Some of these disturbances are more or less predictable, such as the mudslides that have probably occurred regularly ever since the steep slopes in the region were created. Others, such as the effects of fire and man, evade generalizations (Westman 1981, Wells 1962).

In central California, the most common shrub of the coastal scrub is *Baccharis pilularis* subsp. *consanguinea* (DC) C. B. Wolf, often known as coyote brush. Flowering in the period from August to December, it disperses its seeds from October to January, an interval within which the season's first rain usually occurs.

Coyote brush has been studied by several ecologists in its varied habitats. Wright (1928), working in Alameda County, studied the distribution and adaptations of adult plants in relation to their physical environment. In a nearby area, McBride and Heady (1968) documented recent expansion of certain stands and tested the response of young and old plants to fire and grazing by cattle. Biswell (pers. comm.) discovered marked suppression of stand expansion by grazing sheep on the coast north of San Francisco. Finally, McBride (1974) described the role of coyote brush in plant succession in the northeastern part of the San Francisco Bay area.

Human activity caused the introduction and establishment of annual grasses from the Mediterranean region. These grasses, which can themselves be considered pioneer species, are presently found throughout the entire zone where coastal scrub occurs. These naturalized annual species have largely replaced the native California prairie species (Bartolome and Gemmill 1981) and have likely had significant impact on native shrublands as well.

Seedlings of *Baccharis pilularis* are most likely to come into contact with *Bromus mollis* L. (soft chess). It may be the most common of the Mediterranean annual grasses occurring in central coastal California (Heady 1977). Its seeds, which are an order of magnitude heavier than those of coyote brush (10^{-3} g versus 10^{-4} g), normally germinate following the first autumn rains, which may occur before or during seed dispersal of the latter species. *Bromus mollis* has been shown to restrict the seedling survival of another native perennial, the grass *Stipa pulchra* (Bartolome and Gemmill 1981).

In an attempt at applying current ecological theory to the problem of grassland-brushland distribution in California, the following investigation was carried out with the two species *Baccharis pilularis* subsp. *consanguinea* and *Bromus mollis.* Its primary goal was the measurement of the effects of *Bromus mollis* density and moisture stress, singly and in combination, on the germination and seedling establishment of coyote brush. The study supplements the large-scale studies previously reported in the literature with experimental tests of small-scale interactions between the two species.

MATERIALS AND METHODS

Preliminary observations were made on seedlings of *Baccharis* and *Bromus* grown separately but under identical conditions. In order to compare development of very young seedlings, a total of 32 pots 7.5 cm in diameter and 7.5 cm deep were filled with "UC mix" and placed in a greenhouse on the University of California campus. Half were planted with *Baccharis* seeds and half with *Bromus* seeds at a seeding rate calculated to give four seedlings per pot. All seeds had been collected locally during the preceding season. Root and shoot length were measured for plants in successive groups of pots in a destructive sampling program that lasted 17 days. These observations established the comparative seedling development patterns of the two species to be used in the subsequent experiment.

In order to follow development in older seedlings, two glass-sided boxes 10 cm wide, 80 cm long and 50 cm deep were filled with a clay-loam soil and placed in an open-air location on the University campus. One box was planted with *Baccharis* seeds and the other with *Bromus* seeds. Root and shoot length were noted the fifth, seventh, eighth, and ninth weeks after planting.

For the main part of the study, a shelter was constructed adjacent to a natural stand of coyote brush on the University campus. A clear fiberglass roof permitted the entrance of light from the top and light and air from the sides but allowed control of moisture. Forty-eight stainless steel cans 52.5 cm deep and 15.5 cm in diameter were placed inside and filled with native clay-loam soil. All cans were seeded with *Baccharis* at the rate of 200 mg per can (2000 seeds).

Experimental treatments were assigned to these cans according to a completely randomized 4 × 3 factorial design replicated four times. Three levels of seeding with *Bromus mollis* were used, designated zero, 1, and 2. Zero represents no *Bromus,* 1 represents 60 mg (600 seeds) of seed per can, and 2 represents 300 mg (3000 seeds) per can. Four moisture regimes were created by varying the intervals between waterings.

The experiment was timed to allow for as much springtime growth as possible given the amount of rooting space provided. All seeds were planted in late winter (7 March) 1982, and kept continuously moist for eight weeks. Germinated *Bromus* and *Baccharis* seedlings in each can were censused two weeks after planting. At eight weeks after planting, the *Baccharis* seedlings were thinned to the five largest within a ring 1 cm inside the rim of each can. Moisture treatments were then initiated.

Moisture content of the soil was monitored with gypsum blocks (Soil Moisture Corporation, Santa Barbara, CA) placed 10 cm and 30 cm beneath the soil surface in a random sample of cans in each treatment group. After initiation of the moisture treatments, each group of cans was watered only when the top block in its indicator cans showed that the moisture had fallen below a predetermined level. The treatments were designated 1, 2, 3, and 4. Cans in treatment group 1 were kept continuously moist (approximately −⅓ bar). Cans in treatment group 2 were watered when their moisture content dropped to approximately −10 bar at the 10 cm level. Cans in group 3 were watered when the moisture content at the same level dropped to approximately −15 bar. Cans in the fourth group were never watered after the initiation of the moisture treatments, even though eventually moisture fell below −15 bar at the 50 cm depth.

Beginning at the eighth week, regular measurements of *Baccharis* growth were made. Four parameters were measured: number of plants alive per can, total stem length per plant, number of stems per plant, and number of leaves per plant. The final measurements were made eighteen weeks after planting. The aboveground parts of the *Bromus* and *Baccharis* plants from each can were then separately harvested, oven-dried, and weighed.

RESULTS

The preliminary observations indicated that initial root and shoot growth of *Bromus mollis* was faster than that of *Baccharis pilularis.* Table 1 shows the maximum root and shoot growth of the seedlings. Observations on seedlings showed that *Bromus* plants quickly developed box-filling, fibrous root systems that reached 0.5 m in depth in as few as eight weeks. *Baccharis* seedlings developed taproots that grew more slowly than the *Bromus* roots. However, they also reached the 0.5 m depth relatively quickly, in as few as nine weeks. Root-to-shoot ratios for *Baccharis* were greater than those for *Bromus.*

Analyses of variance were performed on all data from the main part of the investigation. Data from the initial census of seedlings were subjected to one-way ANOVA. No significant effects on *Bac-*

TABLE 1. MAXIMUM ROOT AND SHOOT EXTENSION AND ROOT TO SHOOT RATIO (R/S) OF *Bromus mollis* AND *Baccharis pilularis* SEEDLINGS GROWN SEPARATELY IN POTS (PLANTS RECORDED FOR DAYS 6, 13, AND 17) AND IN 50 CM DEEP GLASS-FRONTED BOXES (PLANTS RECORDED FOR 35, 49, 56, AND 63 DAYS).

Age of seedling (days)	*Bromus mollis*			*Baccharis pilularis*		
	Root (cm)	Shoot (cm)	R/S	Root (cm)	Shoot (cm)	R/S
6	7.2	4.3	1.7	9.0	0.15	6.0
13	8.5	6.9	1.2	4.0	0.3	13.3
17	14.0	6.9	2.0	5.6	0.4	14.0
35 (5 weeks)	18.0	6.0	3.0	6.0	0.5	12.0
49 (7 weeks)	40.0	8.0	5.0	12.0	2.0	6.0
56 (8 weeks)	50.0	8.0	6.0	26.0	2.0	13.0
63 (9 weeks)	50.0	8.0	6.0	50.0	2.5	20.0

charis establishment from the different seeding levels of *Bromus* were observed at the 0.05 level. Sampling of seedling densities of *Bromus* showed significant response to the different seeding rates. Mean densities of the three different treatment groups were all significantly different at the 0.05 level when analyzed by Duncan's Multiple Range Test. Treatment 1 had a mean density of 50 seedlings per pot (2650/m^2) and treatment 2 had a mean density of 140 seedlings per pot (7600/m^2).

Data for each *Baccharis* growth parameter were separately analyzed for each measurement date by two-way ANOVA. Significant effects in each data set could have come from up to three sources: moisture treatment, *Bromus* density, and the interaction between the two. Significant effects at the 0.05 level are indicated in Table 2.

TABLE 2. EFFECT OF *Bromus mollis* DENSITY AND SOIL MOISTURE ON GROWTH PARAMETERS OF *Baccharis pilularis* BETWEEN 8 AND 18 WEEKS AFTER PLANTING IN POTS. Capital letters B, M, and I indicate effect significant at $p < 0.05$ as shown by analysis of variance for B = *Bromus* density, M = moisture, I = interaction. [1]Not measured, but see Table 3 for response as dry weight of *Baccharis*.

Weeks after planting	Growth parameters			
	Total stem length	Number of stems	Number of leaves	Mortality
8	none	none	B	none
9	B	none	B	none
10	B	none	B	I
11	B	B	B	I
12	B	B	B	I
14	B	B, I	B	I
16	B, M, I	B, M, I	B, M	I
18	no data[1]	no data[1]	B, M, I	B, M, I

TABLE 3. EFFECT OF *Bromus mollis* DENSITY AND SOIL MOISTURE LEVEL ON DRY WEIGHT OF *Baccharis pilularis* SHOOTS 18 WEEKS AFTER GERMINATION. Lines connect means not significantly different at $p < 0.05$ by Duncan's multiple range test. Density level 1 = 2650 *Bromus* seedlings/m^2 and level 2 = 7600 *Bromus* seedlings/m^2. Soil moisture levels ranged from 1 (high) to 4 (low) as described in text.

	Density of *Bromus mollis*			
	0	1	2	
Dry weight of *Baccharis* shoots (g)	0.62	0.01	0.00	
	Soil moisture level			
	1	2	3	4
Dry weight of *Baccharis* shoots (g)	0.25	0.28	0.24	0.07

Two-way analysis of variance performed on the final dry weights of *Baccharis* showed significant effects at the 0.05 level from moisture regime, *Bromus* density, and the interaction between the two. The *Baccharis* seedlings showed significantly depressed growth only under the greatest moisture stress when grown alone and were significantly inhibited by high densities of *Bromus* (Table 3).

Effects of *Bromus* on *Baccharis* appeared very early and were continued through later growth. Effects due to moisture treatments did not appear until the penultimate measurement date, but at that time they appeared to affect all of the parameters measured. Neither moisture nor *Bromus* caused a significant mortality effect until the last measurement date (Table 4), but evidence of a significant interaction between the two factors appeared early.

TABLE 4. EFFECT OF *Bromus mollis* DENSITY AND SOIL MOISTURE REGIME ON MORTALITY OF *Baccharis* SEEDLINGS EIGHTEEN WEEKS AFTER GERMINATION. Lines connect means not significantly different at $p < 0.05$ by Duncan's multiple range test. Density level 1 = 2650 *Bromus* seedlings/m^2 and level 2 = 7600 *Bromus* seedlings/m^2. Soil moisture levels ranged from 1 (high) to 4 (low) as described in text.

	Density of *Bromus mollis*			
	0	1	2	
Number of survivors of *Baccharis* per can	4.38	3.56	3.00	
	Soil moisture regime			
	1	2	3	4
Number of survivors of *Baccharis* per can	4.33	4.42	4.08	1.75

DISCUSSION

The preliminary observations on *Bromus* and *Baccharis* seedlings indicate that the two species have distinctly different patterns of seedling development. The ability of *Bromus* seedlings to grow faster initially, perhaps due to their greater seed reserves, would seem to be an asset in any interaction with *Baccharis* seedlings. However, *Baccharis* seedlings manage to produce long taproots, as might be expected from a perennial species that must always endure a several-months-long drought in its first season.

Of greater interest are the results from the main part of the study. When the two are grown together, *Bromus* seedlings appear to depress the growth of *Baccharis* seedlings. This effect seems intensified by low soil moisture levels. In time, the growth depression is accompanied by a mortality effect at low moisture levels.

The effects observed can be expected to occur in nature. The highest density of grass seedlings employed in the treatments was within the expected density for a representative annual grassland in California (Bartolome 1978). Although only the most severe moisture regime produced significant growth depression and mortality in the *Baccharis* seedlings, it must be remembered that the experiment was terminated well before a complete summer drought had been simulated. In nature, most plants would face several additional months without added moisture, except perhaps on the immediate coast, where the situation might be ameliorated by summer fog. Thus the treatments employed here do not seem to have exaggerated the possible effects of natural factors—it is possible that even greater effects may occur in nature.

Precise mechanisms for the observed effects cannot be given. It can certainly be said that *Baccharis* suffered from interference with *Bromus,* but whether this interference was of a competitive or allelopathic nature was not investigated. It can also be said that the effects of the interference appeared early and were later heightened by lowered moisture levels of the soil and also that they may be dependent on the demonstrated ability of *Bromus* seedlings to grow faster than *Baccharis* seedlings.

The results obtained in this experiment can be used to correlate some of the variation in the natural environment with variation in vigor of coyote brush stands. This variation may be temporal or spatial. Wet years may favor their establishment, especially those years with late spring rainfall. Years in which the rains are especially early, however, may be unfavorable for *Baccharis* seedlings because of the chance that grass seedlings may become well established before the peak of *Baccharis* seed dispersal. Areas with higher average rainfall or more summer fog may be likewise especially favorable for *Baccharis* seedlings. Particularly favorable sites may also exist in areas permanently free from annual grass seedlings, such as the bare zones observed by Bartholomew (1970). Localized soil disturbances such as mudslides may produce equally good, although temporary, sites. The two factors may compensate for each other, as in a high-rainfall, annual grassland environment.

It is axiomatic that the population dynamics of any species are the result of the interplay of many different factors and different spatial and temporal scales. In *Baccharis pilularis* subsp. *consanguinea,* several of these factors have not been investigated in separate studies. Large-scale effects (fire, cattle grazing, and sheep grazing) were studied previously. The present study adds two additional factors to the group: interference from other plants and soil moisture. These findings verify the prediction of theory. Yet from a demographic standpoint, the work has only begun. Experimental evaluation of factors influencing the structure of different natural populations will provide the clearest answers to questions about coyote brush ecology. We hope these answers will lead to a greater understanding not only of one species, but also of its associates and the factors influencing vegetation composition in general.

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A TAXONOMIC STUDY OF *IPOMOEA TENUILOBA* TORREY (CONVOLVULACEAE), WITH NOTES ON RELATED SPECIES

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Abstract

Morphological study of living and herbarium specimens of perennial, pedatisect morning-glories reveals that the rare *Ipomoea lemmonii* A. Gray is best treated as a variety of *Ipomoea tenuiloba* Torrey. The new combination is made, a description of the species is provided, and the relationship to other species in the group is discussed.

The North American species of *Ipomoea* are a fascinating assemblage of plants of diverse habits and appearances. The group was originally monographed by House (1908), the only attempt to deal with all of the North American species. Since this monumental work, others have studied various groups of species and have added much new information, notably Matuda (1963, 1964, 1965), Shinners (1970), Austin (1978), and McPherson (1981).

In spite of this recent attention, there remain many species groups within the genus that have not been studied since House's monograph. One such group is the collection of pedatisect species. These were placed into the subsection *Pedatisectae* of the section *Batatas* by House (1908) and more recently were reassigned to the series *Pedatisectae* of the section *Orthipomoea* by Austin (1979).

Most students of the Convolvulaceae are in agreement that the *Pedatisectae* is a natural group of closely related species. The features that characterize the *Pedatisectae* are an herbaceous, trailing habit, deeply pedately parted leaves, 2-loculed ovaries, and seeds lacking comae. Two exceptions are *Ipomoea madrensis* S. Watson and *Ipomoea plummerae* A. Gray var. *cuneifolia* (A. Gray) Macbride [=*I. egregia* House; see Soreng and Spellenberg (1981) for discussion], which have cuneate to ligulate leaves with subentire to irregularly lobed margins. These two taxa probably arose from existing species with pedately cleft leaves through secondary fusion of lobes. *I. plummerae* var. *cuneifolia* has been found to grow only within populations of var. *plummerae* and apparently maintains itself through a high degree of inbreeding.

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Within the *Pedatisectae,* taxa are often difficult to recognize, particularly the tuberous perennials, for several reasons: first, several species are uncommon or endemic and, as such, are poorly represented in herbaria. Of the 18 species of *Ipomoea* included by House (1908) within his subsection *Pedatisectae* he cited fewer than 4 collections examined for 11 species. Of these 11, he saw only type collections for 6 and was forced to include 3 species on the basis of literature citations only. A second reason is the generally poor quality of many of the specimens collected. Delicate corollas adhere to pressing paper and are subsequently torn apart. Some species have flowers that close soon after sunrise and few specimens show expanded corollas.

The tuberous species usually grow in rocky soil and have easily disarticulating stem bases, resulting in many rootless collections. For one species, *I. tenuiloba* Torrey, the roots were unknown at the time of description and many subsequent authors (e.g., House 1908, Kearney and Peebles 1960) guessed it was nontuberous until Matuda (1963) recognized its conspecificity with the later-described tuberous species, *I. leptosiphon* S. Watson. More recently, we have observed that the perennial *I. pedatisecta* Martens & Galeotti can also be tuberous.

Finally, when studying the pedatisect morning-glories, one cannot help noticing the great deal of morphological convergence in the group. For many taxa, there is considerable overlap of character states, resulting in subtle species differences. Soreng and Spellenberg (1981) have quantified some of this overlap in their observations on *I. plummerae* and *I. capillacea* (H.B.K.) G. Don. So far, no really acceptable treatment of the *Pedatisectae* has been published, and various authors have arbitrarily chosen to "lump" or "split" taxa, often without adding new data. The species have not been studied cytologically or phytochemically, and it remains for these or other experimental approaches to aid in the clarification of the taxonomy of the group.

This is not to say that morphology should be ignored as a useful tool for taxonomic evaluation in the *Pedatisectae.* Because so few specimens were available to early workers for examination, some species descriptions are as yet imprecise. Diligent field work and careful study of herbarium collections have yielded new records and information on some of the more poorly known species.

One example is *Ipomoea lemmonii* A. Gray. Until recently, this species was known only from the type collection by Lemmon in 1882. Although the species was included in both House's (1908) monograph and Arizona Flora (Kearney and Peebles 1960), it was largely unknown to collectors, who presumably could not distinguish *I. lemmonii* from *I. tenuiloba* in their rootless collections. To avoid further confusion, we decided to study the relationship between these two taxa to determine if a detailed examination of morphological features would support their continued recognition as separate species.

Specimens of *I. lemmonii, I. tenuiloba,* and related species were examined from the following herbaria: ARIZ, ASC, ASU, DES, GH, LL, NMC, NY, TEX, US, and the University of Texas, El Paso (UTEP). Detailed quantitative and qualitative descriptions were compiled from herbarium specimens and supplemented by examination of living plants in the field and greenhouse.

There is considerable overlap in many of the characters examined, and while certain features tend to distinguish the taxa, these are relatively minor and quantitative. There are also a number of intermediate specimens that cannot be assigned conveniently to either of the two species. We therefore feel that evidence does not support the maintenance of *I. lemmonii* and *I. tenuiloba* as separate species, but that the former is better treated as a variety of the latter. The following description of *I. tenuiloba* and its varieties is based on our morphological study.

IPOMOEA TENUILOBA Torrey, U.S. and Mexican Boundary Survey, Botany: 148. 1859.

Herbaceous perennial; roots tuberous, globose to narrowly fusiform, entire to several-parted below, to 60 mm long; stems prostrate-scandent, 1–several, branched at base, sparingly branched above, to over 1 m in length; leaves alternate, glabrous, petiolate, deeply palmatifid to base or nearly so, with 5–9 linear-filiform to lanceolate divisions; pinnae 0.5–6.5 mm wide and 10–71 mm long at maturity, margins entire or slightly wavy; petioles 2–38 mm long at maturity, filiform or slightly thickened (to 1 mm in diameter); flowers axillary, usually solitary, each flower both pedicillate and pedunculate (pedicels sometimes reduced on first flowers of season); pedicels (0–)2.5–8 mm long at anthesis, filiform or slightly thickened, sometimes elongating to 10.5 mm in fruit, subtended by 2 narrowly deltoid-attenuate bracts 1–3 mm long; peduncles 1–39 mm long at anthesis, filiform or apically thickened, not noticeably elongate in fruit; calyx to 14 mm long, deeply lobed, of 5 unequal segments 5–11.5 mm long at anthesis; segments lance-ovate, erect, narrowly to broadly scarious-margined, smooth dorsally or muricate in longitudinal lines, with a soft awn-like mucro at or near apex, spreading in fruit; corolla ca. 35–100 mm long, funnelform (sometimes narrowly so), convoluted in bud, white or with upper $1/5$–$1/2$ variously pink to purple, with 5 shallow lobes and 5 shallow plicae in throat, glabrous externally and sparsely villous internally with weak, crinkly hairs near attachment points of filaments; stamens 5, epipetalous, slightly didynamous; filaments inserted near upper end of tube, free portions 8–19 mm long, sparsely villous near attachment points; anthers basifixed, ca. 2.5 mm long and 1 mm wide, 2-thecate; ovary glabrous, 2–3 mm long and 1.5–2 mm in diameter at anthesis, unlobed; style elongate, variable in length; stigma irregularly globose, situated at or near the level of the anthers in the corolla throat; fruit capsular, globose, glabrous, 6.5–8 mm in diameter at maturity, 2-loculed; dehiscence longitudinal; seeds 1–2 per locule, dark brownish-black, wedge-shaped, with rounded edges and slightly undulate surfaces, 3.5–5 mm long, minutely puberulent with appressed hairs; septum scarious, sometimes persisting after dehiscence of fruit.

IPOMOEA TENUILOBA Torrey var. TENUILOBA.—TYPE: USA, Texas, Valley of the Rio Grande, below Doñana [=Doña Ana, New Mexico], Sep, *Bigelow s.n.* (holotype NY!; isotype US!; photos ARIZ). There are two problems concerning the type citation for *I. tenuiloba* var. *tenuiloba.* House (1908) cited a specimen at GH that he called *Parry 989* as separate from the type collection. This specimen, which is actually at US, bears a label identical to that of the holotype, except for "989" pencilled at the top. There is no evidence that this is a separate collection, so we are accepting it as an isotype. In addition, the species description contains a different type locality from that found on the type collection (USA, Texas, near Puerto de Paysano). The published type locality is in the Anacacho Mountains of Kinney County, which is about 200 km east of the current range of the species and is more than 600 m lower in elevation. The locality data present on the holotype therefore appear to be more correct than those in Torrey's description, which are probably erroneous.

Ipomoea leptosiphon S. Watson, Proc. Amer. Acad. Arts 23:280. 1888.—TYPE: México, Chihuahua, in thin gravelly soil on the foothills of the Sierra Madre, Sep 1887, *Pringle 1337* (holotype GH; isotype US!; photo ARIZ).

The type variety has leaves with 5–7 filiform divisions (to 1.2 mm wide). Petioles are 2–16 mm long in most specimens. Calyces tend to be longer (to 14 mm) than in var. *lemmonii,* as are the corollas (65–100 mm). The corollas also tend to be more narrowly funnelform, and are all white or slightly tinged with pink in the upper ⅕–¼. The free portions of the filaments are 8–11 mm in length and the tubers are usually entire, globose to ovoid, and to 32 mm in length.

This variety is usually found in oak woodland and pinyon-juniper woodland, at elevations above 1700 m. It occurs in southeastern Arizona, southern New Mexico, western Texas, and in the Sierra Madre Occidental of Chihuahua (Fig. 1). The tubers sprout with the advent of summer rains in May–June, the height of flowering is in August–September, and senescence of the above-ground portions of the plant is by the first frost.

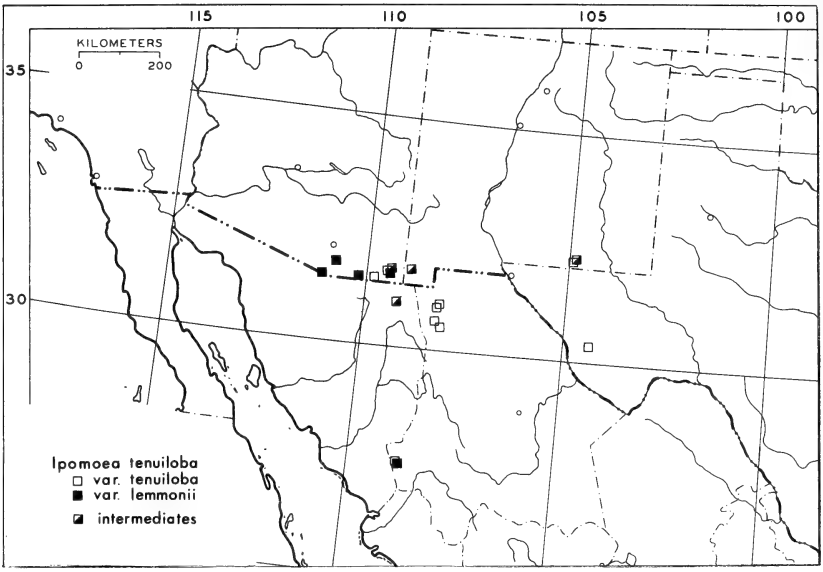

FIG. 1. The geographic distribution of *Ipomoea tenuiloba* and its varieties (plotted on a Goode Series base map, University of Chicago).

Representative specimens. USA, Arizona, Cochise County, Mule Mts., 2.8 mi nw. of old US Highway 80 at Mule Pass, *Reichenbacher 811* (ARIZ); Natural Bridge Trail, Chiricahua Natl. Mon., *Doramus s.n.* (ARIZ). New Mexico, Eddy County, Guadalupe Mts., sw. of Dark Canyon on Ridge Rd., *Higgins 9204* (NY). Texas, Jeff Davis County, near Davis Mts. Resort Headquarters, *Worthington 5020* (UTEP). México, Chihuahua, Majalca, 40 mi nw. of Chihuahua, *White 2385* (ARIZ); 15 mi s. of Guadalupe y Calvo, *Nelson 4822* (US); Colonia Garcia, *Townsend and Barber 271* (US); Sierra Canelo, Rio Mayo Area, *Gentry 2529* (ARIZ, DES).

Ipomoea tenuiloba Torrey var. **lemmonii** (A. Gray) Yatskievych & Mason, stat. et comb. nov.

Ipomoea lemmonii A. Gray, Proc. Amer. Acad. Arts 19:91. 1883.—TYPE: USA, Arizona, Cochise County, ciénega, Tanner's cañon [= Garden Canyon], Huachuca Mts., 1882, *Lemmon 2840* (holotype GH!; isotype US!; photos ARIZ).

This differs from var. *tenuiloba* in having 7–9 leaf segments, which are linear to linear-lanceolate (to 6.5 mm wide). Petioles are 8–38 mm long. Calyces tend to be shorter (to 11 mm long) than in the preceding variety, as are the corollas (35–65 mm). The corollas are funnelform, with the upper ¼–½ purple or bluish-purple. The free portions of the filaments are 14–19 mm in length, and the tubers are ovoid to narrowly fusiform, often several-parted below, and to 60 mm in length. This variety is found in oak woodland and pinyon-juniper woodland, at elevations above 1000 m. It occurs in the mountains of southern Arizona and Chihuahua (Fig. 1). Growth and flowering times are similar to those of var. *tenuiloba.*

Representative specimens. USA, Arizona, Cochise County, ¼ mi se. of Turkey Creek Ranger Station, Chiricahua Mts., *Holler, Mittleman, and Hodgson H1170* (ASU, DES); n. of Wilgus Ranch, Chiricahua Mts., *Blumer V127* (US); Ramsey Canyon, Huachuca Mts., *Toolin 1153* (ARIZ). Santa Cruz County, Madera Canyon, Santa Rita Mts., *Reeves R1045* (ASU, NY); Sycamore Canyon, Pajarito Mts., *Yatskievych & Windham 81-332* (ARIZ). México, Chihuahua, Sierra Canelo, Rio Mayo Area, *Gentry 2503* (ARIZ, DES).

Several additional collections of *Ipomoea tenuiloba* were examined during this study. Some of these could not be determined at the varietal level, due to incompleteness of the collections, whereas others appeared intermediate in morphology between the two varieties. The following specimens are intermediate in morphology between var. *tenuiloba* and var. *lemmonii*: USA, Arizona, Cochise County, Picket Canyon, Chiricahua Natl. Mon., *Clark 8680* (ARIZ). New Mexico, Eddy County, Willow Seep Canyon, Lincoln Natl. Forest, *Chapline 680* (US); Guadalupe Mts., *Bailey 720* (US). Hidalgo County, n. boundary, Bioresearch Ranch, Peloncillo Mts., *Todsen s.n.* (NMC). México, Sonora, Las Tierritas de El Temblor, Sierra de El Tigre, *White 3474* (ARIZ).

Ipomoea tenuiloba is most easily separated from other species of tuberous, perennial, pedatisect morning-glories by its longer corollas. The only other species in the group with corollas commonly longer than 35 mm is *I. madrensis,* which is easily recognized by its non-pedatisect leaves.

I. tenuiloba is most closely related to *I. plummerae,* which differs only in its shorter corollas (25–35 mm) and shorter anthers (ca. 1.5 mm). Both species may have leaf lobes that are linear rather than strictly filiform, as in *I. capillacea* and the problematic *I. patens* (A. Gray) House. There is enough morphological overlap between *I. plummerae* and the latter two species, however, that these three, along with *I. tenuiloba,* must all be considered a very close-knit species complex. Species delimitation within this complex is a fertile subject for future reevaluation.

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A NEW SPECIES OF *ANTENNARIA* (ASTERACEAE) FROM MONTANA AND WYOMING

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ABSTRACT

A new species, **Antennaria aromatica,** from Montana and Wyoming is described and compared with the morphologically similar *A. media, A. umbrinella,* and *A. alpina.*

Because over three hundred North American species of *Antennaria* are listed in the Gray Herbarium Card Index, it is with some trepidation that I describe yet another one. However, field observations, examination of herbarium specimens, and cytological evidence indicate that a distinct species, *Antennaria aromatica,* exists in the mountains of Montana and Wyoming.

Antennaria aromatica Evert, sp. nov.

Herba perennis humilis tomentosa glandifera aromatica, 2–6 cm alta. Folia basalia cuneata vel spatulata, tomentosa, 5–10 mm longa, 3–8 mm lata. Caules tomentosi glandiferi, 2–5 cm longi. Capitula 2–5, in cyma subcapitata. Involucra fuscata, acuta vel obtusa, 4–7 mm alta. Corollae pistillatae 4 mm longae, corollae staminatae 3 mm longae. Achenia tuberculata 1.5–2.0 mm longa. Pappus pistillatus capillaris ca. 4 mm longus, pappus staminatus clavatus 3 mm longus (Fig. 1).

Plants low, mat-forming, short-stoloniferous, tomentose, stipitate-glandular, aromatic in life, dioecious, perennial, 2–6 cm tall, from suffrutescent caudices clothed with marcescent leaves; basal leaves widely cuneate-spatulate to occasionally oblanceolate, densely persistently white-tomentose on both surfaces, glandular, mucronate, 5–10(–13) mm long, 3–8(–10) mm wide; cauline leaves densely to loosely tomentose on both surfaces, glandular, linear-lanceolate to oblanceolate, 0.5–2.0 mm wide, 3–7 mm long, the upper-most frequently with a brown, scarious acute apex; stems loosely tomentose, glandular-puberulent, 2–5 cm long; heads (1–)2–5, in a close corymbiform or sub-capitate cyme, 8–20 mm wide; pistillate involucres 5–7 mm high, basal portions of the phyllaries loosely tomentose-arachnoid, usually glandular, light-green or light-brown, terminal portions scarious-erose, dark to light-brown or dark-green, obtuse or more frequently acute, the base of the terminal scarious portion

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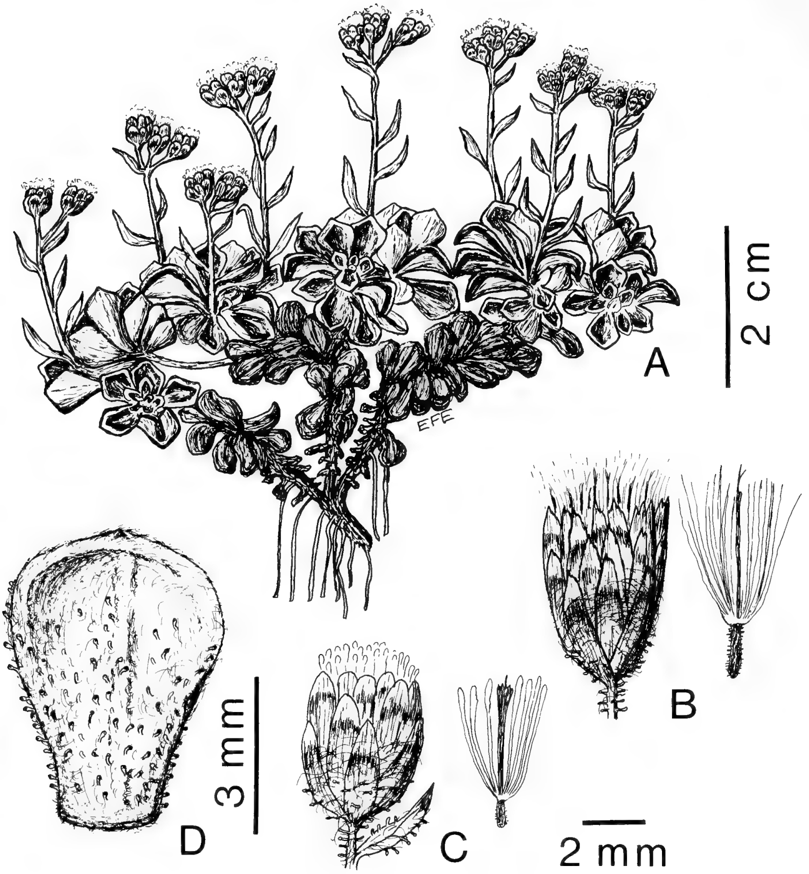

FIG. 1. *Antennaria aromatica.* A. Habit. B. Pistillate capitulum and pappus. C. Staminate capitulum and pappus. D. Leaf. From *Evert 3406.*

often conspicuously darker than the tip; staminate involucres 4–6 mm high, basal portions of the phyllaries frequently glandular, loosely tomentose, brown or green, the terminal scarious portions dark brown below, usually light-brown above, acute or more frequently obtuse; pistillate corollas ca. 4 mm long; staminate corollas ca. 3 mm long; achenes 1.5–2.0 mm long, sparingly tuberculate; pistillate pappus capillary-barbellate, ca. 4 mm long; staminate pappus with clavately dilated tips, ca. 3 mm long; receptacle flat to convex; chromosome number $2n = 28$ (*Bayer and Stebbins 8092*).

TYPE: USA, MT, Carbon Co., Beartooth Range along Hwy. 212, ca. 0.8 km n. of Quad Cr., T9S R19E NW ¼ S20, 2928 m; open, dry scree and talus with *Artemisia michauxiana, Astragalus kentrophyta, Cymopterus hendersonii, Erigeron compositus, Festuca ovina,* *Hulsea algida,* and *Senecio canus,* 5 Aug 1981, *E. F. Evert 3406* (Holotype: RM; isotypes: MO, MONT, MOR, NY, UC).

PARATYPES: USA, MT, Cascade Co., summit of Tiger Butte, limestone, 2135 m, 19 Jul 1887, *Williams 992* (MONT), 11 Jul 1980, *Bayer and Stebbins 8113* (CAS, UC); Gallatin Co., Bridger Range, valley n. of Sacajawea Peak, rock slide, 2592 m, 31 Jul 1938, *Pennell 23835* (F, PH); Carbon Co., along Hwy. 212 at Quad Cr., metamorphic rock, 2592 m, 6 Jul 1980, *Bayer and Stebbins 8092* (DAV, OS); WY, Park Co., along road to Line Cr., 1372 m, 18 Jun 1976, *Robertson 1110* (RM); top of Sheep Mtn., ca. 21 km sw. of Cody, T52N R104W SW ¼ S24, on limestone, 2165 m, 24 May 1980, *Evert 1780* (RM); n. side of Cedar Mtn., ca. 8 km w. of Cody, T52N R102W NE ¼ S8, limestone, 1892 m, 7 Jul 1981, *Evert 3015* (RM); w. summit of Heart Mtn., ca. 32 km n. of Cody, T54N R102W NE ¼ S15, limestone, 2380 m, 30 Jul 1981, *Evert 3333* (RM); limestone ridge, ca. 0.8 km w. of Dead Indian Campground, ca. 40 km nw. of Cody, T55N R104W SE ¼ S7, 2165 m, 6 Aug 1981, *Evert 3420* (RM).

Antennaria aromatica is a sexually reproducing diploid species (Bayer in press) consisting of roughly equal numbers of staminate and pistillate individuals in all populations examined. This *Antennaria* is remarkably uniform morphologically throughout its known range from Cascade Co., Montana south to Park Co., Wyoming. *Antennaria aromatica* most closely resembles *A. media* Greene and *A. umbrinella* Rydb. in its low stature, stoloniferous habit, and dark-colored phyllaries. However, *A. aromatica* can be differentiated from both *A. media* and *A. umbrinella* by its copious and persistent glandulosity, widely cuneate-spatulate basal leaves, and distinctive citronella-like odor. This odor is not detectable in dried material. Furthermore, *A. aromatica* is apparently not abundant in nature and tends to be associated with limestone, where it is found on talus and in rock crevices in exposed xeric habitats at elevations of 1372–2928 m. The relatively ubiquitous *A. media,* a tetraploid species (Bayer and Stebbins 1981), and *A. umbrinella,* with which *A. aromatica* is sympatric through its known range, tend to favor slightly more mesic or alpine habitats and do not display a marked preference for talus or limestone. *Antennaria aromatica* might also be confused with the hexaploid apomict (Halliday 1976), *A. alpina* (L.) Gaertn. *Antennaria alpina* is distinguished from *A. aromatica* by its narrowly spatulate basal leaves, usually glabrous upper leaf surfaces, virtual absence of staminate plants, and more northern, Eurasian and Arctic distribution.

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TYPIFICATION OF *ASTER JESSICAE* PIPER AND REINSTATEMENT OF *A. MOLLIS* RYDBERG (ASTERACEAE)

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ABSTRACT

The two names *Aster jessicae* Piper and *A. mollis* Rydberg are considered synonymous in most currently used floristic works. As the older of the two, the name *A. jessicae* has been adopted. Piper designated (marked) as "type specimen" his own collection No. 2663, from Pullman, Washington (lectotype: US!), not his No. 1604, which was widely distributed prior to publication. Some sheets of the latter have been annotated erroneously as "isotypes" by other botanists. Rediscovery of a large population of *A. mollis* in the vicinity of the type locality (Sheridan County, Wyoming) has prompted a morphological, ecological, and cytological comparison. The results indicate that the two taxa are not conspecific. *Aster jessicae* ($2n = 80$) is endemic to river valleys of the Palouse country at elevations of 1000 m or less, whereas plants of *A. mollis* ($2n = 32$) have been collected only in dry, upper montane meadows of the Big Horn Mountains in north-central Wyoming (2000–3000 m). Evidence is presented that supports reinstatement of *A. mollis* at the rank of species.

INTRODUCTION

In August of 1980, in the Big Horn Mountains of northern Wyoming, I discovered a large population of at least 150 distinct clumps of an aster unknown to me. The affinities were with members of *Aster* subg. *Symphyotrichum* (Nees) A. G. Jones (1980a), but I could not identify the plants with any of the species in that group; nor could I readily suggest a hybrid origin, because there were no other *Aster* species growing nearby in the open, wind-swept, rather dry and sparsely vegetated (mostly bunch-grasses and scattered sagebrush), upper montane meadow. However, *A. occidentalis* (Nutt.) Torr. & Gray and two varieties of *A. foliaceus* Lindl. in DC. came to mind as putative parental taxa occurring in the area. Only later, when scanning the floristic literature, did I discover that my collection (*AGJ 5649*) had been made in or near the type locality of *A. mollis* Rydberg. The type material [Wyoming, Sheridan County, Big Horn Mountains, 7500 ft, 20 Aug 1899, *Tweedy 2029* (Holotype: NY!—Fig. 1; isotype: WS!)] furnished a perfect match to my specimens.

In his original description of *Aster mollis,* Rydberg (1901) cited as a paratype (not to be confused with the nomenclatural type) a collection from Pullman, Washington (*Piper 1604*) that was widely

The written information on this specimen has been abstracted for the TYPE REGISTER PROJECT by K. L. Chambers on July 30, 1973 .

Aster mollis sp. nov

A strict perennial with a horizontal rootstock. Stem densely villous, almost tomentose, or in age more glabrate, 4–8 dm. high, simple below, with short flowering branches above; leaves obovate to oblanceolate, 5–10 cm. long, densely and softly grayish pubescent on both sides, sessile, slightly clasping, and occasionally a little auricled at the base: heads terminating the short branches, hemispherical; disk about 15 mm high and broad; bracts herbaceous, oblong, obtuse, villous-pubescent; rays numerous, bluish purple, about 1 cm. long and 2 mm. wide

This species reaches an elevation of 2200 m

WYOMING: Big-Horn Mountains, 1899, *F. Tweedy, 2029* (type).
WASHINGTON: Pullman, 1893, *C. V. Piper, 1604.*

Bull. Torr. Bot. Club. 28:

UNIVERSITY OF ILLINOIS AT URBANA-CHAMPAIGN

HOLOTYPE of:

Aster mollis Rydberg
Bull. Torr. Bot. Club 28: 22. 1901.

= probably a good species; not identical with the type of A. jessicae Piper (1898) = Piper 1604, which was cited by Rydb. as a paratype. As only the holotype is attached to the name, A. mollis is a legitimate name applying to montane populations of dry habitats in the Bighorn Mountains, Wyoming.

Det. Almut G. Jones, 1982

Aster foliaceus Lindl. in DC.

Annotated: K. L. Chambers July 30, 1973

Note: Aster mollis Rydb. is a nom. illeg., due to the citation of C. V. Piper 1604, which is the type of the earlier published A. jessicae Piper (Erythea 6: 30. 1898).

NEW YORK BOTANICAL GARDEN

Aster mollis Rydb.

Type Bull. Torr. Bot. Club. 28: 22. 190 .
= A. jessicae Piper. [illegible]

FIG. 1. Holotype of *Aster mollis* Rydb. (NY).

distributed under the misapplied name *A. integrifolius* Nutt. (DS! GH! ILL! US! WIS! WS! WTU!). This collection was also cited, however, in the protologue of *A. jessicae* Piper (1898), a species endemic to stream and river valleys of southeastern Washington and adjacent Idaho. Subsequently Rydberg (1917) placed *A. mollis* in synonymy under *A. jessicae,* citing as the habitat "river banks," which does apply to Piper's collections from the environs of Pullman, but not to Tweedy's collection from the Big Horn Mountains. This synonymy was also given by Cronquist (1943) and Ferris in Abrams and Ferris (1960), but not by Cronquist in Hitchcock et al. (1955), Davis (1952), and St. John (1963). In his treatment of the vascular flora of Wyoming, Dorn (1977) did not include either *A. mollis* or *A. jessicae.*

TYPIFICATION OF *ASTER JESSICAE*

In the original publication, Piper's (1898:30) statement on the distribution of *Aster jessicae* reads: "Along the Palouse River at Pullman, Washington, blooming in August and September. Distributed by me under No. 1604 as *Aster integrifolius* Nutt., to which it bears no resemblance. Apparently it is nearest *A. Hendersoni* Fernald."

None of the nine sheets of *Piper 1604* examined was designated by Piper as the type. Only two of the specimens, one at WS, the other at WTU, have the name *Aster integrifolius* crossed out and replaced, in Piper's handwriting, with "*A. jessicae* n.sp." Some sheets were subsequently marked by other botanists as "isotypes" (DS! GH! US! WIS! WTU!), but not the two sheets from Piper's own herbarium at WS. The labels are uniform only in the locality and collection date: "Pullman Wash. Aug. 1893;" habitat information varies from sheet to sheet. The collection was cited as the "type" by Cronquist (1943), Dean (1966), and St. John (1963), but certainly none of the specimens can be regarded as the holotype, and no lectotype has been designated.

Cronquist (1955) pointed out that, although *Piper 1604* is the only collection cited in the original publication, there is another specimen, *Piper 2663,* also from Pullman, that is marked in Piper's own hand as "type specimen" (US 529905!—Fig. 2). The plant was collected by Piper in the year preceding the publication date for *A. jessicae*; it was labelled with that name from the outset, and the locality and habitat information ("Pullman/Along Palouse River/Sept. 1897") coincides with that in the protologue. In my opinion, this is the specimen that persuaded Piper to describe a new species. I suggest that he did not specify a type in the original description, but made special mention of his collection No. 1604 because it was so widely distributed under the misapplied name of *A. integrifolius.*

This specimen (Piper 2663) is the HOLOTYPE of Aster jessicae Piper, Erythea 6: 30. 1898.-- It is the only sheet found that has been marked, by the author himself, as a type, although this collection was not cited in the orig. publication. [Piper 1604 is a Paratype!, cited because it had been widely distributed under the name A. integrifolius. No type was designated in the original description.

det. Almut G. Jones, 1983
University of Illinois Herbarium (ILL)

529905

2663
WASHINGTON FLORA.
Aster jessicae n. sp.
-Type specimen-
Pullman
Along Palouse River
Date Sept. 1897 Collector C. V. Piper

FIG. 2. Lectotype of *Aster jessicae* Piper (US 529905).

One must bear in mind that the type concept was not universally accepted at the turn of the century, although many American botanists, including Piper, did designate types at the time. Rules concerning the typification of names were not formulated until 1904 for submission to the International Botanical Congress, held in Vienna in 1905, where they were rejected by the assembly. They were adopted for the "American Code" in 1907 (cf. Bull. Torrey Bot. Club 34:167–178) and for the international rules of botanical nomenclature in 1930 (cf. Rendle 1934).

The collection in the U.S. National Herbarium, *Piper 2663,* "is the only specimen or other element used by the author or designated by him as the nomenclatural type" (cf. Stafleu et al. 1978:7). Evidently Piper did not keep a specimen of that number for his own herbarium (purchased for WS after his death in 1926), but I have been informed that this was not unusual and that several of Piper's types are not represented at WS (Mastrogiuseppe, pers. comm.). I have designated the sheet at US (No. 529905) as the lectotype. A duplicate of *Piper 2663* (WTU!), lacking habitat information but inscribed with the name *A. jessicae* by Piper, is presumed to be an isolectotype. Specimens of *Piper 1604* are to be regarded as syntypes.

A COMPARISON OF *ASTER JESSICAE* AND *A. MOLLIS*

I have not collected any specimens of *Aster jessicae,* but living plants from two localities were sent to me and are growing in the greenhouse. According to the accompanying information (Mastrogiuseppe, pers. comm.), the plants are considered rare. They grow mostly on shoulders, banks, and slopes in the vicinity of streams and rivers, but apparently some distance (up to 20 m) above the water level on drier ground. The surrounding vegetation includes many weedy species, and the only other aster in the immediate vicinity is *A. occidentalis* var. *intermedius* A. Gray. Some labels on other herbarium collections give roadsides and fields as the habitat. The elevation ranges from 600–1000 m.

Correctly identified collections are known only from Whitman County, Washington and from Latah County, Idaho. Dean (1966) and St. John (1963) also listed only these two counties for *Aster jessicae.*

For his treatment of the flora of Idaho, Davis (1952:704) cited "Streambanks and low ground; S. E. Wash. and adjacent Idaho" as the habitat, but he failed to mention the name *A. latahensis* Henderson (Contr. U.S. Natl. Herb. 5:201. 1899), a species described from Idaho that belongs in synonymy under *A. jessicae* (cf. Cronquist 1943, 1955; Dean 1966, Ferris 1960, and Rydberg 1917). The type was collected "on the prairies or slightly-wooded hills" in Latah County, American Ridge, 5 Sep 1897, *Henderson 2987* (Holotype:

US?—not found; isotypes: GH! RM! WS!). Labels on several sheets of this collection vary in habitat information. In fact, there is another sheet of *Henderson 2987* (ILL!) that differs in the collection data (30 Aug 1898). In addition to the designation "*A. latahensis* n.sp.," the label carries the inscription: "Probably a synonym of *A. jessicae* Piper. Pine-woods and Banks, Latah Co, Idaho." Although the handwriting is the same as on the isotype from RM, this sheet probably should be considered an authentic specimen, perhaps a paratype, rather than an isotype.

Aster jessicae can be characterized as follows: Plants stout, with thick creeping rhizomes. Basal rosette leaves (observed only in greenhouse plants) dark green, somewhat fleshy, with strongly expressed reticulate venation [similar to rosette leaves of *A. eatonii* (A. Gray) Howell], subpetiolate, the blades ca. 3–6(–7) cm long, much smaller than the lower cauline leaves, obovate or broadly spatulate, with rounded apices and entire or shallowly crenate, densely ciliolate margins. Young shoots arising at the tips of fleshy horizontal rhizomes, some distance removed from the old stems. The entire upper half of the plant uniformly and copiously cinereous or lanate, with soft, curled trichomes. Stems erect, not cespitose, up to 1.5 m tall. Lower cauline leaves subpetiolate, the blades ovate-lanceolate, acute or bluntish, to 15 cm long and 3.5–4 cm wide, with usually entire, undulate, or sometimes shallowly serrate margins. Leaves gradually reduced in size, the middle cauline leaves narrowed toward a sessile, clasping, often dilated and auricled base. Capitulescence ample, very leafy, typically elongate-paniculate (in this regard, too, resembling plants of *A. eatonii*). Ultimate rameal leaves on the peduncles several to many, foliar, mostly unlike the phyllaries, but often one or two closely subtending the involucre. Peduncles variable in length, 0.5–4 cm. Heads relatively large, the involucres 8–10(–12) mm high. Receptacles deeply alveolate, the teeth sharp and bristle-tipped (a characteristic shared with plants of *A. laevis* L.). Phyllaries typically graduated in (4–)5–6 series, appressed to somewhat loose but not squarrose, strongly pubescent on both surfaces, linear or somewhat dilated at the base, the apex acute or bluntish, not conspicuously mucronulate; outer phyllaries entirely herbaceous, those of the second whorl with a chartaceous basal portion of ca. 30–40% (specimens of *Piper 1604* have the phyllaries more herbaceous and not as strongly graduated as the lectotype and most other specimens examined). Ligules 20–30(–32), violet or blue, 12–20 mm long and 2 mm wide. Disk florets numbering at least 40, the corollas 6–7(–8) mm long, the lobe/limb fraction less than 0.2. Pappus sordid or at least somewhat discolored, soft, about as long as the disk corollas. Achenes purple, slightly compressed, 3.5–4(–4.5) mm long, thinly strigillose, with 4–5 straw-colored ribs.

Chromosome number $2n = 80$ [reported first by Dean (1966), and confirmed by me from two populations (*Mastrogiuseppe 3401* and *3402*—ILL, WS)].

The affinities lie with *Aster cusickii* A. Gray, *A. subspicatus* Nees, and *A. laevis.* Dean (1966) suggested that the species may be of allopolyploid origin as a result of hybridization between a tetraploid ($2n = 4x = 16_{II}$) and a hexaploid ($2n = 6x = 24_{II}$) plant, with subsequent doubling of the chromosomes. Such a derivative conceivably could have been produced from a hybrid between a tetraploid plant of *A. cusickii* and a hexaploid plant of either *A. subspicatus* or *A. laevis.* Chromosome counts for such populations were reported by Allen (1984), Dean (1966), Dean and Chambers (1983), and Jones (1980b).

In addition to the type material of *Aster jessicae* and *A. latahensis* mentioned before, the following specimens of *A. jessicae* were examined. IDAHO: Latah Co., 1 mi s. of Troy, *Constance 1811* (GH, WS), *1812* (WTU); S17 T39N R3W, midslope on se. hillside of Little Bear Cr., *Heidel s.n.* (WS). WASHINGTON: Whitman Co., Armstrong, *King 52-153* (WS); S6 T14N R45E, on s. side of Hwy. 195, *Mastrogiuseppe 2506* (WS); (same place) on n. side of Hwy. 195, *Mastrogiuseppe 2507* (WS); (ca. same place) just w. of Pullman off Hwy. 195, *Mastrogiuseppe 3401* (ILL, WS); along Union Flat Cr., sw. of Ewartsville, *Mastrogiuseppe 3402* (ILL, WS); Pullman, *Pickett 355* (WS); w. of Pullman, *Pickett 1302* (WS, WTU); Pullman, *Piper s.n.* (10 sheets at GH, some annotated by Cronquist as "topotype"); w. of Pullman, *Warren 126* (WS).

Aster mollis Rydberg can be distinguished from *A. jessicae* as follows: Plants forming cespitose clumps of several to many comparatively slender stems. Rhizomes short, tangled, and strongly lignified. Rosette leaves often arising close to the base of old stems (*AGJ* and *Chance 5951*), light grayish green, not conspicuously reticulate-veined, subpetiolate, the blades ca. 1.5–4 cm long. Pubescence typically copious, soft, lanate, sometimes almost pilose, especially on the petioles and peduncles. Stems usually ascending at an angle, not erect, 30–50(–60) cm tall, not nearly as leafy as the stems of *A. jessicae.* Larger cauline leaves subpetiolate, the blades oblanceolate, to 10 cm long and 2.5 cm wide; middle and upper cauline leaves slightly clasping at the base but not auricled, those of the capitulescence relatively few in number, the peduncles often lacking rameal leaves. Capitulescences averaging fewer heads than those of *A. jessicae,* forming broad, open, corymbiform panicles. Heads medium-large, the involucres 8–9 mm high. Receptacles alveolate, the teeth pointed but not bristle-tipped. Phyllaries conspicuously squarrose, graduated in 4–5(–6) series, oblanceolate, i.e., somewhat constricted below the oblong or oblanceolate chlorophyllous areole, the apex acute, usually with a minute purple mucro, the outer at least somewhat chartaceous at the base, those of the second whorl chartaceous over ca. one third or more of the area. Ligules similar to those of *A. jessicae.* Disk florets often very numerous, 40–70, 5.5–6.5 mm long, the lobe/limb fraction less than 0.2. Pappus soft, whitish or only slightly discolored. Achenes 2.5–3.5 mm long, similar to those of *A. jessicae,* except for size.

Chromosome number $2n = 32$ (*AGJ 5649, 6412; AGJ and Chance 5951*—ILL).

The affinities of *Aster mollis* seem to lie with *A. foliaceus* var. *apricus* A. Gray and var. *parryi* (D. C. Eaton) A. Gray, as well as with *A. occidentalis* and, more distantly, *A. ascendens* Lindl. in Hook. However, the combination of certain characteristics does not fit well within the circumscription of any of these taxa, e.g., the cespitose habit, the copious, uniform, lanate pubescence, the almost naked, flat-topped capitulescence with relatively many-flowered heads, and the strongly squarrose phyllaries. Furthermore, the populations in the Big Horn Mountains seem to be separated by ecological factors. Some collections of *A. mollis* were made in June (*AGJ and Chance 5951*), when the snow had just receded and the meadows were moist, but at flowering time in August, the meadow habitat was quite dry. Plants of *A. foliaceus* and *A. occidentalis* also grow in montane meadows but always in more mesic situations near streams and rivers; plants of *A. ascendens* invariably are found in disturbed, somewhat weedy habitats, along roads and ditches, or about towns.

All collections of *Aster mollis* examined came from the Big Horn Mountains of Wyoming: Big Horn, Sheridan, and Washakie Counties. Plants with intermediacy toward *A. foliaceus* var. *apricus* were recorded from Natrona County (*B. E. Nelson 4257*—RM) and from Sheridan County (*AGJ 6408*—ILL), and plants approaching *A. occidentalis* from Big Horn County (*G. Fonken 714*—RM) and Sheridan County (*B. E. Nelson 4363*—RM). I have annotated a specimen from Fremont County, elevation ca. 2000 m, as "*A. ascendens* or near, with possible influence of *A. mollis*" (*B. E. Nelson 4244*—RM). In addition to the type material, the following collections are representative of *A. mollis.* Big Horn Co.: ca. 34 air mi ese. of Greybull and 12.5 air mi ne. of Hyattville, *B. E. Nelson 4910* (ILL, RM). Sheridan Co.: ca. 7 air mi sw. of Big Horn, S28 T54N R85W, *Hartman 10770* (ILL, RM); Freezeout Stock Trail, S29 T57N R87W, *Hartman 10780* (RM); above Dayton at 2200 m, *AGJ 5649,* with *Blanz and Oberwinkler* (ILL, NY, TUB); 13 mi above Dayton, *AGJ 6412, 6413* (ILL); near Arrowhead Lodge, *AGJ 6411* (ILL). Washakie Co.: at the head of Tensleep Canyon, ca. 12.5 air mi ne. Tensleep, S7 T48N R86W, *B. E. Nelson and G. Fonken 7099* (ILL, RM).

DISCUSSION

Both *Aster jessicae* and *A. mollis* are members of *A.* subg. *Symphyotrichum,* a group characterized by a basic chromosome number of $x = 8$ (cf. Jones 1980a). However, results of this study indicate that the two taxa almost certainly were not derived from the same parental lineages. The principal characteristic shared by the two taxa is that of copious, uniformly distributed, lanate pubescence, but many specimens of *A. cusickii, A. hendersonii,* and *A. subspicatus* also exhibit copious soft pubescence. Morphologically, *Aster jessicae* seems to be more closely related to these three taxa than to *A. mollis.*

The two taxa under study are readily distinguishable by several characteristics of habit and of the inflorescence, and they are further separated by a significant difference in chromosome number. An allopolyploid origin is hypothesized for and suggested by the high decaploid chromosome number of $2n = 80$ obtained for *Aster jessicae.* On the other hand, the relatively low tetraploid number of $2n = 32$ recorded for *A. mollis,* coupled with normal behavior of the chromosomes at meiosis, may be indicative of an origin by way of reticulate evolution, rather than allotetraploidy. This notion is supported by the fact that a relatively large number of individuals were recorded at the collection localities. Mature plants showed ample production of viable achenes that could readily be germinated without stratification. Several seedlings have been successfully grown to maturity. The plants are indistinguishable from the seed parents; they certainly are not hybrids.

Most of all, *Aster jessicae* and *A. mollis* are isolated geographically and ecologically. The former is a rare endemic of the Palouse country of Washington and Idaho, found at elevations of 1000 m or less. The plants grow in river bank habitats, often associated with a somewhat weedy vegetation. By contrast, *A. mollis* has been collected only in the Big Horn Mountains of north-central Wyoming. The plants are restricted to dry, upper montane meadows at elevations of 2000–3000 m, but they form a significant and conspicuous element of a vegetation composed almost entirely of native species.

I propose that *Aster mollis* be taxonomically recognized and reinstated at the rank of species. The populations are morphologically distinct and ecologically isolated from related *Aster* species; they appear to be maintained by sexual reproduction generation after generation.

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NOTEWORTHY COLLECTIONS

ARIZONA

HELIOTROPIUM PRINGLEI Robbinson (BORAGINACEAE).—Cochise Co., 8.5 km w. New Mexico, and 5.2 km n. Mexico (T34S R31E S1), 1360 m, 20 Sep 1982, *Soreng & Salazar 1895* (NMC, UCS) (Det. by M. Frohlich).

Significance. First record for the US, representing a 450 km range extension to the nw. Previously known from Mexico to Guatemala, it is widespread in cent. Mexico, reaching cent. Chihuahua, near Cd. Chihuahua.—R. J. SORENG, Biology Dept., New Mexico State Univ., Las Cruces 88003.

CALIFORNIA

SPIRODELA PUNCTATA (G. F. W. Meyer) Thompson (LEMNACEAE).—USA, CA, San Diego Co., N. Twin Oaks Valley, pond e. side of N. Twin Oaks Valley Road, 2.4 km n. of junction with Hwy. S-12 (33°12′N, 117°10′W), 244 m, 4 Jul 1983, *Armstrong 1145* (RSA, SD). Forming dense colonies at surface of large pond covering at least 1.5 ha, associated with *Lemna minuscula* and *L. gibba* with combined density of 12–18 per cm^2 of water surface.

Previous knowledge. Widely distributed in tropical and temperate regions of both hemispheres. Often associated with *Lemna, Wolffia,* and *Azolla.* It was first recorded by G. F. W. Meyer in 1814 along the Essequibo River in what is now Guyana, South America. This species is listed as *S. oligorrhiza* by Daubs (Ill. Biol. Monogr. 34. 1965; Rhodora 64. 1962) and Mason (A fl. marshes Calif. 1957). According to Daubs, it has been introduced into the United States, apparently as an aquarium plant, and is now widespread. It is reported in California from the vicinity of Berkeley and from Fresno Co. It has undoubtedly been overlooked by botanists because of its superficial resemblance to certain species of *Lemna.* (Herbaria consulted: RSA, SD.)

Significance. First record of *Spirodela punctata* in s. CA, a se. extension of 470 km from the San Joaquin River, Fresno Co. This species is clearly distinguished from species of *Lemna* by its multiple roots, small ventral scale covering base of roots, brown pigment cells (visible only in dead fronds), and both raphide and druse crystals of calcium oxalate throughout the parenchyma. In addition, the fronds appear darker green than in *Lemna* and are conspicuously reddish on the ventral surface. It is distinguished from *S. polyrrhiza* by its smaller size and fewer roots, usually only 2 or 3 (Fig. 1).—WAYNE P. ARMSTRONG, Palomar College, San Marcos, CA 92069.

NEVADA

ARABIS CUSICKII S. Wats. (BRASSICACEAE).—Elko Co., Independence Mts., ridge e. of Gance Creek, ca. 5.6 km nw. of Saval Ranch, growing in rock outcrops (T40N R53E S25–26), 2500 m, 20 Jun 1979, *Tiehm & Birdsey 5163* (GH). (Det. by R. C. Rollins.)

Significance. First record for NV and is an extension of over 160 km s. from central ID.

ARTEMISIA PAPPOSA Blake & Cronq. (ASTERACEAE).—Elko Co., Independence Mts., meadow s. of Mahala Creek, 3.9 km n. of Saval Ranch, growing with *Artemisia* in drying meadow areas (T40N R54E S29), 2012 m, 23 Jun 1979, *Tiehm & Birdsey 5256* (CAS, CIC, MO, NY, RENO, UTC); ne. end of Sunflower Flat, 0.8 km w. of Bieroth Spring, growing in drying meadow areas (T45N R55E S14), 2012 m, 26 Jun 1980, *Tiehm & Read 6094* (CAS, CIC, MO, NY, RSA, UTC).

Significance. First records for NV and an extension of over 90 km s.

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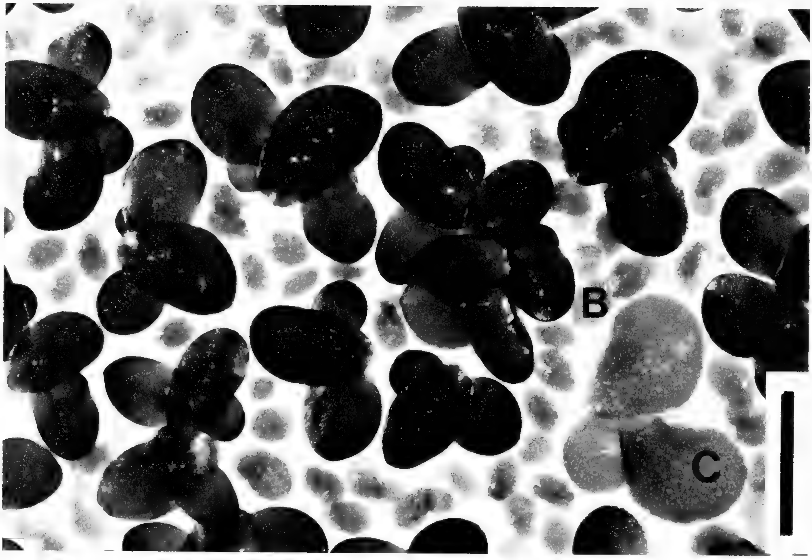

FIG. 1. Dense population of *Spirodela* and *Lemna* from pond in North Twin Oaks Valley, San Diego Co., CA. A. *Spirodela punctata*. B. *Lemna minuscula*. C. *L. gibba*. Scale bar is 5 mm. (See Armstrong, p. 123).

ASTRAGALUS DIVERSIFOLIUS A. Gray (FABACEAE).—White Pine Co., Spring Valley, North Spring area, growing with *Chrysothamnus* at the edge of seepage areas (T12N R67E S18), 1750 m, 17 Jun 1982, *Tiehm & Williams 7200* (CAS, MO, NY, RM, RSA, UTC). (Verified by R. C. Barneby.)

Significance. First record for NV and an extension of 125 km ssw. from the Ibapah region of UT.

ASTRAGALUS SALMONIS M. E. Jones (FABACEAE).—Elko Co., Bull Run Mts., NV hwy. 11, 40 km s. of Owyhee, 26 km sw. of Mountain City, 1707 m, 30 May 1971, *N. H. & P. K. Holmgren 4919* (NY); Independence Mts., 0.5 km ne. of Saval Ranch, just n. of the main road, growing with *Artemisia* on rocky flats (T39N R54E S4), 1920 m, 19 May 1980, *Tiehm & Birdsey 5623* (CAS, NY, RENO, UTC) (Det. by R. C. Barneby); 1.3 km ne. of Saval Ranch, growing with *Artemisia* on rocky flats (T40N R54E S33), 1920 m, 26 Jun 1980, *Tiehm & Read 6103* (CAS, NY, RSA, UTC).

Significance. First records for NV and an extension of over 145 km s.

BIDENS LAEVIS (L.) B.S.P. (ASTERACEAE).—Lincoln Co., Pahranagat Valley, Crystal Spgs. along Hwy. 25, growing along the runoff from the springs (T5S R60E S10), 1170 m, 4 Oct 1980, *Tiehm 6334* (CAS, NY, UTC).

Significance. First record for NV and is an extension of over 240 km nnw. from Yavapi Co., AZ.

CYPSELEA HUMIFUSA Turp. (AIZOACEAE).—Lyon Co., Lahontan Reservoir, 14 Sep 1975, *Tiehm 1905* (RENO); Lahontan Reservoir at the end of 9th St., 29 Sep 1976, *Lott 89* (RENO); Churchill Co., n. end of Lahontan Reservoir near "the Cove," 14 Jul 1977, *Tiehm & Lott 3612* (CAS, NY, RENO); Lahontan Reservoir by "the Cove," 5 Oct 1976, *Lott 86* (RENO); all collections are from the exposed mud flats at the edge of the reservoir at around 1250 m.

Significance. First records for NV.

DALEA LANATA Spreng. var. TERMINALIS (M. E. Jones) Barneby (FABACEAE).—Clark Co., St. Thomas Gap area sw. of Whitney Ridge, 0.8 km n. of Grand Gulch road on reservoir road, growing on deep red sand (T17S R71E S32), 730 m, 14 May 1982, *Tiehm 6856* (CAS, NY, MO, RSA, UTC). (Verified by R. C. Barneby.)

Significance. First record for NV and a small extension w. from adjacent AZ.

ERIGERON LATUS (Nels. & Macbr.) Cronq. (ASTERACEAE).—Elko Co., Point of Rock, w. side of Sunflower Flat, growing on gravelly hillsides (T45N R55E S20), 1950 m, 24 Jun 1979, *Tiehm et al. 5272A* (CAS, CIC, NY, RSA, UTC). (Det. by A. Cronquist); hills on the e. side of Hwy. 51 at the south end of Wildhorse Reservoir, growing with *Artemisia* on gravelly hills (T43N R55E S9), 1890 m, 26 Jun 1980, *Tiehm & Read 6082* (CAS, CIC, NY, RSA, UTC); just n. of Poorman Creek, n. of Wildhorse Reservoir, 5.6 km nw. of Mendive Ranch, growing with *Artemisia* on gravelly hills, 26 Jun 1980, *Tiehm & Read 6087* (CAS, CIC, NY, RSA, UTC).

Significance. First records for NV and an extension of about 65 km s.

HYMENOPAPPUS FILIFOLIUS Hook. var. TOMENTOSUS (Rydb.) Turner (ASTERACEAE).—Clark Co., St. Thomas Gap area sw. of Whitney Ridge, 0.8 km n. of Grand Gulch road on reservoir road, growing on deep red sand (T17S R71E S32), 730 m, 14 May 1982, *Tiehm 6858* (CAS, NY, MO, RSA, TEX, UTC). (Verified by B. L. Turner.)

Significance. First record for NV and an extension of over 80 km sw. from the St. George area of Washington Co., UT.

MENTZELIA MOLLIS Peck (LOASACEAE).—Humboldt Co., Black Rock Range, Copper Canyon area about 11 km nearly due s. of Soldier Meadows Ranch, growing with *Atriplex* on brown clay hills (T39N R25E S15), 1400 m, 25 May 1982, *Tiehm & Williams 7030* (CAS, NY, OSU, RSA, UTC). (Verified by H. J. Thompson.)

Significance. First record for NV and an extension of 250 km sw.—A. TIEHM, 790 N. Maddux Dr., Reno, NV 89512.

NEW MEXICO

CYANCHUM ARIZONICUM (Gray) Shinners (ASCLEPIADACEAE).—Hidalgo Co., Guadalupe Canyon (NW ¼ S4 T34S R21W), 1500 m, 16 Aug 1979, *Spellenberg and Repass 5353* (NMC). At base of rock on steep sw-facing rocky slope.

Significance. First report from NM, a range extension of ca. 200 km. Previously reported in the U.S. from southern AZ only.

TEPHROSIA TENELLA Gray (FABACEAE).—Hidalgo Co., Peloncillo Mts., Skeleton Canyon (S24 T31S R22W), 1500 m, 7 Sep 1981, *Spellenberg and Spellenberg 6334* (NMC); Guadalupe Canyon drainage (S23 T34S R22W), 1350 m, 21 Sep 1983, *Todsen 8316-11* (NMC). In level gravelly soil pockets on rocky slopes.

Significance. First reports from NM.

MECARDONIA VANDELLIOIDES (H.B.K.) Penn. (SCROPHULARIACEAE).—Hidalgo Co., ¼ mi ne. of U.S. Border Monument 77, 1350 m, 17 Aug 1979, *Spellenberg and Repass 5364* (NMC); Side canyon of Guadalupe Canyon (S23 T34S R22W), 1300 m, 21 Sep 1983, *Todsen 8316-10* (NMC). In rock crevices in canyon bottom.

Significance. First reports from NM.—THOMAS K. TODSEN, Dept. of Biology, New Mexico State Univ., Las Cruces 88003.

PUCCINELLIA PARISHII A. Hitchc. (POACEAE).—Grant Co., se. corner, 40 km due se. Silver City, 1.7 km ne. of Faywood Hotsprings, 5.2 km ne. of US Hwy. 180 on NM Hwy. 61 (T20S R11W s. cent. S16), 1650 m, 23 May 1983, *Soreng & Ward 2158* (NMC, NMCR, US, WTU).

Significance. Extension of known range about 500 km se. from nearest location in AZ, and a reported location from Taos Co., NM 500 km sw. Previously known from a few locations in s. CA, two collections Coconino and Navajo Cos., AZ. Report for Taos Co., NM (Correll & Correll. 1972. Aquatic and Wetland Plants of Southwestern United States, p. 180), is questionable.

ASTRAGALUS VACCARUM Gray (FABACEAE).—Hidalgo Co., 25 km due se. Animas, w. edge Las Playas Lake (T28S R17W S28), 1640 m, 23 Aug 1982, *Soreng & Salazar 1921* (NMC, UNM).

Significance. First Hidalgo Co. record, this filling in a 300 km gap between the nearest NM and Mexico distributions reported by Barneby (1964. Mem. New York Bot. Gard., vol. 13, p. 1095). The two previous records in New Mexico (Grant Co., Luna Co.) are now well over 100 years old. (Erroneously reported from Hidalgo Co. in Martin & Hutchins. 1981. A Flora of New Mexico, vol. 1, p. 1059.)

ERIOGONUM ATRORUBENS Engelm. var. ATRORUBENS (POLYGONACEAE).—Hidalgo Co., w. slope San Luis Mts. ca. 0.25 km n. of United States border, 1800 m, 10 Oct 1982, *Spellenberg & Soreng 6832* (NMC).

Significance. First verifiable record from the US.

ERIOGONUM SCABRELLUM Reveal (POLYGONACEAE).—San Juan Co., ca. 22.5 km sw. of Fruitland, due e. of s. end of Hogback Mt., 1730 m, 7 Jun 1983, *Spellenberg & Soreng 7100* (US, NMC) (Verified by J. L. Reveal); thirty km sw. Fruitland, n. side Cottonwood Arroyo, *Spellenberg & Ward 7587* and *7594.*

Significance. First record for NM, and a 70-km se. range extension. This rarely collected species was previously known from e. cent. and se. UT, and from w. cent. and extreme sw. CO, primarily from along the Colorado and San Juan River drainages (Reveal. 1976. Phytologia 34:409–484).

ERIOGONUM HOOKERI S. Wats. (POLYGONACEAE).—Same location as second collections of *E. scabrellum* (above), 1710 m, 10 Sep 1983, *Spellenberg & Ward 7595* (NMC).

Significance. First record for NM. This species occurs infrequently from e. CA, to sw. WY, to w. CO, and n. AZ.

PHACELIA DEMISSA Gray (HYDROPHYLLACEAE).—San Juan Co., 17 km s. Waterflow, 1.7 km e. of Chaco River (on Navajo Coal Mine lease between mine boundary corners L72 and L68), 1750 m, 7 Jun 1983, *Spellenberg & Soreng 7093* (NMC). Rare on barren badlands of the Fruitland Formation.

Significance. First record for NM. Known from ne. AZ, UT, and WY.

MENTZELIA THOMPSONII Glad (LOASACEAE).—Same location and date as above, *Spellenberg & Soreng 7090* (NMC, LA, NY, COLO, UNM). (Dup. det. by H. J. Thompson.)

Significance. First record for NM. Range extension of 75 km se. from sw. CO. Known from e. cent. and ne. Utah, and w. cent. and sw. Colorado, primarily along the Green, Colorado, and Gunnison river drainages (Glad. 1976. Madroño 23:283–292).—R. J. SORENG, Biology Dept., New Mexico State Univ., Las Cruces 88003.

WYOMING

SAUSSUREA WEBERI Hultén (ASTERACEAE).—Sublette Co., Wind River Range, above Green River Lakes, ne. ridge of Big Sheep Mt. (T39N R109W), 3100 m, 18 Aug 1981, *Soreng 1705* (COLO, RM). (Det. W. A. Weber.)

Significance. This collection lies between the known CO and MT ranges of this rare alpine species, and represents the first record of the genus in WY. The herbaria consulted (COLO, MONTU, RM) generated the following collections only. Colorado: Park and Summit Cos., 6 collections. Montana: Deer Lodge Co., 2 collections, same location. *Saussurea weberi* is currently listed in the *Federal Register* (15 Dec 1980) in Cat. 2.—R. J. SORENG, Biology Dept., New Mexico State Univ., Las Cruces 88003.

ANNOUNCEMENT

The Flora of the Central Wasatch Front, Utah, 2nd Ed., by Arnow, Albee, and Wyckoff [reviewed in Madroño 30(3):199] is available from the Utah Museum of Natural History, University of Utah, Salt Lake City 84112. (Softbound $14.95)

ANNOUNCEMENT

XIV INTERNATIONAL BOTANICAL CONGRESS

Under the auspices of the International Union of Biological Sciences
Berlin (West), Germany, 24th July to 1st August 1987

The Programme will comprise 6 Divisions: metabolic botany, developmental botany, genetics and plant breeding, structural botany, systematic and evolutionary botany, and environmental botany. All plant groups will be considered, and aspects of both pure and applied research will be covered. Special emphasis will be laid on inter- and multidisciplinary topics. There will be plenary sessions, symposia, and sessions for submitted contributions (posters).

The Nomenclature Section will convene in Berlin on 20th to 24th July 1987.

Pre- and post-congress scientific Field Trips will be arranged to various parts of Central, South and North Europe.

The First Circular, containing further details and a preliminary registration form, is now available. Send your name and full address to ensure your inclusion on the mailing list. Your early reply will be appreciated.

Chairman of the Organizing Committee: Prof. Dr. Dr. h.c. K. Esser.

Enquiries should be sent to the Secretary of the Organizing Committee, Prof. Dr. W. Greuter.

Congress Address: XIV IBC, Bot. Garden & Museum, Königin-Luise-Str. 6-8, D-1000 Berlin (West) 33, Germany.

ANNOUNCEMENT

The Shrub Research Consortium is sponsoring a Wildland Shrub Symposium on the "Biology of *Artemisia* and *Chrysothamnus*" on 9–13 July 1984 at Brigham Young University, Provo, UT.

Papers are invited that deal with any aspect of the biology of *Artemisia* or *Chrysothamnus,* including ecology, physiology, genetics, evolution, taxonomy, management, horticulture, manipulation, distribution, uses, and impact of pathogens or insects. Presentations will be limited to 20 minutes. The proceedings will be published. A 2-day (9–10 July) field trip to south-central Utah will precede three days of papers. If you would like to present a paper, send the title and abstract by 15 April 1984 to: Dr. E. D. McArthur, Chairman, Shrub Research Consortium, Shrub Sciences Laboratory, 735 North 500 East, Provo, UT 84601.

For further information about the symposium and facilities, please write to: Dr. Robert Hales, Conferences and Workshops, Brigham Young University, 297 CONF, Provo, UT 84602.

New Manual of California Plants from Jepson Herbarium

A revision of W. L. Jepson's MANUAL is underway, with a planned publication date of 1993. The single-volume MANUAL will cover about 8000 taxa, have about 2000 representative illustrations, incorporate current revisionary results while remaining unified in style and philosophy, and be produced using computers to allow easy revision. Authored treatments are solicited from all specialists with interests in California flora; draft copy must be available at latest by end of 1988. For more details, write James C. Hickman, Editor, Jepson Herbarium, Botany Department, Univ. of California, Berkeley 94720 USA.

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All members of the California Botanical Society are allotted eight pages in MADROÑO over a two year period. Joint authors are each assessed the full page number. Beyond that number of pages a required editorial fee of $60.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

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GRADIENT ANALYSIS OF A NORTH SLOPE MONTANE FOREST IN THE WESTERN TRANSVERSE RANGES OF SOUTHERN CALIFORNIA

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Abstract

Detrended correspondence analysis, an indirect ordination technique, and two-way indicator species analysis, a classification method, were employed to analyze tree cover data from mixed conifer and mixed evergreen forests on the north slope of Pine Mountain in the western Transverse Ranges. The first and second axes of the indirect ordination were correlated with elevation and topography, respectively.

The distributions of seven tree species are presented in two-dimensional population nomograms along gradients of elevation and topography. Five species, *Abies concolor, Calocedrus decurrens, Pinus lambertiana, P. ponderosa* and *Pseudotsuga macrocarpa* attain maximum importance on more north-facing exposures on the topographic gradient, although at different elevations; whereas, *P. jeffreyi* and *Quercus chrysolepis* are best represented on more south-facing exposures at higher and lower elevations, respectively.

Sixteen forest types were identified within the montane forest. The types are described and their positions arrayed in a mosaic diagram in the same two-dimensional gradient framework.

In the western Transverse Ranges of southern California, mixed conifer and mixed evergreen forests often dominate steep, north-facing mountain slopes above 1650 m. Although the species composition of these forests is variable, mixed conifer forest usually consists of single and mixed-species stands of the following conifers: *Abies concolor, Pinus jeffreyi, P. ponderosa, P. lambertiana,* and *Calocedrus decurrens.* The principal non-coniferous species outside of riparian areas are *Quercus kellogii* and *Q. chrysolepis. Quercus chrysolepis* is by far the most abundant of the oak species, forming extensive pure stands or combining with *Pseudotsuga macrocarpa* in mixed evergreen forests (Sawyer et al. 1977).

General descriptions of montane forests in the Transverse Ranges have been presented by Horton (1960), Minnich (1976), Vogl (1976), and Thorne (1977). Wanting, however, are descriptions of the compositional variation often encompassed within these broad montane forest types. This study describes the tree species distributions and resultant vegetation pattern within north-slope mixed conifer and mixed evergreen forests on Pine Mountain.

Madroño, Vol. 31, No. 3, pp. 129–139, 30 July 1984

THE STUDY AREA

Located 20 km north of Ojai, in Ventura County, Pine Mountain is an east-west oriented narrow ridge that rises 915 m to a maximum elevation of 2290 m (Reyes Peak). The ascent is abrupt, rising to the ridge top within a horizontal distance of 5 km from the Cuyama Valley to the north, and the Sespe River to the south. Slopes in the study area average 53%. The range is composed of folded and faulted layers of Eocene sandstone and shale bedrock. Soils in the study area are well-drained, slightly acidic sandy loams derived from hard sandstone (U.S. Forest Service data on file at the Supervisor's Office, Goleta).

The climate is Mediterranean. Most precipitation falls between November and March, an unknown amount of which is snow. The mountains create a rainshadow in the more interior Cuyama and Lockwood Valleys as illustrated by a south to north precipitation profile of the mountain. Near the base of the south slope (1280 m), precipitation averages 60 cm, increasing only slightly to 61 cm at the ridge top (2100 m). From the north slope of the mountain to the Cuyama Valley (1100 m), precipitation decreases sharply to 36 cm (Ventura Co. Water Resources Dept. data). Temperature data are not available for the study area.

The 500 ha study area, situated 4 km west of Reyes Peak, includes Snail Canyon, and another unnamed canyon containing Raspberry Springs. The ridge has no history of logging, and the last major fire swept the study area in 1932.

METHODS

Data from 126 sample plots used in the analysis and descriptions were taken entirely from the north slope of Pine Mountain between 1675 m and 2135 m. Qualitative information was recorded on the less diverse south-slope forests between 1940 m and 2135 m.

In homogeneous 0.07 ha circular plots all trees larger than 5 cm dbh were counted by species and their diameters measured at 1.4 m. Sample stands were selected from representative slope directions along contours spaced at elevation intervals of 75 m. Slope and exposure were recorded for each plot. The range of azimuths sampled varied between 216° (south-southwest) and 126° (east-southeast). Only tree coverage was used in the analysis because understory herbaceous and shrub cover were usually sparse or absent. Species importance values (IV's) for each stand were computed as one-half the sum of relative density and relative basal area (del Moral 1978, Golden 1981).

The data were analyzed in two steps. First, two-way indicator species analysis (TWINSPAN), a polythetic divisive technique, was used to classify the samples (Hill 1979b). This method first ordinates samples using reciprocal averaging (RA) (Hill 1973). The ordinated samples then are divided into two segments by breaking the RA axis near its middle. A differential species is identified on each side of the dichotomy and an improved ordination is constructed using the differential species as a basis. Each of the two refined ordinations is split again to produce another two groups, four in all, and the improved ordination repeated for each group. The process continues until each group has no more than a minimum number of members. A species classification is produced along with the sample classification and both are used to reorder the data matrix (Gauch and Whittaker 1981). TWINSPAN classified the 126 samples into 28 stand groups composed of at least two stands.

Samples were arranged along compositional gradients by the indirect ordination technique, detrended correspondence analysis (DCA) (Hill 1979a). Detrended correspondence analysis, a derivative of RA, is considered among the most successful of ecological ordinations because (1) it provides consistently interpretable species and sample ordinations, (2) the ordination axes are scaled, and (3) the higher axes distortions of RA are avoided (Hill and Gauch 1980). The best results were obtained by transforming the IV's to the Domin scale.

Detrended correspondence analysis produced interpretable ordinations along two axes. Stands similar in composition tended to form discernible clusters in the ordination space. These clusters were connected by lower densities of stands intermediate in composition. Field observations, together with the TWINSPAN classification, guided the partitioning of stands in the ordination space into 16 forest types. Nine samples were eliminated from the analysis of forest types as outliers (single stand groups). Forest type, as used in this study, refers to a group of stands that (1) have a similar composition, (2) generally recur in a predictable but relatively limited range of topographic settings and elevations, and (3) are recognizable in the field.

Stand ordination values along the first axis are correlated with elevation ($r = -0.784$, $p < 0.01$), a common outcome in mountain vegetation ordinations (Parker 1982, Vankat 1982). When the mean elevation of each forest type is compared to its corresponding mean first axis score, the relationship is improved ($r = -0.872$; $p < 0.01$).

We interpret the second ordination axis as a topographic gradient. In steep mountainous terrain, topography, as expressed in slope and aspect, has a significant influence on vegetation patterns (Day and Monk 1974, Sawyer and Kinraide 1980). Potential annual solar irradiation (PASI) (from the tables of Frank and Lee 1966) integrates slope and aspect into a single factor that can be used to estimate topography. The correlation between stand PASI values and second axis scores is weak ($r = -0.400$, $p < 0.01$), but significant. The low correlation coefficient is not entirely unexpected, however, because PASI does not account for some important local topographic influences on the vegetation, such as soil drainage, or topographic position, i.e., stand proximity to canyon bottoms or ridges. Another even greater source of variability is the tendency for forest types to occupy a variety of exposures at elevations where growing conditions are optimal, but then to become progressively restricted to one or two exposures at elevations away from the optimum. A comparison of mean forest type PASI values to their corresponding mean second axis scores reduces some of this variability, and the postulated relationship between forest types and topography becomes clearer ($r = -0.782$; $p < 0.01$).

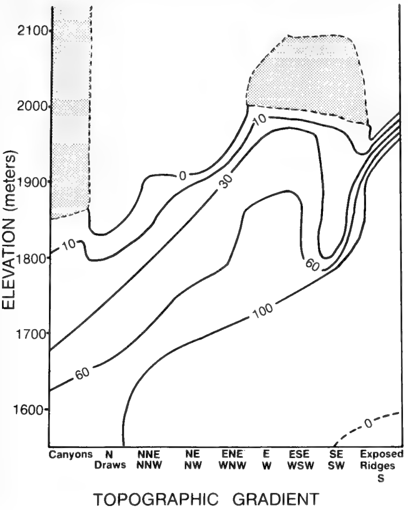
The results of the ordination are displayed as species population nomograms and a forest type mosaic diagram. Species population nomograms (Figs. 1–7) were constructed by directly ordinating stand sample IV's for each species according to elevation and position along a gradient of increasing PASI (canyons to south slopes and ridges), expressed as slope direction. The mosaic diagram of forest types (Fig. 8) was constructed in a similar way, but instead of species IV's, stand groups were plotted along the environmental gradients.

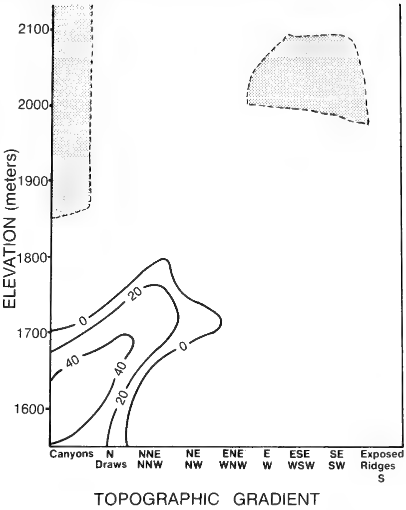
Stands in canyons and on ridges did not regularly have the lowest and highest PASI values, respectively. Nevertheless, they are placed at the extremes of the topographic (PASI) gradient because forest types that dominate canyons and ridges formed the endpoints of the ordination. Plots were not taken from south-southeast and south-southwest exposures, which were rare in the study area.

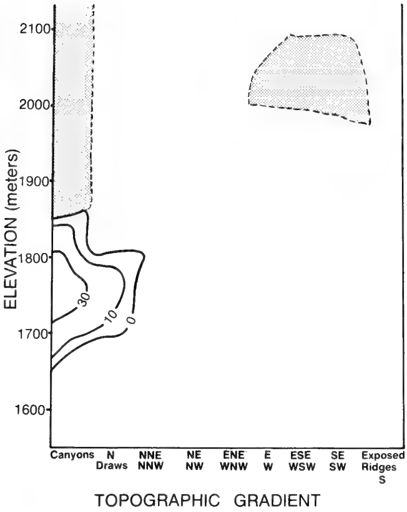
RESULTS AND DISCUSSION

Quercus chrysolepis. Quercus chrysolepis IV's decrease with increasing elevation. However, the decrease is steeper in canyons and draws and on more north-facing exposures than on ridges and more south-facing exposures (Fig. 1). Between 1500 m and 1825 m, *Q. chrysolepis* forms a continuous uneven forest belt that separates high-elevation conifer forest from lowland chaparral (Fig. 8). Below 1500 m, *Q. chrysolepis* is a riparian codominant on canyon bottom slopes, whereas above 1825 m, it is a common mixed conifer associate to 1980 m. On the south slope of the mountain, *Q. chrysolepis* codominates with *Pinus jeffreyi* between 2000 m and 2100 m.

Pseudotsuga macrocarpa. Along the lower slopes of canyon bottoms, in draws bordering ephemeral streams, and on open slopes to 1700 m, *Pseudotsuga macrocarpa* grows as patchily distributed forest stands with *Q. chrysolepis* (Fig. 2). *Pinus lambertiana* is also a common associate, but its abundance is usually low (IV's < 0.05). Although *Pseudotsuga macrocarpa* achieves its highest IV's in these topographic settings, tree density (97 plants/ha) and basal area (8.06







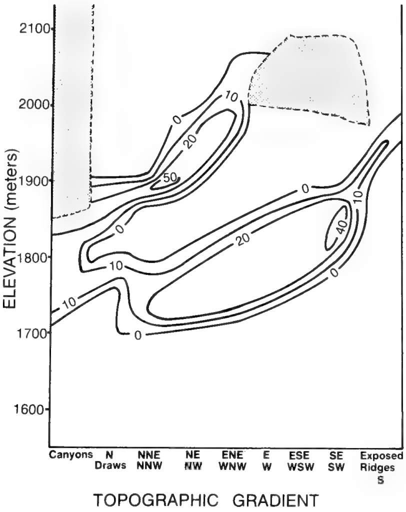


FIG. 1. Isolines of *Quercus chrysolepis* IV's. Importance values are ×100. The dashed zero isoline in the lower right was estimated from aerial photos. In all Figs., shaded areas are not represented in the study area.

FIG. 2. Isolines of *Pseudotsuga macrocarpa* IV's. Importance values are ×100.

FIG. 3. Isolines of *Calocedrus decurrens* IV's. Importance values are ×100.

FIG. 4. Isolines of *Pinus ponderosa* IV's. Importance values are ×100.

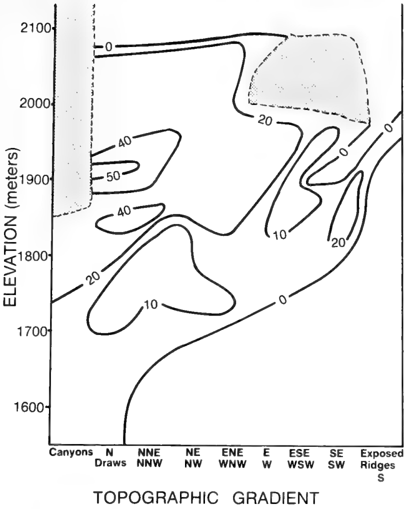
m^2/ha) are both at the low end of the ranges of these values for this species in southern California (McDonald and Littrell 1976). Near 1760 m, on open northeast, north-northeast and north-northwest slopes, *Pseudotsuga macrocarpa* reaches the upper limits of its distribution in the study area. Here, it frequently occurs with *Pinus ponderosa* and becomes a minor element of the mixed conifer forest.

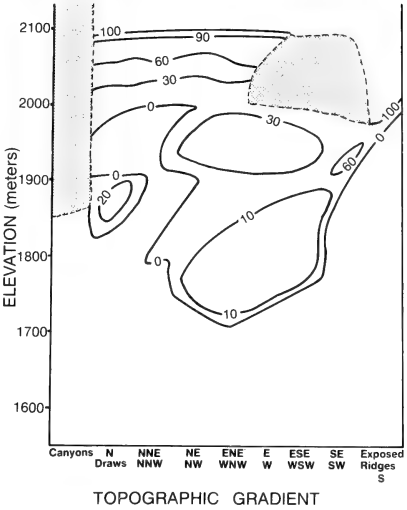
Calocedrus decurrens. At a somewhat higher elevation, *Pseudotsuga macrocarpa* gives way to *C. decurrens,* which is confined almost entirely to the canyons and lateral draws of the major streams (Fig. 3). This species occurs either as scattered individuals in a matrix of *Q. chrysolepis* along the rocky canyon slopes, or as small groves lining the water courses. In the San Jacinto Mountains *C. decurrens* borders water courses and follows canyon bottoms that carry subterranean water (Hanawalt and Whittaker 1976, Vogl 1976). In this study the densest stands with the largest trees also grow where water intermittently appears at the streambed surface. Away from the deeper canyons, however, *C. decurrens* occurs only as occasional individuals or small groups of trees in draws, or just below lateral ridges.

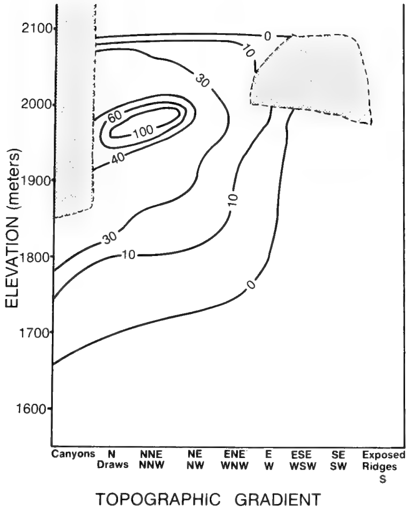
Pinus ponderosa. The distribution of *P. ponderosa* is notable for the presence of two separate zones of importance: the first occurs from 1700–1900 m, whereas the second extends from 1850–2000 m (Fig. 4). Regardless of location, however, the overall trend of IV's within both zones is from more north-facing, low-elevation sites to relatively more south-facing, high-elevation sites. In the southern Sierra Nevada, the same general trend occurs in the altitudinal distribution of *P. ponderosa.* For example, in Sequoia National Park, ponderosa pine forest shows a gradual shift to relatively drier conditions above 1500 m (Rundel et al. 1977, Vankat 1982). Similarly, in Yosemite National Park, *P. ponderosa* occupies steep, dry, south-facing slopes above 1600 m (Parker 1982). In the present study xeric, high-elevation sites, ostensibly suitable for *P. ponderosa,* are occupied by *P. jeffreyi,* suggesting, as some have (Haller 1959, Thorne 1977), that *P. jeffreyi* outcompetes *P. ponderosa* in the colder, drier, high-elevation habitats of southern California mountains.

Pinus lambertiana. This is the most widespread species in the study area (Fig. 5), as it often is in mixed conifer forests throughout southern California (Thorne 1977). Like *P. ponderosa,* it is best represented on more north-facing exposures around 1900 m; unlike *P. ponderosa,* however, *P. lambertiana* is most abundant on much steeper, north to north-northeast-facing slopes.

Pinus jeffreyi. Beginning about 1700 m, *P. jeffreyi* appears in the mid-portion of the topographic gradient (Fig. 6). With increased elevation, *P. jeffreyi* IV's increase, until gradually it expands to occupy most of the topographic gradient. Near 2080 m, parklike Jeffrey pine forest dominates the main ridge, although it also can extend







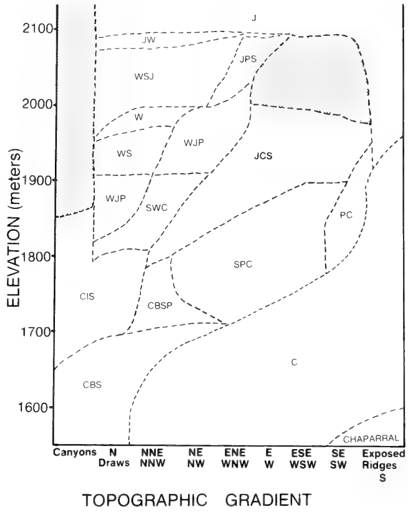


FIG. 5. Isolines of *Pinus lambertiana* IV's. Importance values are ×100.

FIG. 6. Isolines of *Pinus jeffreyi* IV's. Importance values are ×100.

FIG. 7. Isolines of *Abies concolor* IV's. Importance values are ×100.

FIG. 8. Vegetation diagram illustrating the distribution of forest types according to elevation and topographic conditions of a north-slope montane forest on Pine Mountain, California. Species symbols: B, *Pseudotsuga macrocarpa*; C, *Quercus chrysolepis*; J, *Pinus jeffreyi*; P, *Pinus ponderosa*; S, *Pinus lambertiana*; and W, *Abies concolor*.

down to 1950 m on major lateral ridges. The high-elevation position of Jeffrey pine forest presented here agrees with vegetation descriptions for the southern Sierra Nevada (Rundel et al. 1977, Vankat 1982) and the San Jacinto Mountains of southern California (Hanawalt and Whittaker 1976). In fact, *P. jeffreyi* appears to occupy a wider variety of environmental settings on Pine Mountain than in the southern Sierra Nevada (Rundel et al. 1977, Haller pers. comm.).

Abies concolor. Although the elevational distribution of *A. concolor* is extensive, its coverage of the topographic gradient is the narrowest of the species group (Fig. 7). Like *P. ponderosa* and *P. lambertiana,* it achieves the maximum IV's on more north-facing exposures, although at a somewhat higher elevation.

When the species population distributions are displayed in terms of nomograms, several patterns emerge. First, *A. concolor, P jeffreyi, P. lambertiana, Q. chrysolepis,* and, to a lesser extent, *P. ponderosa* have broad elevational distributions; whereas, *C. decurrens* and *Pseudotsuga macrocarpa* are restricted to the lower elevations. The latter two species, along with *Q. chrysolepis,* continue to the Cuyama Valley floor as riparian elements.

Along the topographic gradient, five species, *A. concolor, C. decurrens, P. lambertiana, P. ponderosa* and *Pseudotsuga macrocarpa* attain maximum IV's in the portion of the gradient with lower PASI's (more north-facing exposures), although at different elevations. *Pinus jeffreyi* and *Q. chrysolepis,* on the other hand, are generally best represented in the portion of the gradient with higher PASI's (more south-facing exposures), which they broadly dominate at the highest and lowest elevations, respectively. Hanawalt and Whittaker (1976) have employed a similar vegetation diagram to show the mean position of the major vegetation types in the San Jacinto Mountains. The relative positions of species maxima in this study for *A. concolor,*

TABLE 1. TREE DATA AND DESCRIPTIONS FOR FOREST TYPES OF THE LOW-ELEVATION (1500 M–1880 M) STRATUM. Key: n, stand sample size; D, density in individuals per hectare; BA, basal area in m^2 per hectare. Species symbols: C, *Quercus chrysolepis*; B, *Pseudotsuga macrocarpa*; I, *Calocedrus decurrens*; S, *Pinus lambertiana*; and P, *Pinus ponderosa.*

Forest type	Description	n	D	BA
C	Continuous uneven forest belt covering all exposures	3	496	26.0
CBS	Small stands (<0.5 ha) bordering ephemeral streams and on open slopes; continuous ribbons along canyon bottoms	5	391	36.4
CIS	Best developed in major canyons; replaces CBS at higher elevations	6	445	48.7
CBSP	Open, boulder-strewn slopes above canyons	4	352	35.2

TABLE 2. TREE DATA AND DESCRIPTIONS FOR FOREST TYPES OF THE MID-ELEVATION (1780 M–1910 M) STRATUM. Key: n, stand sample size; D, density in individuals per hectare; BA, basal area in m^2 per hectare. Species symbols: P, *Pinus ponderosa*; C, *Quercus chrysolepis*; S, *Pinus lambertiana*; J, *Pinus jeffreyi*; and W, *Abies concolor.*

Forest type	Description	n	D	BA
PC	Small stands at the margin of oak forest; extensive stands at higher elevations where *P. lambertiana* is a common associate	5	275	35.2
SPC	Tops and gentle side slopes of knolls and benches; intermingles with live oak forest at lower elevations	13	312	33.6
JCS	Widespread; *A. concolor* is a component at higher elevations	13	294	77.9
SWC	Patchily distributed on steep (70%) active slopes; most common on north-northeast exposures	5	221	59.0
WS	Almost entirely on steep (62%) protected slopes; high elevation counterpart of SPC	5	153	43.5
PWS	Moderately steep (52%), open slopes; occasionally on the lower slopes of deeper drainages	8	277	31.1
WJP	Benches and knolls, small gently sloping (20%) valleys, and ephemeral stream courses	15	339	50.8

C. decurrens, P. jeffreyi, P. ponderosa, and *Q. chrysolepis* agree well with their placement of these species. Unfortunately, however, they did not present details of species distributions.

Forest types. The 16 forest types are displayed in Fig. 8. The major attributes of each type are presented in Tables 1–3. The forest types have been divided into low-elevation (1500 m–1880 m) (Table 1), mid-elevation (1780 m–1910 m) (Table 2), and high-elevation (1920 m–2135 m) (Table 3) strata.

In the diagram forest types are portrayed as discrete, continuous units; but in the field, most occur as variable sized stands interspersed among stands of other types represented at the same elevation. This mosaic configuration to a large extent reflects the interplay of elevation, topography, and other local modifying conditions that shape the vegetation pattern.

Elevation, and the complex of environmental factors associated with it, exerts the controlling influence on both the species distributions and resultant vegetation pattern. Topographic effects are more subtle, largely because most slope exposures are variations of north, especially at the higher elevations. In this regard, DCA proved to be particularly useful for elucidating the postulated topographic gradient.

In other gradient analysis vegetation studies, PASI, in combination with other topographic variables, has been employed as an indirect measure of site moisture conditions (Loucks 1962, Golden

TABLE 3. TREE DATA AND DESCRIPTIONS FOR FOREST TYPES OF THE HIGH ELEVATION (1920 M–2135 M) STRATUM. Key: n, stand sample size; D, density in individuals per hectare; BA, basal area in m^2 per hectare. Species symbols: J, *Pinus jeffreyi*; P, *Pinus ponderosa*; W, *Abies concolor*; and S, *Pinus lambertiana*.

Forest type	Description	n	D	BA
J	Dominant type on the main ridge and spur ridges	4	185	60.8
JPS	East-northeast-facing slopes and benches	4	258	56.3
JW	On a variety of exposures just below J forest	8	257	60.3
WSJ	The densest and most widespread high elevation forest	16	367	52.4
W	Small (<1.0 ha) widely scattered stands on moderate (45%) slopes; concave bowls at the heads of small drainages	3	350	32.6

1981, Peet 1981). In this study, the increase from low to high PASI values could be interpreted as roughly equivalent to a change from mesic to xeric conditions. Viewed in these terms, there is a heavy concentration of forest types and species IV maxima in the mesic end of the gradient, especially between 1800 m and 2000 m.

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PENSTEMON ABSAROKENSIS, A NEW SPECIES OF SCROPHULARIACEAE FROM WYOMING

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ABSTRACT

A new species, **Penstemon absarokensis,** from Wyoming is described and compared with the morphologically similar *P. alpinus, P. glaber,* and *P. paysoniorum.*

Penstemon absarokensis was first collected by the author in 1974 during floristic studies of the North Fork Shoshone River drainage area in northwest Wyoming. This distinctive species is ecologically restricted to shifting scree and is known only from Park and Fremont Counties, Wyoming.

Penstemon absarokensis Evert, sp. nov.

Planta perennis caulibus pluribus, 7–18 cm alta. Folia integra sursum minime reducta elliptica vel lanceolata, 2.5–7.0 cm longa, 7–20 mm lata. Thyrsus compactus secundus multiflorus, 3–10 cm longus, pedicellis glandulosis. Calyx 7–12 mm longus, segmenta acuminata inferne scariosa erosa marginata. Corolla caerulea glabra, 18–33 mm longa. Staminodium leviter expansum pubescens vel glabrum apice. Antherae loculi 1.5–2.0 mm longi hispidi reflexi (Fig. 1).

Plants perennial, low, glabrous (the inflorescence minutely glandular), several-stemmed, 7–18 cm tall, clustered from a slender or more frequently thickened, unbranched, suffrutescent caudex surmounting numerous fibrous roots; leaves little reduced upwards, entire, somewhat fleshy and slightly glossy, the margins papillate, the lower leaves petiolate, obtuse, elliptic-lanceolate or oblanceolate, the upper sessile, acute, elliptic to oblanceolate or ovate, 2.5–7.0 (–9) cm long, 7–20(–25) mm wide; inflorescence a compact, broad thyrse of 1–4 verticillasters, leafy, 3–10 cm long, 3–5 cm wide, the cymes 2–8 flowered, ± secund, the pedicels minutely glandular; sepals 7–12 mm long, prominently scarious-erose margined, ovate or lanceolate with a long caudate-acuminate tip, the tip equaling or exceeding the basal portion, the basal portion minutely glandular; corolla 18–33 mm long, moderately ampliate, glabrous externally and within, obscurely bilabiate, the throat 7–11 mm wide (in pressed specimens), the tube 14–25 mm long, purplish-blue, the limb 4–8 mm long, bright blue, the upper lobes reflexed on living specimens;

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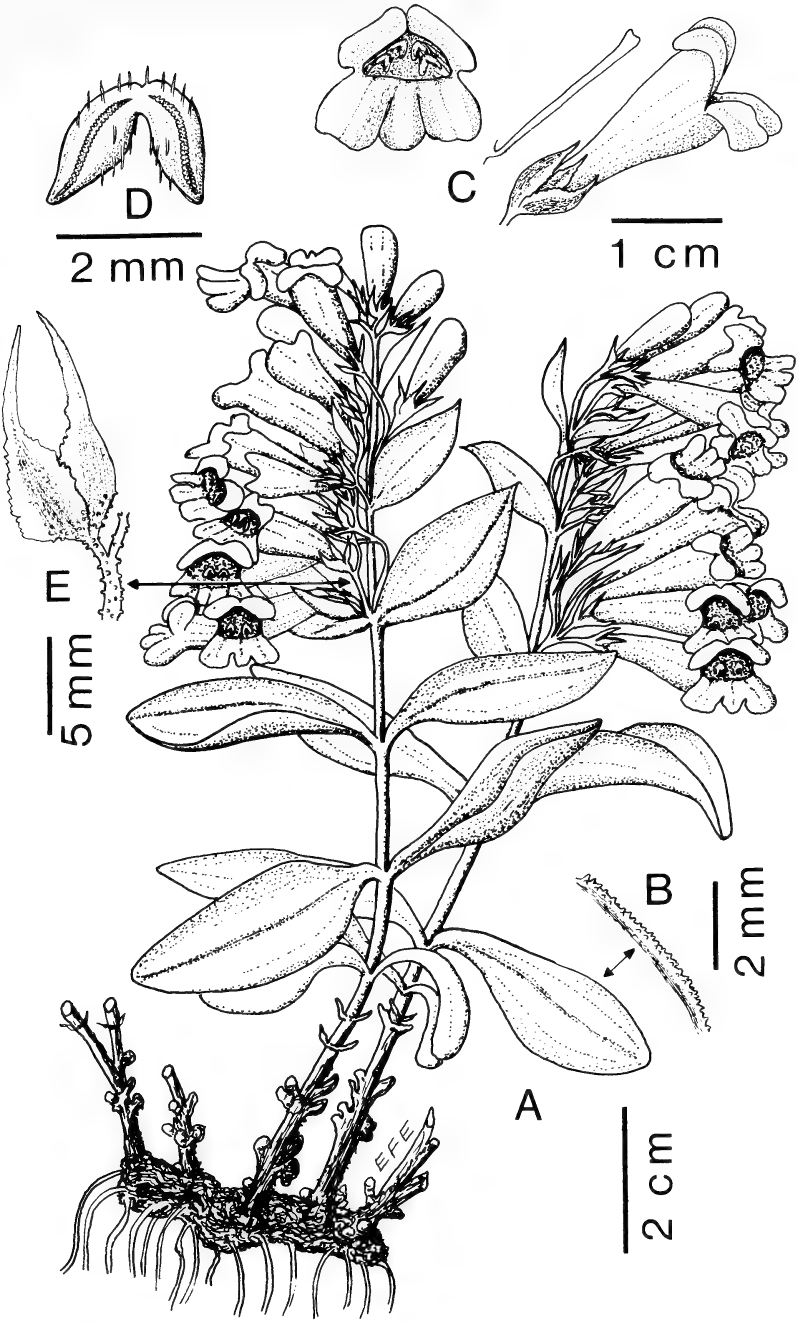

FIG. 1. *Penstemon absarokensis* Evert. A. Habit. B. Detail showing papillate leaf margin. C. Corolla and staminode. D. Anther sacs. E. Detail showing glandular pedicels and sepals. From *Evert 4345*.

staminode just reaching the orifice, slightly expanded and slightly lobed apically, sparsely bearded or glabrous apically; fertile stamens (anterior pair) projecting 2–4 mm beyond the orifice (in pressed specimens), the anther sacs 1.5–2.0 mm long, not explanate, reflexed, sparingly hispidulous over the entire surface, dehiscing nearly the entire length but not next to the connective, the suture margins papillate; mature capsules ovoid, acuminate, 8–12 mm long; seeds dark-brown, alveolate-reticulate, narrowly winged, 2–4 mm long.

TYPE: USA, WYOMING, Park Co., Absaroka Range, w. side of Clayton Mtn., ca. 5 km s. of Hwy. 14, T51N R107W S9 NW ¼, 2684 m; open, dry, shifting volcanic scree with *Astragalus vexilliflexus, Chaenactis alpina, Haplopappus acaulis, Lupinus argenteus, Oenothera caespitosa, Oryzopsis hymenoides,* and *Phacelia hastata,* 20 Jul 1982, *E. F. Evert 4345* (Holotype: RM; isotypes: MO, NY).

PARATYPES: USA, WYOMING, Fremont Co., on bluff ca. 23 km se. of Dubois, 1936 m, 30 Jun 1947, *Ripley and Barneby 8923* (NY); Park Co., Absaroka Range, on divide between Newton and Moss Crs. ca. 5 km n. of Hwy. 14, T52N R107W S5 SW ¼, 2623 m, 9 Jul 1979, *Evert 1479* (RM); ridge e. of Elk Fork Cr., ca. 1.6 km s. of Hwy. 14, T52N R106W S28 SW ¼, 2013 m, 16 Jun 1981, *Evert 2703* (RM); near the source of Canyon Cr., ca. 8 km s. of Hwy. 14, T51N R105W S18 SW ¼, 2928 m, 14 Jul 1981, *Evert 3162* (NY, RM); on divide above Cougar and Pagoda Crs., ca. 8 km s. of Hwy. 14, T51N R106W S15 NW ¼; 3044 m, 22 Jul 1981, *Evert 3258* (UC, RM); ridge e. of Sweetwater Cr., ca. 6.5 km s. of Hwy. 14, T52N R106W S6 NE ¼, 1982 m, 27 Jun 1982, *Evert 4051* (RM); ridge e. of Post Cr., ca. 8 km e. of Wapiti, T52N R104W S28 NE ¼, 1946 m, 11 Jul 1982, *Evert 4165* (RM); ridge e. of Newton Cr., ca. 0.8 km n. of Hwy. 14, T52N R107W S21 SW ¼, 2074 m, 7 Aug 1982, *Evert 4686* (RM).

Penstemon absarokensis grows on open, dry shifting, scree derived from volcanic material or rarely on river gravels at elevations of 1936–3044 m in or along the Absaroka Range, Park Co. and Fremont Co., Wyoming. It flowers from mid-June through July depending on elevation. The name is given in reference to the Absaroka Range of northwestern Wyoming.

Penstemon absarokensis is allied to the species comprising section *Glabri* (Rydb.) Pennell and most closely resembles *P. paysoniorum* Keck, *P. glaber* Pursh, and *P. alpinus* Torr. *Penstemon absarokensis* resembles *P. paysoniorum,* a southwestern Wyoming endemic, in its low stature, tufted habit, and sepal shape but differs in its significantly larger, glabrous corollas, larger sepals, wider leaves, and larger, sparsely short-pubescent, reflexed anthers. Both *P. glaber,* which is widespread in Wyoming, and *P. alpinus,* which is restricted to the southeastern part of the state, resemble *P. absarokensis* in flower size but differ in larger stature, more completely dehiscent anthers, sepal shape and length, and in their usually internally pubescent corollas. Furthermore, these two species are not restricted ecologically to shifting scree slope habitats as *P. absarokensis* apparently is. With its consistently low stature, large glabrous flowers, and somewhat fleshy thickened leaves, *P. absarokensis* is a highly distinctive and easily recognized species.

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CROSSABILITY AND RELATIONSHIPS OF WASHOE PINE

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ABSTRACT

Washoe pine, related to ponderosa pine but occurring at higher elevations along the western edge of the Great Basin, crosses freely with the Rocky Mountain race of ponderosa despite evidence of long-term separation. Washoe is morphologically distinct from the parapatric Pacific race of ponderosa pine, and the two taxa are kept separate partly by genetic barriers that reduce seed yield by about two-thirds. Washoe pine most closely resembles North Plateau ponderosa pine, and may be a late-Pleistocene offshoot of this race, which occupies the Pacific Northwest interior.

Washoe pine (*Pinus washoensis* Mason and Stockwell) is the most recently described and one of the most puzzling of California's remarkable assortment of pines. It is a western yellow pine in subsection *Ponderosae* (subgenus *Pinus,* section *Pinus*: Critchfield and Little 1966), and there is general agreement that it is allied to two other members of *Ponderosae*: ponderosa and Jeffrey pines (*P. ponderosa* Dougl. ex Laws., *P. jeffreyi* Grev. & Balf.). Widely divergent views have been expressed concerning its origin and taxonomic status, however. J. R. Haller, one of the first students of Washoe pine, has questioned its species status (1965a), and has proposed that it originated either from hybridization between ponderosa and Jeffrey pines (1959) or from hybridization between races of ponderosa pine in the Pacific and Rocky Mountain regions (1965a). Mirov (1961) dismissed Jeffrey pine as a possible ancestor on chemical and morphological grounds, and suggested that Washoe pine is "a variety or mutant" of ponderosa pine. Smith (1967b, 1971) concluded from resin composition that Washoe pine may be most closely related to Rocky Mountain ponderosa pine, from which it is separated by much of the Great Basin.

Washoe pine was discovered in 1938 on the east slopes of Mt. Rose, Nevada, the highest peak in the mountains north and east of Lake Tahoe. In their description, Mason and Stockwell (1945) likened it to a small-coned version of Jeffrey pine, with which it is associated on Mt. Rose, and asked the question: "Whence came this pine?" We now know much more about Washoe pine—its distribution (Haller 1961, Critchfield and Allenbaugh 1965), ecology (Talley 1977), adult morphology (Haller 1957), seedling morphology

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and physiology (Wells 1964, Jenkinson 1980), resin composition (Mirov 1961; Smith 1967b, 1971), seed proteins (Prager et al. 1976), and ability to cross with other pines (Critchfield 1966). This paper reviews our knowledge of the species and presents a fuller account of its crossing behavior. Summarized are all crosses involving Washoe pine and all crosses between ponderosa pine races carried out by the Institute of Forest Genetics (IFG), near Placerville, California. Despite contradictions between different kinds of evidence, these data provide a tentative answer to the question posed by Mason and Stockwell: Washoe pine is probably not of hybrid origin, but most likely originated as a Pleistocene derivative of the North Plateau race of ponderosa pine, which now occupies the interior Pacific Northwest.

THE WESTERN YELLOW PINES OF THE U.S.

Subsection *Ponderosae,* a large and predominantly Mexican group, includes only three taxa with distributions centered in the western U.S.: Jeffrey, ponderosa, and Washoe pines. Jeffrey pine is widely distributed in California, mostly at upper elevations, and extends into Oregon, Nevada, and Baja California (Fig. 1). The distributions of ponderosa and Washoe pines are sharply contrasting: they are respectively the most widespread and most narrowly restricted taxa in *Ponderosae* (Critchfield and Little 1966).

The distribution of ponderosa pine encompasses much of the montane West (Fig. 1). The western (var. *ponderosa*) and eastern (var. *scopulorum* Engelm.) parts of this broad distribution are widely separated from each other except in central Montana, where they meet and intergrade.

Each variety is made up of two or three discrete geographic races. These races are delimited by differences in adult morphology and growth in natural stands and in a common environment (Weidman 1939), seed and seedling characters (Wells 1964, Read 1980), and monoterpenes of xylem resin (Smith et al. 1969, Smith 1977). Included in var. *ponderosa* are the North Plateau, Pacific, and southern California races. The Rocky Mountain and Southwestern (South Plateau) races comprise var. *scopulorum.*

All three northern races—North Plateau, Pacific, and Rocky Mountain—have been implicated in the ancestry of Washoe pine. The Continental Divide has traditionally been accepted as the eastern limit of the North Plateau race (and that of var. *ponderosa*); but in Read's (1980) transect across Montana, the most abrupt change was near the 110th meridian, about 200 km east of the Divide. In northeastern California the North Plateau race is replaced by the Pacific race through a zone extending from the Cascades to the western edge of the Great Basin. This zone is best defined by shifts

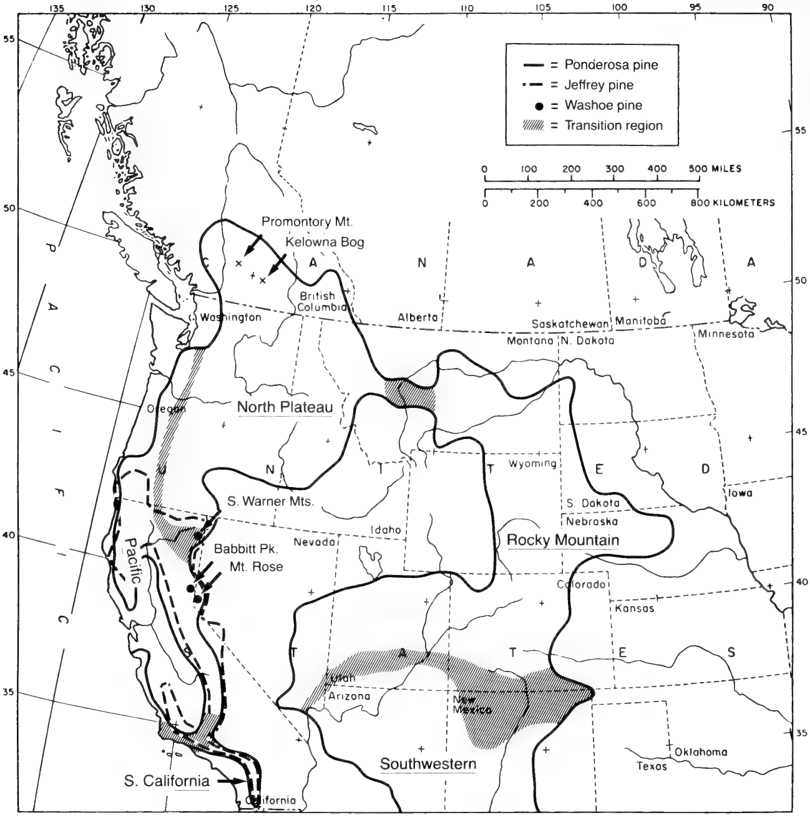

Fig. 1. Distribution of western yellow pines in the U.S. and Canada. Geographic races of ponderosa pine are underlined.

in two well-studied characters: resin composition (Smith 1977, Sturgeon 1979) and color of immature seed cones (Smith 1981). The Pacific race is distributed throughout most of California and extends north to include most or all of the stands west of the Cascades in Oregon and Washington (Sturgeon 1979, Wells 1964). Populations in the southern California mountains are here considered a separate race, primarily because of their distinctive resin composition (Smith 1977).

The Rocky Mountain race, to which the varietal name *scopulorum* was originally restricted (Engelmann 1880), reaches its western limits in Nevada, where scattered stands in isolated mountain ranges of the eastern and southern Great Basin are separated from the nearest Washoe pines by about 400 km of sagebrush steppe (Fig. 1). Engelmann described the needles of var. *scopulorum* as "often in pairs," and this useful character distinguishes most populations of the Rocky Mountain race from all other ponderosa races, which have most or all of their needles in fascicles of three (Haller 1965b). The Rocky Mountain and Southwestern races intergrade in southern Utah, southern Colorado, and northern New Mexico. The replacement of the Southwestern race near the Mexican border by a complex of poorly defined, predominantly Mexican taxa is beyond the scope of this paper.

The three well-known populations of Washoe pine are located at the eastern edge of the coniferous forests that cover the mountains of the Pacific Slope, and are all within sight of the Great Basin sagebrush steppe (Fig. 1). In addition to the type locality on Mt. Rose, Washoe pine stands have been found at two California localities: the Babbitt Pk. area, about 30 km northwest of Mt. Rose (Critchfield and Allenbaugh 1965), and the southern Warner Mts., in the northeastern corner of California about 200 km north of Mt. Rose (Haller 1961). Elsewhere in northeastern California, Washoe characteristics are sometimes present in variable stands of ponderosa pine (Haller 1961, Griffin and Critchfield 1976). Trees resembling Washoe pine occur at scattered localities in eastern Oregon (Haller 1965a), and another stand of Washoe pine has been found in southern British Columbia (J. R. Haller, pers. comm., Oct. 1981).

Washoe pine grows at higher elevations than ponderosa pine, which reaches its upper limits at about 2000 m in this region. On Mt. Rose, mixed stands of Washoe and Jeffrey pines extend above 2500 m to the subalpine forest zone. Washoe pine reaches its lower limits at about 2100 m on Mt. Rose, but pure stands of Jeffrey pine extend down to 1600 m, where they are replaced by sagebrush. The distribution of ponderosa pine is sporadic in the Tahoe–Mt. Rose region; one stand at 1950 m is less than 2 km east of the nearest Washoe pines (Haller 1957). A more extensive ponderosa stand is at Incline, 13 km to the southwest on the north shore of Lake Tahoe. At Babbitt Pk., Washoe pine grows in nearly pure stands at 2400 to 2600 m; at lower elevations (down to 2300 m) it is associated with other conifers (Talley 1977). Jeffrey pine is not common in this area, but below 2450 m it is sometimes a minor component. Ponderosa pine stands have not been observed in the immediate vicinity of Washoe pine in the Babbitt Pk. area, but they are present within a few km (Griffin and Critchfield 1976).

In the Warner Mts., Washoe pine occurs at lower elevations (about 1950 to 2400 m) than at the two southern localities. Jeffrey pine is mostly restricted to a narrow zone below Washoe pine (Haller 1961). Ponderosa pine is common at lower elevations in this region, which is in the transition zone between the Pacific and North Plateau races.

The Babbitt Pk. and Warner Mts. stands have not been heavily logged, but the Mt. Rose stand is mostly second-growth. The forests on the east slopes of Mt. Rose were the nearest major source of timber to the mining center of Virginia City, Nevada, and were clearcut during the exploitation of the Comstock Lode in the 1860s and 1870s. Washoe pines that predate logging are not rare, however. The oldest tree I have found in the Mt. Rose area, on the northeast slope of Slide Mountain, had an estimated age exceeding 300 years in 1962. In the same stand as the tree from which we believe the type specimen was collected, several trees had estimated ages of 100 to 250 years.

Mason and Stockwell (1945), in what was intended to be the first in a series of reports on Washoe pine, provided a fairly complete description of the species but gave little indication of how it differed from ponderosa or Jeffrey pines. They noted that it had short, stout needles; short, red-purple pollen cones; small seed cones with many cone scales; and seeds with short wings.

Haller (1957) contrasted Mt. Rose Washoe pine with ponderosa and Jeffrey pines in several quantitative characteristics. He sampled ponderosa and Jeffrey pines on Mt. Rose and ponderosa in eastern Nevada and central Montana. Washoe pine resembled the Rocky Mountain trees—and differed from local ponderosa and Jeffrey pines—in its short, stout needles and small cones. It differed from all ponderosa (but not Jeffrey) in its dense cones, and had relatively shorter seed wings than the other pines. Haller concluded that Washoe pine was most like the Rocky Mountain race of ponderosa, differing from it in the direction of Jeffrey pine.

The dissimilarity of Washoe pine and Pacific ponderosa pine was also underscored in Wells's (1964) rangewide provenance test of ponderosa pine, which included Washoe pine from Mt. Rose. This study was based on 1- and 2-year-old seedlings grown in Michigan. Washoe seedlings differed from nearly all ponderosa provenances in their lesser height, shorter secondary needles, and greener foliage at 2 years. They suffered much less winter injury than most western provenances, and differed from eastern provenances in the delayed production of secondary needles and in having fewer lateral buds at 2 years. In a multi-character analysis (Summation of Differences = SD) restricted to western provenances (var. *ponderosa*), Washoe pine was more like the North Plateau race (SD 23–42) than the Pacific race (SD 50–69), differing from the nearby Incline stand by SD 50.

Washoe pine also differs from Pacific ponderosa pine in the ability of its dormant seedlings to produce new roots after one growing season in the IFG nursery (Jenkinson 1980). Ponderosa seedlings from central and northern California, lifted and tested at intervals throughout the winter, had a single peak or plateau in root production. Mt. Rose Washoe pine resembled most Jeffrey provenances in its two-peaked pattern of root production, with one peak in late fall or early winter and the other in late winter. Most ponderosa seedlings of other provenances (including south-central Oregon and eastern Nevada) also had a single peak or plateau in root production; the two-peaked pattern was restricted to one Rocky Mountain provenance (Wyoming) and all four provenances of the southern California race.

Seedlings of Washoe pine allocate a larger fraction of growth to the root system than Pacific ponderosa or Jeffrey pine seedlings (S. H. Strauss, pers. comm., Jan 1983). Seedlings grown from Mt. Rose seed had a mean shoot-root ratio of 0.60 at 5 months, compared with ratios of 1.03 and 0.98 for ponderosa and Jeffrey seedlings from the west slope of the Sierra Nevada.

Washoe pine is completely different from Jeffrey pine in the composition of the turpentine (low-boiling-point) fraction of its wood resin, but within the range of variation of ponderosa pine. Jeffrey pine turpentine consists mostly (89–99%) of heptane (Smith 1967b). Washoe pine lacks this hydrocarbon, and ponderosa resin only occasionally has trace amounts (Smith 1977). Five monoterpenes—alpha-pinene, beta-pinene, 3-carene, myrcene, and limonene—are the major constituents of ponderosa and Washoe turpentine, and all are highly variable within and between ponderosa races (Smith 1977).

Washoe pine turpentine is characteristically high in 3-carene (more than 55%) and low in limonene (less than 2.4%). Of 24 trees sampled on Mt. Rose, 20 were of this type (Smith 1967b). This combination is rare in Pacific ponderosa pine, which typically has moderate amounts of all five monoterpenes (Smith 1977). Among 951 trees of this race sampled by Smith (1964, 1977, and unpubl. data), fewer than 1% had both low limonene and high 3-carene. A transect of 47 trees on the west slope of the central Sierra Nevada included no low-limonene trees and only one with high 3-carene (Smith 1964). In a smaller sample near Incline on Lake Tahoe, 11 of 12 trees were like the west-slope trees, but one resembled Washoe pine in its low limonene and high 3-carene.

The contrast between Washoe and ponderosa pines is less marked in the Warner Mts. region, where ponderosa is transitional between Pacific and North Plateau races. Trees with low limonene and high 3-carene—rare in the Pacific region—are common throughout the North Plateau region, and ponderosa of the south Warner Mts. is intermediate. Below 1830 m, 57% of 74 trees were low in limonene and 26% were high in 3-carene (Smith 1971). Above 1950 m, in the Washoe zone, 93% of 63 trees were low in limonene and 83% were high in 3-carene.

Throughout the broad distribution of ponderosa pine, only the North Plateau and Rocky Mountain races have frequencies of low-limonene, high-carene trees approaching that of Washoe pine. This combination was most common in 627 North Plateau trees sampled by Smith (1977, and unpubl. data): 47% overall, ranging from a high of 56% (near Bend, Oregon) to a low of 34% (Bitterroot Mountains, Idaho). The Rocky Mountain race is more variable. Overall frequency of low-limonene, high-carene trees was 29% (of 1165 trees), decreasing from a high of 73% in the east (Wyoming) to a low of 13% in the eastern Great Basin (389 trees).

Previous Reports of Hybridization

In the lower part of its distribution on Mt. Rose, Washoe pine appears to have been influenced by ponderosa pine (Haller 1957, 1959), and in the Warner Mts. the two taxa form what Haller (1965a) described as a morphological continuum. The elevational change from ponderosa to Washoe pines in the Warner Mts. is best documented for resin composition (described above) and immature cone color (Smith 1981). The deeply pigmented, dark red-purple to purple-black cones of Washoe pine contrast with the green cones of Pacific ponderosa pine, and the stands of this region form a gradient from predominantly green cones at low elevations to predominantly dark purple cones at high elevations.

Washoe pine also hybridizes with Jeffrey pine, but natural hybrids are uncommon. Of 124 trees sampled as Washoe pine on Mt. Rose, two trees about 0.5 km apart had turpentine consisting of 80–85% heptane, with 3-carene as the next most abundant constituent (5–6%) (R. H. Smith, pers. comm., Feb 1981). This level of heptane is more than twice that of F_1 hybrids between Jeffrey and either Washoe or ponderosa pines (Smith 1967a), and these trees were probably backcrosses of Washoe-Jeffrey hybrids to Jeffrey pine.

Verified F_1 hybrids of Washoe and California ponderosa pines from controlled crosses in both directions were first reported by Righter and Duffield (1951), Jeffrey × Washoe hybrids by Liddicoet and Righter (1960), and Washoe × Rocky Mountain ponderosa hybrids by Keng and Little (1961). Needle characteristics of these combinations were described by Keng and Little (1961), and other morphological and growth attributes by Little and Righter (1965). Smith (1967a) described the turpentine composition of a Jeffrey × Washoe F_1 (32% heptane, 45% 3-carene, 1% limonene) and a California ponderosa × Washoe F_1 (much like the female parent). Critchfield (1966) reported that crossability was high in crosses of Washoe with ponderosa and low in crosses with Jeffrey pine or Apache pine (*P. engelmannii* Carr.), the latter a member of *Ponderosae* native to northern Mexico and southern Arizona. No hybrids were obtained from crosses of Washoe pine with Coulter pine (*P. coulteri* D. Don), a California species in subsection *Macrocarpae.*

METHODS

Parent trees. All crosses involving Washoe pine were made between 1941 and 1967 on female parents in natural stands (Table 1). Exploratory crosses between 1941 and 1948 were made with Washoe parents on Mt. Rose, the only population known then. The identity of Washoe pine was still uncertain when the first crosses were made, and the parent trees were initially labeled Jeffrey pine. The "type" tree, from which the type specimen probably came, was used as a parent in 1941 and most subsequent breeding seasons. These early crosses did not include within-species control crosses. Most crosses were made with freshly collected pollen, and within-species pollinations were often difficult or impossible to execute during short pollinating seasons.

A second series of crosses between 1962 and 1967 included within-species controls. Female parents were the type tree and three others in the same stand. From 1961 on, pollen was routinely collected and deep-frozen a year before pollinations were made, and control crosses were no longer a problem. Pollen parents of 1962 controls were other Washoe pines in the same stand as the female parents. In a 1965 set of crosses between Washoe populations, pollen parents were four trees in a Mt. Rose stand 1 km from the female parents, two trees 1 km apart near Babbitt Pk., and five trees in two stands 5 km apart in the Warner Mts. Most of the crop from these crosses was lost to Clark's nutcrackers and seed insects during the following season, and the crosses were not repeated. Pollen parents of 1967 control crosses were in the same Mt. Rose stand as the 1965 pollen parents.

Crosses between geographic races of ponderosa pine were made between 1941 and 1967 on native ponderosa pines growing near the IFG in the central Sierra Nevada. Mature trees of other races are well represented in the IFG arboretum, and have been used as pollen parents in interracial crosses (Table 1). Attempts to use them as female parents have not been successful, however. Many trees of Rocky Mountain and North Plateau origins produce few or no cones in California, and when cones are produced the seed yield is abnormally low. A total of 27 Rocky Mountain × California crosses, made in five seasons, produced an average of fewer than 7 sound (filled) seeds and 14 total seeds per cone, with maxima of 21 sound and 30 total seeds per cone. Mean seed yields in natural stands of the Rocky Mountain region are much higher: 30 germinable seeds and 42 total seeds per cone in central Colorado (Roeser 1941), 20 sound seeds per cone in northern Colorado (unpubl. data, IFG), and 32 to 55 sound seeds per cone in the Black Hills (Van Deusen and Beagle 1970). The large reduction in both sound and hollow seed yield from female parents of Rocky Mountain origin might be at-

TABLE 1. PARENT TREES OF CROSSES SUMMARIZED IN TABLES 2 AND 3 AND IN TEXT. ( ) = number of localities; + = some crosses made with mixes of pollen from unspecified number of male parents.

Species or race	Number of parents		Location or geographic origin
	Female	Male	
Natural stands:			
Washoe	6	8+	Mt. Rose (2)
		2	Babbitt Pk. (2)
		5	Warner Mts. (2)
Pacific ponderosa	12	9	Central Sierra Nevada (11)
		7+	Lake, Modoc, Santa Cruz, Siskiyou Cos., California, s.w. Oregon (2)
Jeffrey	1	3	Central Sierra Nevada (2)
Lodgepole	2	2+	Central Sierra Nevada (2)
Arboretum trees:			
Rocky Mt. ponderosa		7	Colorado (3)
		7	Nebraska (3)
		4	Wyoming
		1	South Dakota
		1	e. Montana
		1	e. Nevada
North Plateau ponderosa		2+	British Columbia
		2+	Bitterroot Mts.
		1	Washington
		1	w. Montana
Apache		2	Arizona
Coulter		3	Unknown

tributed to an unusual sequence of reproductive barriers in these interracial crosses, except that five control crosses between Rocky Mountain trees produced slightly fewer seeds than accompanying interracial crosses (8 sound and 15 total seeds per cone, compared with 9 sound and 18 total). Two crosses of North Plateau females (Bitterroot Mts. origin) with California pollen parents were even less successful, producing fewer than 3 sound and 5 total seeds per cone. In a natural stand in the North Plateau region (central Oregon), ponderosa pine averaged 75 sound and 100 total seeds per cone (Sorensen 1970).

Techniques and terminology. Breeding and seed-processing techniques have been described elsewhere (Critchfield 1966). Except as noted, the data summaries (Tables 2 and 3) include all cone-producing crosses for which the following information was available: numbers of female strobili pollinated, cones harvested, and sound and hollow seeds.

An *attempt* is the pollination in a single season of a single female parent with pollen from one male parent or with a mixture of pollen from two or more males. Mean number of seeds per cone is the unweighted average of all individual attempts. *Crossability* is the mean number of sound seeds per cone of all crosses (attempts) between taxa or races, expressed as a percent of the mean sound seed yield of control crosses within the maternal-parent taxon. Control crosses summarized in Tables 2 and 3 were made on the same seed parent in the same season as crosses between taxa.

Other observations. Several characteristics were studied in trees growing in the IFG arboretum and in natural stands, or in collections in the IFG herbarium:

Pollen cones—Most observations of ponderosa pine in the arboretum were made in a single season (1981). Color and length of pollen cones were recorded for 42 Rocky Mountain trees (18 provenances scattered throughout the region), 10 North Plateau trees (10 provenances), and five native trees on the IFG grounds. In other years, observations were made in natural stands of Washoe and ponderosa pines. Color was noted just before the pollen cone elongated and the pollen was shed. For arboretum trees, length was measured when the cone was fully elongated and most or all of the pollen had been shed, but most field observations were made after the elongated cone had dried up. For all trees, the longest pollen cone of a 5- to 8-cone sample is reported.

Seed cones—Color of immature seed cones was observed on five Rocky Mountain trees in the arboretum (Nebraska, Colorado, and eastern Nevada) and in natural stands of Washoe and ponderosa pines. Observations were made during the summer of the second season of cone development, after the cones reach their full size but before they turn brown at maturity in late summer or fall.

Unpublished data on other characteristics are from a rangewide study of ponderosa pine that included a sample of Washoe pine. The study was organized by R. Z. Callaham, and the data are on file at the IFG. Characters included: number of needles per fascicle, length of needles, fascicle radius (=needle thickness), seed length, and the ratio of seed + wing length to seed length. Cone scales were counted on single cones from each tree in a few 8- to 10-tree samples from the same study.

RESULTS

Crosses of Washoe pine. Washoe pine crosses readily only with ponderosa pine. In combination with other western pines, its crossing behavior is much like that of ponderosa pine (Critchfield 1966). It has been hybridized with Jeffrey and Apache pines, but crossability is low in both combinations. Verified hybrids were produced in an early Jeffrey × Washoe cross, but no germinable seeds were obtained

TABLE 2. CROSSES BETWEEN WASHOE PINE AND OTHER SPECIES (EXCLUDING PONDEROSA PINE). ND = no data; ( ) = range of individual attempts; ___ = verified hybrid; * = no further record of sound seed.

Parent								
Female	Male	Attempts	Minimum tree × tree combinations	Attempts producing sound seed	Female strobili pollinated	Strobili producing cones	Mean sound seed per cone	Mean total seed per cone
1) Crosses lacking controls (1945, 1948):								
Lodgepole	Washoe	2	4	0	37	17	0	ND
Washoe	Lodgepole	2	4	0	33	2	0	41.5
Washoe	Coulter	1	2	1	28	6	0.2*	74.8
Washoe	Apache	1	2	1	15	2	1.5*	106.5
Jeffrey	Washoe	1	5	1	14	10	3.4	172.8
2) Crosses with controls (1962):								
Washoe	Apache	3	6	1	20	13	0.1	76.6 (55–105)
Washoe	Coulter	3	9	0	22	16	0	65.1 (40–83)
Washoe	Jeffrey	3	9	0	23	13	0	49.2 (16–85)
Washoe	Washoe	3	9	3	25	14	48.9 (26–78)	95.8 (68–122)

from later crosses with Washoe pine as female parent (Table 2). Sound seeds were produced twice in crosses with Apache pine. The fate of the seeds from an early cross was not recorded, but a later cross yielded a single verified hybrid.

Crosses between Washoe pine and species in other subsections were unsuccessful. A single seed from an early Washoe × Coulter cross is unaccounted for, but later crosses in the same direction produced no sound seeds (Table 2). Lodgepole pine (*P. contorta* Dougl. ex Loud.), the only representative of subsect. *Contortae* in the western U.S., has not been successfully crossed with any other western pine. The combination of lodgepole and Washoe pines, tried in both directions, produced only hollow seeds (Table 2).

Most crosses made on Washoe pine with species other than ponderosa pine produced fewer total seeds per cone than Washoe × Washoe control crosses (Table 2). Pine seed coats form at about the time of fertilization (Buchholz 1945), so the reduced number of seed coats from crosses with other species suggests that ovules pollinated with foreign pollen aborted at a higher frequency during the first year of cone development, between pollination and fertilization. The reduction is fairly consistent and sometimes large (e.g., Washoe × Jeffrey), but the data are insufficient to establish its significance.

In contrast to its low crossability with other western yellow pines, Washoe pine is fully crossable with the Rocky Mountain race of ponderosa pine (Table 3). Crossability exceeds 100%: significantly more sound seeds per cone were harvested from Washoe × Rocky Mountain crosses than from Washoe × Washoe controls (*t* test, $p = <0.05$). Interspecific crosses produced more sound seeds per cone than controls in 11 of 13 attempts and in both seasons the crosses were made, although most pollen parents and some female parents differed between years. Interspecific crosses also produced more total seeds per cone, but this smaller difference was not statistically significant.

The Pacific race of ponderosa pine, unlike the Rocky Mountain race, is partially isolated from Washoe pine by reproductive barriers (Table 3). Washoe × California ponderosa crosses showed large and highly significant reductions in sound seed yields compared to Washoe controls ($p = <0.01$). Among eight crosses with controls, estimated crossability ranged from 6 to 61%, with a mean of 30%. Mean crossability was the same in both years the crosses were made. Total number of seeds per cone was also substantially reduced: 64.1 in crosses with California ponderosa compared with 76.2 in control crosses. The size of this reduction suggests that reproductive barriers expressed before seed coat formation produced differential ovule abortion in some combinations, but overall the reduction was not statistically significant. Early Washoe × California ponderosa crosses lacking controls produced more sound seeds per cone (17.7) than

TABLE 3. INTERSPECIFIC AND INTERRACIAL CROSSES OF WASHOE AND PONDEROSA PINES. All attempts produced sound seed. ND = data incomplete or lacking; ( ) = range of individual attempts.

Parent							
Female	Male	Attempts	Minimum tree × tree combinations	Female strobili pollinated	Strobili producing cones	Mean sound seed per cone	Mean total seed per cone
1) Crosses lacking controls (1941–1972):							
Washoe	ponderosa (Pacific)	10	11	366	78	17.7 (2–35)	46.7 (5–91)
Washoe	ponderosa (Rocky Mt.)	1	3	15	1	26	126
ponderosa (Pacific)	Washoe	1	1	ND	15	18.1	73.1
ponderosa (Pacific)	ponderosa (Rocky Mt.)	9	12	808	508	32.1 (6–64)	63.1 (8–95)
2) Washoe × ponderosa crosses with controls (1962, 1967):							
Washoe	ponderosa (Pacific)	8	11	134	63	12.1 (3–35)	64.1 (26–116)
Washoe	ponderosa (Rocky Mt.)	13	18	215	113	57.5 (9–120)	81.5 (27–135)
Washoe	Washoe	6	10	92	35	41.9 (24–78)	76.2 (47–122)
3) Interracial ponderosa crosses with controls (1941–1967):							
Pacific	Rocky Mt.	20	24	557	271	17.1 (2–41)	51.3 (7–107)
Pacific	N. Plateau	7	10	162	83	23.2 (11–38)	ND
Pacific	Pacific	17	17	605	188	48.6 (6–94)	58.6 (13–103)

later crosses with controls (12.1), a difference that can perhaps be attributed to choice of parent trees.

Crosses between Washoe pine populations were made in a single season on Mt. Rose female parents using pollen from all three populations, but most of the crop was lost. Three cones on one tree survived, one cone each from crosses with pollen from Babbitt Pk., the Warner Mts., and another stand on Mt. Rose. The highest yield of sound seed was from the Babbitt Pk. cross, followed by the Warner Mts. cross. Many cones were harvested from another tree, but insect damage was heavy, and the eight crosses on the tree produced only 0–9 sound seeds per cone. Four crosses with Warner Mts. pollen produced the fewest sound seeds per cone, and three crosses with Mt. Rose pollen produced the most. These sketchy and inconsistent results show that Washoe pine populations can be intercrossed successfully, but they provide no basis for estimating crossability.

Compared with other western yellow pines, Washoe pine produces unusually large numbers of hollow seeds in intraspecific crosses. Cones harvested from controlled pollinations of Mt. Rose trees averaged a high percentage of hollow seed in all combinations: 51% with pollen parents in the same stand, 40% with parents in another Mt. Rose stand, and 54% with Warner Mts. and Babbitt Pk. trees. Overall, crosses between Mt. Rose trees averaged 45% hollow seed (Table 3), with individual combinations ranging from 30 to 62%. The proportion of hollow seed was even higher in open-pollinated cones from Mt. Rose trees (11 collections in 6 seasons). Total seed yield was low, averaging 51 seeds per cone. All collections averaged 73% hollow seed, ranging from 43 to 100%. The type tree was particularly unproductive, yielding 93 to 100% hollow seed in three different seasons. These data show that a large fraction of Washoe pine's reproductive potential is lost before the cones mature, and the significantly higher yield of sound seed from Washoe × Rocky Mountain ponderosa crosses suggests that the factors responsible for these losses are diminished or eliminated when Washoe pine is replaced as pollen parent by the Rocky Mountain race of ponderosa pine.

This large reduction in reproductive capacity is not matched by other western yellow pines. Control-pollinated cones of North Plateau ponderosa pine produced 33% hollow seed (Sorensen 1970), and California ponderosa is variously estimated to produce 17% (Table 3) and 10% hollow seed (Critchfield 1966) in controlled crosses. Digger pine (*P. sabiniana* Dougl.: subsect. *Macrocarpae*) and Jeffrey pine produced 13 and 12% hollow seed in controlled within-species crosses (Critchfield 1966). Estimates of hollow seed in open-pollinated ponderosa cones are 25% in central Oregon (Sorensen 1970), 29% in Colorado (Roeser 1941), and 27% in 20 collections from Sierra Nevada trees (unpubl. data, IFG).

Crosses between ponderosa pine races. Pacific ponderosa pine is partially isolated by reproductive barriers from the Rocky Mountain race, just as it is from Washoe pine, and crossability is similar in both combinations. The reduction in sound seed was highly significant ($p = <0.01$) in California × Rocky Mountain crosses compared with their controls (Table 3), and estimated crossability was 35%. California × Rocky Mountain crosses lacking controls, some of them carried out on a large scale in the 1970s, yielded much more sound seed per cone (Table 3), and this discrepancy too must be attributed to choice of parent trees.

The provenance of pollen parents had little effect on sound seed yield. Among 20 crosses with controls, 4 or more attempts were made with trees originating in each of three states: Colorado, Wyoming, and Nebraska. All three sets of crosses gave crossability estimates between 33 and 39%.

A few crosses between Pacific and North Plateau trees suggest that these races too are partially isolated by reproductive barriers (Table 3). These crosses, carried out in a single season on two Sierra Nevada trees in different stands, were accompanied by control crosses made with pollen from a single tree of southwestern Oregon provenance (Josephine County). Mean crossability was 50%, and individual attempts ranged from 38 to 75%. Although these data indicate the probable existence of a genetic barrier, they are too limited for a reliable estimate of its magnitude.

Reproductive phenology. The mean pollination date of Mt. Rose Washoe pine over six seasons was 28 June, with the earliest on 3 June and the latest on 9 July. In a single season (1964), all three Washoe populations (Mt. Rose, Babbitt Pk., and Warner Mts.) began to shed pollen between 24 June and 4 July.

The Mt. Rose populations of Washoe, Jeffrey, and ponderosa pines all have opportunities to intercross, although both Washoe and ponderosa are pollinated earlier than Jeffrey pine in the same stand. Jeffrey pine occupies an elevational span of nearly 1000 m on the steep eastern slopes of Mt. Rose, and in most seasons pollen must be shedding somewhere in this span through most or all of the pollination periods of ponderosa and Washoe pines. Ponderosa on Mt. Rose, below the lower limits of Washoe pine, precedes but overlaps the latter in pollen shedding. On 22 June of one year (1963), ponderosa pine at 1950 m was past its peak of pollen shedding, and a few Jeffrey pines in the same stand were just beginning to shed. In a stand 2.2 km away and 365 m higher, some Washoe pines were beginning to shed pollen and bore receptive female strobili. The pollen strobili of Jeffrey pines in this stand were estimated to be at a meiotic stage, at least two weeks before pollen shedding.

Foliage characteristics. Washoe pine needles are shorter and stouter than those of Pacific ponderosa pine, but they can be matched or approximated by both North Plateau and Rocky Mountain races. Needle length has been extensively studied in the ponderosa group, and comparisons between provenances planted in Idaho and corresponding natural populations have shown that it is a moderately heritable trait (Weidman 1939). Mason and Stockwell (1945) described Washoe needles as 10 to 15 cm long, and the Mt. Rose population has been variously estimated to average 15.1 cm (Haller 1957) and 14.4 cm (unpubl. data, IFG). Mt. Rose ponderosa and Jeffrey pines both have longer needles: 20.5 and 20.0 cm (Haller 1957). Other populations of Pacific ponderosa also have significantly longer needles than Washoe pine ($p = <0.05$), with means of 16.1–24.3 cm in 27 stands (unpubl. data, IFG). The North Plateau race has slightly shorter needles than the Pacific race, with means of 43 samples ranging from 13.0–20.5 cm. Populations with the shortest needles, in southern British Columbia and in eastern Oregon and adjacent Idaho, have mean lengths (13.0–15.7 cm) that do not differ significantly from that of Washoe pine. Most Rocky Mountain stands have significantly shorter needles than Washoe pine or the other races of ponderosa pine, but the range of mean lengths (8.7–17.9 cm in 31 populations) also includes that of Washoe pine. Populations equaling or exceeding Washoe pine in needle length are mostly in the eastern part of the Rocky Mountain region (unpubl. data, IFG), but include an isolated stand in eastern Nevada (Haller 1957).

The short needles of Washoe pine are wider than those of Jeffrey or ponderosa pines on Mt. Rose—8 and 20% on the average (Haller 1957). Washoe pine also has wider needles than Jeffrey pine in the Warner Mts., but the difference is not significant (Haller 1961). Washoe pine has significantly thicker needles than most populations of ponderosa pine (unpubl. data, IFG). Exceptions are five North Plateau populations—three on the east slope of the Cascades and one each in northeastern Oregon and southeastern British Columbia—and two Rocky Mountain stands in central Utah.

In number of needles per fascicle, Washoe pine differs from the Rocky Mountain race but not from the other races of ponderosa pine. This trait too is moderately heritable (Weidman 1939), although it is influenced by tree age, by branch vigor, and in some places by climatic fluctuations (Haller 1965b). Mature Washoe pines uniformly have three needles per fascicle on Mt. Rose (unpubl. data, IFG) and in the Warner Mts. (Haller 1965b). Fascicles with two needles are uncommon in the Pacific and North Plateau races, occurring at frequencies up to 1.4% (Haller 1965b; J. R. Haller, pers. comm., Oct 1981; unpubl. data, IFG). The Rocky Mountain race, in contrast, usually has moderate to high frequencies of two-needled fascicles: 19 to 75% in the region from central Montana to central Colorado, and 17 to 39% in most populations of the eastern Great Basin (Haller 1965b). On the Colorado Plateau in western Colorado and eastern Utah, however, the frequency of two-needled fascicles drops to less than 3% in most stands (Haller 1965b; unpubl. data, IFG).

Cone and seed characteristics. Pollen cones of Washoe pine are short, stout, and deeply pigmented. Mason and Stockwell (1945) described them as red-purple and 10–20 mm long. Fully elongated pollen cones of five trees on Mt. Rose and one in the Warner Mts. were 21–27 mm long and 7–12 mm in diameter, ranging in color from red-purple to purplish-black. Pacific ponderosa pines have longer, more slender pollen cones. On three Mt. Rose trees they were 36–46 mm long and 6–8 mm in diameter. Native ponderosa pines at IFG had pollen cones 71–93 mm long, and dried cones of six trees in four other Sierra Nevada stands were 38–67 mm long. In all California trees observed, color ranges from dark red to red-purple. North Plateau trees in the IFG arboretum also have deeply pigmented cones, but in length they fall between Washoe and Pacific ponderosa pines. On 10 widely scattered North Plateau trees they were 28–69 mm long, averaging 46 mm. Rocky Mountain trees in the arboretum have pollen cones as short as those of Washoe pine, but at maturity most are unpigmented (yellow) or lightly pigmented (pink). Of 36 trees, the cones of 35 were 17–40 mm long; on one eastern Nevada tree they were 51 mm long. Only 4 of 36 trees, all of eastern origin (Nebraska, Wyoming), had red or purple pollen cones, but some Rocky Mountain populations have a higher frequency of trees with pigmented cones. In an eastern Nevada stand, R. H. Smith (pers. comm., Feb 1983) counted 15 trees with purple and 19 with yellow pollen cones.

The seed cones of Washoe pine are 5–8 cm long (Mason and Stockwell 1945). Haller (1957) estimated that their volume was 69% of Mt. Rose ponderosa cones and 19% of Jeffrey cones, but about the same as that of ponderosa cones from eastern Nevada and central Montana. In the same samples, Washoe cones were about equal in density to Jeffrey cones, and the heavy cones of both species had mean densities 32–61% greater than those of ponderosa cones. In other samples (unpubl. data, IFG), Washoe pine had shorter cones (mean length 6.4 cm) than any western population of ponderosa pine (means 7.3–12.2 cm), and the differences were significant with one exception: an eastern Oregon stand with cones 7.3 cm long. Northern and eastern Rocky Mountain stands also had small cones (means 5.2–7.9 cm), but populations nearest Washoe pine (eastern Great Basin, Colorado Plateau) had significantly longer cones than Washoe pine (means 7.8–9.3 cm).

Despite their small size, Washoe cones have more scales than most ponderosa cones. Mason and Stockwell's (1945) estimate of scale number was 160 to 190, and in a 10-tree sample from Mt. Rose I counted a mean of 173 scales per cone. In this feature, Washoe pine significantly exceeded ponderosa samples from three Rocky Mountain stands (Utah, Colorado, eastern Montana), with means of 112–141 scales, as well as samples from nearby Incline, southeastern British Columbia, and western Montana-northern Idaho, with means of 134–137 scales per cone. It also exceeded, but not significantly, ponderosa from the Sierra Nevada west slope and from central Oregon (159 and 157 scales per cone). A single North Plateau stand, in the Okanagan region of southern British Columbia, had the same mean number of scales per cone as Washoe pine.

Ponderosa pine is polymorphic in immature seed-cone color, but deeply pigmented cones like those of Washoe pine have not been observed in the Pacific race. Smith (1981) reported no ponderosa pines with purple cones in the region from the central Sierra Nevada to southern Oregon west of the Cascades. Only in and near the transition zone of northeastern California did he encounter low frequencies of trees with purple cones. The ponderosa stand on Mt. Rose is also polymorphic in cone color. Of six trees I observed, four had green cones and two had reddish-brown cones.

Trees with cones ranging in color from reddish-brown to dark purple predominate in the North Plateau region. Smith (1981) found high frequencies of trees with purple cones in southern Oregon just north of the transition zone. Sargent (1897) noted that one western Montana stand was a mixture of green- and purple-coned trees, but in another stand most trees had purple cones. Not all trees are readily classifiable: in an Idaho stand Maki (1940) counted 3 trees with green cones, 7 with deep purplish-brown cones, and 10 with varying degrees of pigmentation. In some British Columbia stands, however, all trees have dark purple cones (J. R. Haller, pers. comm., Oct 1981).

Not much information is available on seed-cone color in Rocky Mountain ponderosa pine, but purple cones have not been reported. Haller saw only green cones in central Colorado and southern Montana stands (pers. comm., Oct 1981 and Sept 1983), and five arboretum trees of Rocky Mountain provenances (eastern Nevada, Colorado, Nebraska) all had green cones.

Washoe pine has large seeds with relatively short wings. Mason and Stockwell (1945) described the seed as 8 mm long, with a wing (measured from wing tip to seed) 1.5 to 2 times as long as the seed. Mean length of Mt. Rose Washoe seed was 8.1 mm (unpubl. data, IFG), significantly longer than all 25 Rocky Mountain samples (means 5.4–7.2 mm) and 14 of 19 Pacific samples (6.5–8.1 mm), but only 2 of 10 samples from the North Plateau region (means 6.7–8.4 mm).

TABLE 4. COMPARISON OF WASHOE PINE WITH NORTHERN RACES OF PONDEROSA PINE. 1 = most similar; 3 = least similar; ND = no data. Western = eastern Great Basin, and Colorado Plateau in Utah and Colorado; eastern = central Montana to Nebraska and central Colorado; column in between represents Rocky Mt. region as a whole.

			Rocky Mountain		
	Pacific	North Plateau	Western		Eastern
Seedlings (Wells 1964)	2	1		ND	
Terpenes (Smith 1977)	3	1	2		1
Needles:					
Length	2	1		1	
Thickness	3	1	2		3
Number per fascicle	1	1	2		3
Pollen cones:					
Length	3	2		1	
Color	1	1		2	
Seed cones:					
Volume (Haller 1957)	2	ND		1	
Length	3	2	2		1
Number of scales	2	1		3	
Color	2	1		2	
Seeds:					
Length	2	1		3	
Wing length : seed length	3	1	3		2

Seed weight differences in the same set of samples were much less striking: most western stands and two eastern Rocky Mountain stands had heavier seeds than Washoe pine (Wells 1964).

The seed of Washoe pine has shorter wings, relative to seed length, than most ponderosa pines outside the North Plateau region. The mean ratio of wing to seed length in Haller's (1957) Mt. Rose sample was 1.9, compared with means of 3.2, 3.0, and 2.3 in ponderosa from Mt. Rose, eastern Nevada, and central Montana. In other samples (unpubl. data, IFG), this ratio was 2.0 in Mt. Rose Washoe pine, 3.0–3.9 in the Pacific region, 2.1–3.4 in the Rocky Mountain region, and 1.9–2.5 in the North Plateau region. Expressed as the ratio of total (wing + seed) length to seed length, the mean ratio of Washoe pine was significantly smaller than that of all Pacific samples, all western (eastern Great Basin, Colorado Plateau) and most eastern Rocky Mountain samples, and 2 of 10 North Plateau samples.

DISCUSSION

The two kinds of data assembled in this paper—crossing, and all other—suggest different hypotheses concerning the origin of Washoe pine. In its ability to cross with other taxa, Washoe pine behaves like a fragment of the Rocky Mountain race stranded at the western edge of the Great Basin. But most other evidence supports the hypothesis that Washoe pine is most closely linked to the North Plateau race of ponderosa pine (Table 4).

The data are in agreement, however, in narrowing the field of ancestral candidates. Mirov's (1961) conclusion that Jeffrey pine was not involved in the ancestry of Washoe pine was based primarily on the absence of heptane in Washoe wood resin, but his view is supported by morphological evidence and by the strong crossing barrier between these taxa. Among the northern races of ponderosa pine, the least likely ancestral candidate is the Pacific race. Although it is essentially parapatric with Washoe pine, in nearly all of its attributes it is less similar to Washoe pine than are the other two northern races (Table 4). The Pacific race and Washoe pine exchange genes, but the extent and consequences of hybridization appear to be limited by moderately strong reproductive barriers, by differences in pollination time, and perhaps by selection against hybrids and their derivatives in the rigorous environments to which Washoe pine is restricted.

The available crossing data provide a less than complete picture of crossability among elements of the ponderosa pine complex, including Washoe pine. The data are most complete for the Pacific race, and least so for the North Plateau race. No crosses have been made between the latter and either Washoe pine or the Rocky Mountain race, but the few Pacific × North Plateau crosses suggest that these two geographic races are partly isolated by reproductive barriers. The Pacific race is, in fact, genetically isolated to varying degrees from all other northern elements of the ponderosa complex. It is in genetic contact with both Washoe pine and the North Plateau race, and may have been in the past. In these instances the barriers could have evolved either during isolation or by selection against the products of hybridization. The latter explanation is hardly applicable to barriers of the same magnitude between Pacific and Rocky Mountain races, which are more likely to have evolved as a byproduct of geographic isolation. These well-differentiated races have been separated by the western Great Basin since at least the late Pleistocene (see below), and possibly for much longer.

Genetic barriers between geographic races are not common in *Pinus,* but they have been encountered in at least one other species. The northern "blue" race of the Californian *P. muricata* D. Don is isolated from southern populations by reproductive barriers that are absolute or nearly so (Critchfield 1967). The more common situation in the genus, however, is exemplified by the absence of reproductive barriers between coastal and Sierra Nevada races of lodgepole pine, although these taxa are so different they are sometimes considered separate species (Critchfield 1980).

The hypothesis that Washoe pine is a geographically isolated offshoot of the Rocky Mountain race is based primarily on crossing behavior. Not only are the two taxa fully crossable, but in combination with the Pacific race they give almost identical results: 30% crossability for Washoe pine and 35% for the Rocky Mountain race. As an indicator of relationship, however, these results are inconclusive in the absence of comparable crossing data for the North Plateau race.

Morphological and biochemical characters provide only limited support for the hypothesis that Washoe pine derives from a Rocky Mountain-like ancestor. The closest similarities are in size (needles, pollen cones, and seed cones), and the most conspicuous differences in other kinds of characters: color (pollen- and seed-cone) and number (needles per fascicle and scales per cone). In several respects (resin composition; needle, seed-cone, and seed length; relative length of seed wings), Washoe pine resembles the geographically remote eastern populations of the Rocky Mountain race more than it does the populations in the eastern Great Basin (Table 4). This tendency suggests that involvement of the Rocky Mountain race in the ancestry of Washoe pine, if any, must have been remote in time, and in circumstances that have been obscured by subsequent displacement and migration.

The history of vegetation in the Great Basin region has been substantially revised in the past two decades, and the possibility that ponderosa pine migrated across the Great Basin in late Quaternary time is no longer tenable. This historical revision is based on radiocarbon-dated macrofossils recovered from hundreds of wood-rat (*Neotoma*) middens. The midden record is most complete for the Southwest and parts of the Great Basin (e.g., Thompson and Mead 1982, Van Devender and Spaulding 1979, Wells 1983), but it includes sites as far north as the central Rocky Mts. and southern Columbia Plateau (Wells 1983) and as far west as the Sierra Nevada (Cole 1983).

No aspect of Western vegetation history has been more drastically reinterpreted than the role of ponderosa pine. Fossil pollen data were the principal source of information before the midden work began, and one reconstruction of full-glacial vegetation mapped ponderosa pine forests across the southern Great Basin and throughout much of the Southwest (Martin and Mehringer 1965). This interpretation has been discarded as negative evidence from middens has accumulated. With two possible exceptions, macrofossils of ponderosa pine have not been found in any Pleistocene midden. Needles of either ponderosa or Jeffrey pine were recovered from full- and late-glacial middens in Kings Canyon, on the west side of the southern Sierra Nevada (Cole 1983). In the Southwest, "*Pinus* cf. *ponderosa*" was reported in Pleistocene middens in the Santa Catalina Mts. of southeastern Arizona (Thompson and Van Devender 1980).

The identity of this find has still to be established; ponderosa pine is present in the region today, but so are the closely similar Arizona pine (*P. arizonica* Engelm.) and Apache pine. The absence of ponderosa pine from the Pleistocene record of much of the interior West led Wells (1983) to speculate that in the late Pleistocene the species "must have been far south of its present range, possibly on the southern High Plains (Wells 1970) and in the mountains of the Southwest in and near northern Mexico."

The first postglacial record of ponderosa pine is from the Sheep Range in southern Nevada, where it was present in a midden dated 10,060 B.P. but absent from older middens at the same site (Van Devender and Spaulding 1979). The species was sparsely represented in the eastern Grand Canyon by 9070 B.P., but lacking in middens with dates of 20,630 to 9400 B.P. (Cole 1982). Ponderosa pine grew in Chaco Canyon, northern New Mexico, by 8300 B.P. (J. L. Betancourt, pers. comm., Nov 1982), and in the same region the fossil pollen record (identified to pine species) shows that it reoccupied the crest of the Chuska Mts. by about 5000 to 6000 B.P. (Wright et al. 1973). The species reached the Snake Range of eastern Nevada between 9180 and 6120 B.P. (Thompson 1979, Wells 1983), and the Rocky Mountain race, represented by two-needled fascicles, was in southeastern Wyoming by 4060 B.P. (Wells 1970). It is not known when this race reached its northern and northwestern limits in Montana, but a recent arrival is suggested by this sequence of dates and by the moderately abrupt transition between Rocky Mountain and North Plateau races in central Montana.

The anomalous absence of ponderosa pine from most of the interior West during the latter part of the Pleistocene virtually eliminates the possibility that eastern and western populations have been in contact across the Great Basin during the past 40,000 years—the span of radiocarbon time. And if the last glacial and present interglacial periods are representative of earlier glacial-interglacial sequences, the western Great Basin and the deserts to the south of it may have been a barrier to east-west migration of ponderosa pine for a much longer time, perhaps since the Tertiary.

Evidence of long-term separation between eastern and western segments of ponderosa pine strengthens the alternative hypothesis: that Washoe pine originated from North Plateau ponderosa pine. The close resemblance of Washoe pine to this race was first pointed out by Haller (1965a). At scattered localities in eastern Oregon, he found that occasional trees in predominantly ponderosa stands were within the morphological range of Washoe pine. He speculated that these variable populations might have originated from hybridization of local ponderosa pine with the Rocky Mountain race, and concluded that Washoe pine "could be a segregate from these hybrid populations, maintained in isolation in the south but only partially differentiated in the north." He later found a stand consisting entirely of Washoe pines in south-central British Columbia, growing on Promontory Mountain (Fig. 1) at the relatively high elevation of 1460 m (J. R. Haller, pers. comm., Oct 1981). Haller now believes that Washoe pine originated in the interior of the Pacific Northwest and "migrated southward into California along the Sierra-Cascade crest, probably during one of the glacial phases of the Pleistocene" (J. R. Haller, pers. comm., Sept 1983).

Although the data summarized in Table 4 confirm the overall similarity of Washoe pine and the North Plateau race, they do not support the degree of taxonomic congruence suggested by Haller (1965a). In Wells's (1964) analysis of seedling traits, Washoe pine was unique in its distinctness from the other western populations. It differed significantly from most or all North Plateau provenances in five seedling traits: height at two years, for example, was only 41–65% of seedling height in North Plateau samples. In resin composition, North Plateau populations approach but do not equal Washoe pine's high frequency of trees with high carene and low limonene. In other adult characteristics, Washoe pine was distinct from 43 of 45 North Plateau populations in a combination of needle traits and from 33 of 34 populations in length of seed cones. The exceptions were all upper-elevation populations: two in eastern Oregon (1430 and 1800 m) and one in southeastern British Columbia (1000 m). In limited data on length of pollen cones, all Washoe pines differed from all western ponderosa pines. Seed traits are less discriminating; the only North Plateau populations that differed significantly from Washoe pine were in the eastern part of the region (Idaho, western Montana). None of the North Plateau populations was identical to Washoe pine in an array of characters, although some may have included individuals within Washoe's range of variation.

Haller's observations in the Northwest suggest the following speculative reconstruction: Washoe pine is better adapted than ponderosa pine to the harsh climates that prevailed in the periglacial environments of the interior Northwest, and is most likely to have evolved from an isolated fragment of the North Plateau race during the Wisconsin or an earlier glacial period. Near the end of the Pleistocene, Washoe pine comprised a string of scattered populations extending from eastern Oregon to the Mt. Rose region. It was geographically separated from ponderosa pine, and grew at lower elevations than it does today. In the warmer climate of the early Holocene, it migrated north on to deglaciated terrain in southern British Columbia as the ice receded from its full-glacial limits in northern Washington. In the south it moved to higher elevations where suitable sites were available, and it still occupies some of these sites. Most remnants of Washoe pine in the interior Northwest were replaced or absorbed by the North Plateau race as the latter expanded throughout the region from unknown refugia, but at least one population (Promontory Mountain) may have survived intact on a high-elevation site in British Columbia.

The late Quaternary vegetation history of the interior Northwest provides one piece of evidence supporting this reconstruction. This history is based entirely on fossil pollen, and in most studies of radiocarbon-dated sequences the pollen of *Diploxylon* pines (lodgepole and ponderosa in this region) is lumped (e.g., Mack et al. 1979). An exception is Alley's (1976) analysis of Kelowna Bog, in the Okanagan Valley of southern British Columbia (Fig. 1). A forest dominated by *Diploxylon* pine occupied the site before 8400 B.P., and may have been contemporaneous with ice in the nearby valley bottom. Alley identified the *Diploxylon* pollen as ponderosa pine, using a combination of morphological and size characteristics. Mack et al. (1979) questioned Alley's identification on ecological grounds, because of lodgepole pine's well-documented role as a pioneer on deglaciated terrain in parts of the Northwest. Washoe pollen has not been studied, but if it falls within the range of ponderosa pine in size and morphology, this taxon, rather than ponderosa or lodgepole pines, may have been the early postglacial *Diploxylon* pine in the Okanagan region. The influence of Washoe on ponderosa pine is more marked in southern British Columbia than in any other part of the North Plateau region except eastern Oregon (J. R. Haller, pers. comm., Oct. 1981), and the Kelowna Bog site is only 100 km east of the Washoe pine stand on Promontory Mountain.

According to this reconstruction, Washoe pine is the product of major displacements that occurred during the Pleistocene, and may have originated as recently as within the past 100,000 years. A more direct estimate of its antiquity is based on an immunological investigation of differences in seed proteins (Prager et al. 1976). Washoe pine from Mt. Rose had an antigenic distance of 0.6 from Sierra Nevada ponderosa pine (seed origins from IFG files). This was greater than the distances of Jeffrey and Digger pines from ponderosa (0.4, 0.5), but less than the values for Coulter and Apache pines (0.8, 1.0). Rough estimates of rates of protein evolution based on these and other values suggest that the lineages represented by Washoe and Pacific ponderosa pines separated long before the Pleistocene, possibly as much as 20 million to 30 million years ago. This estimate does not conflict with the hypothesis that Washoe pine is a recent derivative of the North Plateau race, however, if it actually estimates the time of divergence between North Plateau and Pacific races of ponderosa pine.

A recent origin is in better agreement with other attributes of Washoe pine, which are suggestive of a brief and unsuccessful experiment in speciation. This taxon exists as a distinct entity only in a narrow range of forest sites, on which it retains a precarious hold.

And if the low seed production of the Mt. Rose population is characteristic of other populations, Washoe pine is poorly equipped to survive even in these limited habitats. The consistency of poor seed yield from year to year appears to preclude an environmental explanation, such as the production of functionally impaired pollen under harsh climatic conditions. A genetic basis is more likely, but the available data are insufficient to discriminate among alternatives. If low seed production is restricted to Mt. Rose, it may be related to the near-destruction of this population in the 19th century. If the population regenerated from a few closely related seed parents, a high level of inbreeding could account for large reductions in seed yield. An alternative is that Washoe pine has accumulated unusually high frequencies of deleterious genes, many of them acting to produce embryo death. Critical genetic tests (interpopulation crosses, selfing) are lacking, and either genetic explanation is compatible with the increased yield of sound seed when Rocky Mountain ponderosa pine are used as pollen parents.

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THE GENUS *WOLFFIA* (LEMNACEAE) IN CALIFORNIA

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ABSTRACT

Three species of *Wolffia* occur in California: *W. columbiana, W. globosa* and *W. borealis.* Because of their small size and relatively few critical morphological characteristics they have often been misidentified, and confusion has resulted from several different published epithets for each taxon. They are distributed throughout the state in marshes and ponds, often in disjunct clonal populations. All three species have extensive geographical distributions outside the state.

INTRODUCTION

The genus *Wolffia* Horkel (Lemnaceae) includes the smallest and structurally simplest of all angiosperms. Individuals of these free-floating, rootless plants are barely visible without magnification. They occur in dense, homogeneous populations forming a greenish layer at the surface of quiet streams and ponds (Armstrong 1982), and are commonly associated with *Lemna, Spirodela, Wolffiella* and *Azolla.* Of the nine species of *Wolffia* (Landolt 1980a), three appear to occur in California. The primary objective of this paper is to clarify exactly which species occur in California and to elucidate their distribution within the state.

Several taxonomic studies of the Lemnaceae have been published during the past three decades, and there is considerable disagreement among California and other authors over which species occur in California (Mason 1957; Landolt 1957, 1980a, 1980b; Daubs 1965; den Hartog and van der Plas 1970; Clark 1979). The occurrence of *Wolffia columbiana* Karst. is agreed upon by all the authorities cited above. *Wolffia globosa* (Roxb.) Hartog & Plas was listed as *W. cylindracea* Hegelm. by Galen Smith in Mason (1957) and *W. punctata* Griseb. by Landolt (1957). Daubs (1965) considered *W. cylindracea* synonymous with *W. arrhiza* (L.) Horkel ex Wimmer, a European species that does not occur in North America. Probably the greatest confusion concerns the correct usage of *W. punctata.* According to Landolt (1980a), the original *W. punctata* described by Grisebach in 1864, and *W. papulifera* Thompson described in 1898, are synonymous with *W. brasiliensis* Weddell, described earlier in 1849. *Wolffia brasiliensis* occurs throughout the southeastern

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United States and in Central and South America, but does not occur in California. Vegetative fronds of this species are distinguished by a prominent central papule on the dorsal surface. The *W. punctata* referred to by most American authorities is actually *W. borealis* (Engelm.) Landolt, a North American species closely related to *W. brasiliensis.* It was originally listed as *W. brasiliensis* var. *borealis* Engelm. ex Hegelmaier (1868) and later changed to *W. borealis* (Landolt and Wildi 1977).

Some confusion between *Wolffia brasiliensis* and its complex of synonyms may be due to early publications of Weddell (1849), Hegelmaier (1868) and Thompson (1898), which do not show the prominent central papule. According to Landolt (pers. comm., 29 Dec 1983) the type collection of *W. brasiliensis* from Mato Grosso, Brazil contains flowering and fruiting fronds that do not show a papule. The few vegetative fronds in the collection also do not show a very prominent papule. The other specimens Hegelmaier saw for his monograph, in addition to the type collection, originated from the northern United States and belong to *W. borealis.* Without the dorsal papule, fronds of *W. brasiliensis* easily can be mistaken for *W. borealis* or one of its synonyms, and these errors have been perpetuated in the literature for more than a century.

METHODS AND MATERIALS

Herbarium specimens of *Wolffia* species in California were compared and previous collection sites were revisited during the summer and fall of 1980–83. New collections were made, including several range extensions. Since the fronds become barely recognizable after pressing, photomicrographs of living plants were included on herbarium sheets. For positive identification, living samples of all collections were compared with clonal cultures from the laboratory of Dr. E. Landolt, Geobotanical Institute, Zurich.

RESULTS AND DISCUSSION

Species of *Wolffia* are often difficult to separate in a taxonomic key. They have relatively few critical morphological characteristics and are rarely found with flowers or fruits. Often there is overlap in size and shape of fronds. Ideally, it is best to compare species floating in a shallow container, preferably through a dissecting microscope (Figs. 1, 2). The California species of *Wolffia* may be identified by use of the following key:

A. Fronds ovoid to ellipsoid with flattened dorsal surface, apex ± pointed (acute) and slightly upturned, floating with entire dorsal surface above water; greatest width of frond near water surface; brownish pigment cells present (visible only on dead fronds . . . . 1. *W. borealis* (Engelm.) Landolt

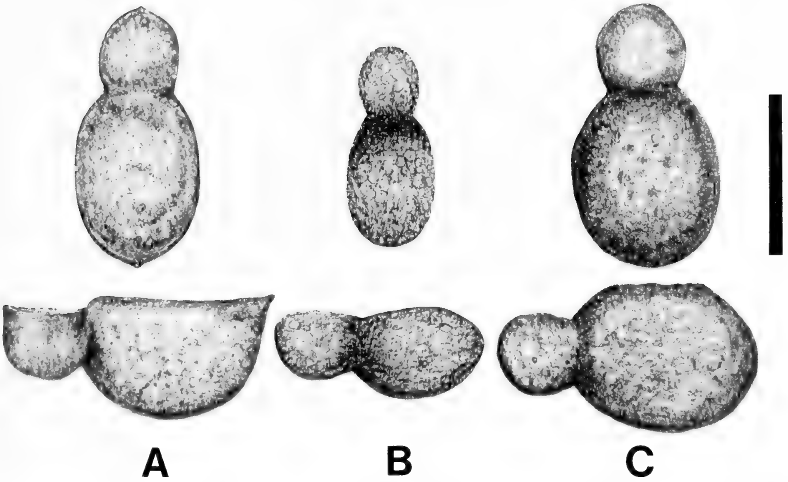

FIG. 1. Dorsal and lateral views of *Wolffia* species. A. *W. borealis*. B. *W. globosa*. C. *W. columbiana*. Scale bar is 1 mm.

AA. Fronds ovoid or globoid (often ellipsoid or cylindrical in *W. globosa*), apex of fronds rounded, floating with only the central portion of dorsal surface above water; submerged body of frond wider than dorsal surface; brown pigment cells lacking.
  B. Fronds 0.8 to 1.3 mm long; dorsal surface rounded or slightly flattened, minutely roughened by enlarged cells . . . . 2. *W. columbiana* Karst.
  BB. Fronds 0.4 to 0.9 mm long; dorsal surface flattened and minutely roughened by a few enlarged cells . . . . 3. *W. globosa* (Roxb.) Hartog & Plas

When fronds of all three species are viewed from above (Fig. 1), *Wolffia borealis* appears darker green with a pointed apex. Fronds of *W. columbiana* and *W. globosa* are distinctly light, transparent green with a rounded apex. Fronds of *W. globosa,* rivaled in minuteness only by the Australian species *W. angusta* Landolt, are smaller and more cylindrical (narrow) than in *W. columbiana.* With substage lighting, the densely pigmented fronds of *W. borealis* appear black. However, in photographs with substage lighting and lighting from above, the transparent fronds of *W. columbiana* and *W. globosa* often appear darker than those of *W. borealis* (Fig. 2).

With the exception of *W. borealis,* which has brownish pigment cells, dried, pressed specimens are often difficult to identify. Ideally, herbarium sheets should include detailed notes on shape and size

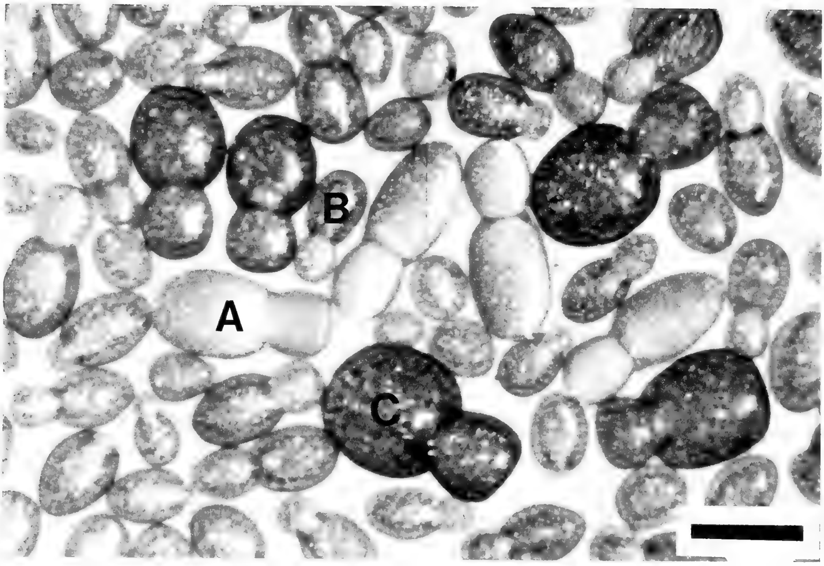

FIG. 2. Dorsal view of *Wolffia* species showing relative size and shape of fronds. A. *W. borealis*. B. *W. globosa*. C. *W. columbiana*. Scale bar is 1 mm.

of fronds, and preferably photomicrographs or references to duplicate specimens preserved in fluid. Plants may remain alive in aerated containers for several days, but should be placed in a preservative for long-term storage. Fronds retain their original shapes in FAA or ethanol. Formalin is not advisable because the plants become very fragile (van der Plas 1971).

DISTRIBUTION

Stations for *Wolffia* known to the authors in California are shown in Fig. 3. Because of their small size, generally 0.6 to 1.2 mm long, they are easily overlooked. Diligent field work could probably fill many gaps in the distribution patterns of all three species. Collections of *Wolffia* in California are cited by Mason (1957), Landolt (1957), Daubs (1965), Landolt and Urbanska-Worytkiewicz (1980) and Armstrong (1981a, 1981b). In addition, Urbanska-Worytkiewicz (1980) reports chromosome numbers for all species, including several polyploid populations in California.

Wolffia columbiana occurs in San Diego County (Lake Hodges and San Dieguito River) and in San Luis Obispo County (Oso Flaco Lake and perhaps other lakes and ponds of the Nipomo Mesa area, and near Oceano). It also occurs sparingly in Fresno County (sloughs along the San Joaquin River) and in Stanislaus County (west of Modesto).

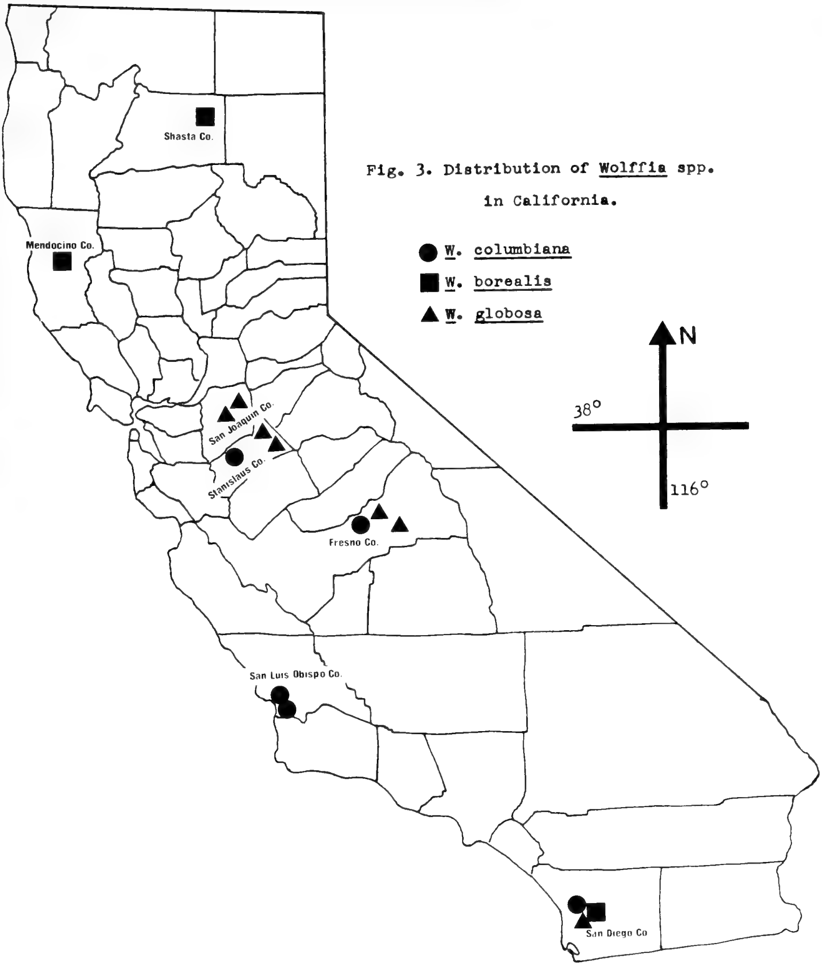

FIG. 3. Map showing the distribution of *Wolffia* species in California.

California: FRESNO CO.: San Joaquin River, *Nobs and Smith 992a* (ARIZ, MO, WIS). SAN DIEGO CO.: pond s. of Lake Hodges, *Armstrong 1195* (RSA, SD); San Dieguito River, *Armstrong 1124, 1167, 1176, 1183* (RSA, SD). SAN LUIS OBISPO CO.: Dune Lake, *Mason 12864* (MICH, RM, UC); near Oceano, *Nobs and Smith 676* (UC); Oso Flaco Lake, *Armstrong 1133* (RSA, SD), *Landolt 6859, 8143* (ZT), *Piehl 63781* (RSA). STANISLAUS CO.: w. of Modesto, *Smith 2660* (UC).

Wolffia globosa is apparently confined to ditches and ponds of the extreme northern and central San Joaquin Valley, and in sloughs along rivers draining the Sierra Nevada. It occurs in northeastern

San Joaquin County (southwest of Ione), Stanislaus County (Knights Ferry and La Grange), and Fresno County (northwest of Clovis and near Minkler). It was recently collected in a small pond (south of Lake Hodges) in San Diego County (see Noteworthy Collections, p. 191).

California: FRESNO CO.: Minkler, *Landolt* (ZT); San Joaquin River, *Armstrong 1135* (RSA, SD), *Landolt 6724, 8152* (ZT), *Nobs and Smith 992a* (ARIZ, MO). SAN DIEGO CO.: s. of Lake Hodges, *Armstrong 1196, 1197* (RSA, SD). SAN JOAQUIN CO.: sw. of Ione, *Russell and Swader s.n.* (RSA); sw. of Lockeford, *Landolt 8180* (ZT). STANISLAUS CO.: Knights Ferry, *Landolt 6592* (ZT); La Grange, *Landolt* (ZT).

Wolffia borealis occurs at each end of the state in remarkably disjunct populations, including Shasta County (Fall River Mills) and San Diego County (Lake Hodges and San Dieguito River). A third site was recently discovered in Mendocino County by D. Richards (Humboldt State University), who plans to publish a note on it.

California: MENDOCINO CO.: s. of Willits, *Richards 104* (HSU, RSA, SD). SAN DIEGO CO.: Lake Hodges, *Armstrong 1123* (SD); San Dieguito River, *Armstrong 1124, 1167, 1183* (RSA, SD). SHASTA CO.: Fall River Mills, *Mason 14629* (MO, RSA, UC).

These species of *Wolffia* have rather extensive distributions outside the state and are undoubtedly much more abundant than data from collection sites indicate. Fronds and seeds of *Wolffia* and other members of the Lemnaceae may be dispersed over short distances by waterfowl (Jacobs 1947, van der Plas 1971, Wolek 1981). According to Thompson (1896), fronds of *Wolffiella lingulata* (Hegelm.) Hegelm. may have gradually been carried to California from central Mexico by migratory birds. Although survival of vegetative fronds of *Wolffia* for several hours out of water is unlikely due to desiccation, some could possibly survive in clods of mud and debris or under feathers where they are protected from the wind. At 20–21°C and relative humidity 55–60%, a mass of *W. arrhiza* weighing 1.0 g can survive almost 6 hours of desiccation (Godziemba-Czyz 1970). Under similar conditions single individuals of *W. arrhiza* can survive only 20–30 minutes of desiccation (Wolek 1981). Disseminules may also be transported by river currents, flood waters, and possibly by man when lakes are stocked with fish and in the shipment of aquarium cultures. North American species also produce starch-filled, dormant fronds called turions that sink to the bottom and survive cold winters (Landolt 1981).

Wolffia columbiana occurs in the Pacific states from southern California to Oregon and throughout the eastern United States and Ontario, Canada, extending sporadically south in Mexico, El Salvador, Guatemala, Colombia, Venezuela, Uruguay and Argentina

(Daubs 1965; Hitchcock, Cronquist and Ownbey 1969; Landolt and Urbanska-Worytkiewicz 1980). *Wolffia borealis* is essentially a boreal species of the Pacific, midwestern, and eastern United States and southern Canada (Landolt and Urbanska-Worytkiewicz 1980). It is also reported (as *W. punctata*) from eastern Texas, Georgia, and southeastern United States (Thorne 1956, Correll and Correll 1975, Clark 1979). According to Landolt (pers. comm. 10 May 1983), these southern populations may actually be of *W. brasiliensis.*

Wolffia globosa has the most widespread distribution of all, although restricted in North America to the Central Valley of California, San Diego County and to Southern Florida. A recent collection in Pinellas Co. (*Armstrong 1182*) may be the first record of this species in Florida. It also occurs in southern and eastern Africa, Sri Lanka, India, eastern and southeastern Asia, Japan, Indonesia, Malaysia, Philippines, and the Hawaiian Islands (Landolt and Urbanska-Worytkiewicz 1980). Records of *W. arrhiza* in southeast Asia are probably *W. globosa,* a species that may occur in Australia (van der Plas 1971). Landolt (1980a) lists only two species from Australia, *W. angusta* Landolt and *W. australiana* (Benth.) Hartog and Plas. It is possible that some collections from Australia labeled *W. globosa* are actually the closely related *W. angusta.* The occurrence of *W. globosa* in the Central Valley of California is perplexing. According to Landolt (1981) it may not be indigenous to North America. Possibly, like other aquatic "weeds" from Asia, *W. globosa* first became naturalized in rice fields in the Central Valley. Some of these Asian introductions are *Eriocaulon cinereum* R. Br., *Najas graminea* Raff.-Delile, *Scirpus mucronatus* L., *S. tuberosus* Desf., *Eleocharis atropurpurea* (Retz.) Kunth., *Cyperus difformis* L., *Elatine ambigua* Wight, and *Monochoria vaginalis* (Burm. f.) Presl.

CONCLUSIONS

Vegetative propagation predominates in the Lemnaceae, and different geographical populations of the same species may differ in general appearance (Landolt 1957). Under 10–20× magnification the California species of *Wolffia* are sufficiently different from each other to be distinguished on the basis of size and shape of their fronds. Brown pigment cells in the epidermis of *W. borealis* are clearly evident in dried specimens. Although soaking dried specimens in water is useful for identification of *Lemna* species, it is inadequate for *Wolffia* because the fronds generally remain flat and deformed. Ideally, it is perhaps best to examine living plants or fronds preserved in FAA or ethanol. Flowers and fruits are probably too infrequently observed to be of much value in identifying species of *Wolffia.* Proterogyny has been reported for most species (den

Hartog and van der Plas 1970) and this also appears to be the case with *W. borealis* in San Diego County (Armstrong 1982).

As in other members of the Lemnaceae, there may be considerable ecophysiological and cytogenetic variation among different species of *Wolffia,* and among different geographical populations of the same species (Landolt 1957, 1981, 1982; Hillman 1961; Landolt and Wildi 1977; Urbanska-Worytkiewicz 1980). Urbanska-Worytkiewicz (1980) reported a tetraploid number of 40 for *W. columbiana* from Oso Flaco Lake, and polyploid numbers of 30 and 60 for populations of *W. globosa* from the San Joaquin Valley. Future cytological and physiological studies may provide a better understanding of the ecological requirements and distribution of *Wolffia* species in California. Additional studies on the distribution of all three species along waterfowl migration routes and the survival of fronds under conditions of desiccation may elucidate the possible role of waterfowl in exozoic dispersal of *Wolffia* species in California.

ACKNOWLEDGMENTS

The authors are especially grateful for the invaluable contributions and axenic cultures provided by Dr. E. Landolt of the Geobotanical Institute, Zurich. We also wish to thank the staff of the herbarium at the University of California, Berkeley for their kind assistance and Dr. Howard L. Clark of the University of Georgia, Institute of Ecology for his helpful review of the manuscript. The illustration of the three species of *Wolffia* was prepared by F. E. Collins of the Instructional Resources Department, Palomar College.

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A NEW SPECIES OF *JATROPHA* (EUPHORBIACEAE) FROM COASTAL JALISCO, MEXICO

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ABSTRACT

Jatropha bullockii from Jalisco, México, is described and illustrated and its relationships are discussed. The species is assigned to sect. *Platyphyllae* and appears most closely related to *J. moranii.*

Tropical deciduous forest dominates the Pacific slope of Mesoamerica. Knowledge of the flora from locally intensive studies is still sparse, but a florula is in preparation for a 1600-ha reserve in coastal Jalisco, the Estación de Biología Chamela. In the course of this project it has become clear that Leguminosae and Euphorbiaceae are the most species-rich families in the area. Particularly in the latter several species new to science have been found (e.g., Pérez Jiménez 1982), one of which is described here.

Jatropha bullockii E. J. Lott, sp. nov.

Sect. *Platyphyllae*; a *J. moranii* foliis eglandulosis glabris, corolla intus pilosa, petalis albis vel roseis, staminibus 8 (nec 10) differt (Fig. 1).

Shrub 0.5–3 m tall, branches erect to sprawling, young branches flexible. Bark pale grayish-brown, fissured, thin, easily peeled (not exfoliating), latex clear, becoming reddish, bright red on drying, younger branches and growing tips densely white-puberulent with straight hairs 0.1–0.2 mm long, older branches glabrescent, short shoots sometimes present. Leaves alternate, broadly obovate to usually palmately 3–5-lobed, the lobes and apex occasionally terminating in a tooth ca. 0.2 mm long, margins entire (glands lacking), blades shiny above, paler beneath, glabrous or with a few scattered hairs on midvein near base on upper surface, covered with a fine whitish cuticle when very young, 2–4.5 cm long, 2–4 cm wide, palmatinerved with 5 main veins, the 2 laterals sometimes less prominent, base cordate, apex acute; petioles slender, 1–4 cm long, often bearing remnants of a transparent cuticular covering, especially near the base, stipules absent, axils villous with reddish hairs 0.3–0.5 mm long. Plants monoecious; inflorescence mixed, subterminal, lateral, or on short shoots, very reduced, subsessile to pe-

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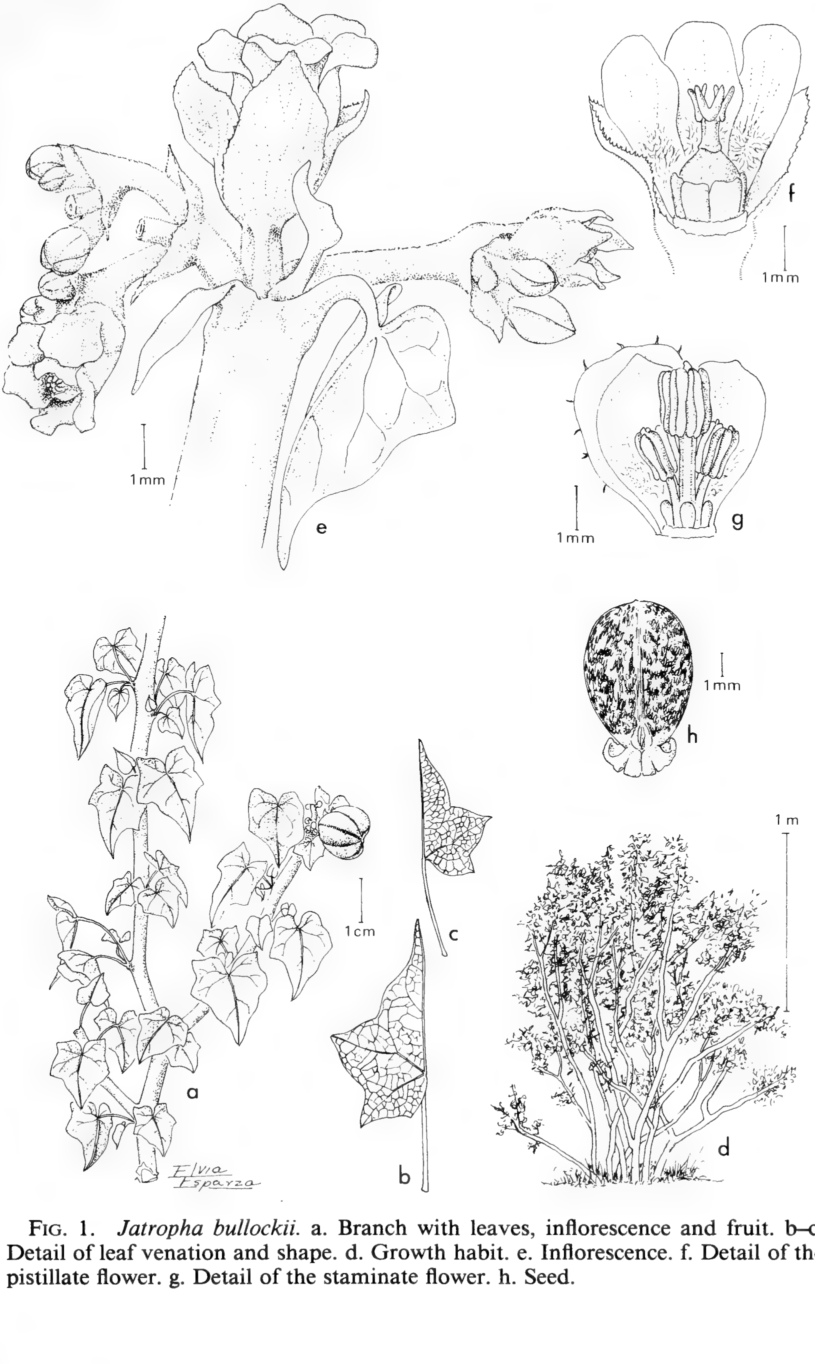

FIG. 1. *Jatropha bullockii.* a. Branch with leaves, inflorescence and fruit. b–c. Detail of leaf venation and shape. d. Growth habit. e. Inflorescence. f. Detail of the pistillate flower. g. Detail of the staminate flower. h. Seed.

dunculate, peduncles 1–20 mm long, densely white-puberulent, bracts of the inflorescence (1–)2–8 mm long, 1–1.5 mm wide, lance-linear to lance-ovate. Staminate flowers: sessile in compound dichasia; bracts lance-ovate, ciliate (not glandular), green or reddish, acute to acuminate, 0.8–2 mm long, 0.5–0.8 mm wide; calyx 1.5–2 mm long, often reddish, lobes 5, rounded, ciliate, 1–1.3 mm long, 1–1.5 mm wide, imbricate; corolla cream-white to pink, campanulate, 3–3.5 mm long, lobes (1.5–)2–2.5 mm long, 1–1.3 mm wide, recurved at anthesis, glabrous without, tube densely white-pilose within; disc glands 5, reddish, oblong, smooth, glabrous, 0.8–1 mm long, very conspicuous; stamens 8, monadelphous, biseriate, total staminal column ca. 3 mm tall, outer (lower) 5 stamens with filaments free ca. ½ their length, free portion 0.6 mm long, inner (upper) 3 stamens with filaments fused, 1.3 mm long, anthers 0.7–0.8 mm long, glandular-mucronate at tip of connective. Pistillate flowers: larger than staminate, single and terminal but much surpassed by male branches; pedicel stout, 0.5–2 mm long, 1.5–2 mm wide, to 8 mm long in fruit, densely white-puberulent; calyx 3–5 mm long, glabrous, more or less foliaceous, lobes 5, imbricate, ovate-lanceolate, acute, erect, green to reddish, 2–4(–4.5) mm long, 2 mm wide, ciliate; corolla campanulate, cream to pink, 3.5–4.3 mm long, 2.5 mm broad at base, fused ca. ½ its length, lobes 1.8–2.5 mm long, 2 mm wide, recurved at anthesis, glabrous without, pilose within proximally; disc lobes 5, green to purplish-red, rectangular, 0.5 mm long, 0.5–0.8 mm wide; ovary trilocular, conspicuously 3-lobate, 1.2 mm tall, smooth, glabrous; styles 3, fused, 0.5–0.6 mm long, bifid, glabrous, stigma lobes 0.7 mm long, narrow, glabrous. Capsule 3-locular, yellow-brown, 3-lobed, abruptly angled when immature, the lobes somewhat rounded on drying, 9 mm long, 9 mm broad, verruculose. Seeds 3, golden to brown with reddish-brown mottling, oblong-elliptic, 8 mm long, 5–6 mm broad, caruncle yellow, lacerate, 2–3 mm long, 2.4–4 mm wide.

TYPE: Mexico. JALISCO. Mpio. La Huerta: Estación de Biología Chamela (UNAM), 19°30′N, 105°03′W, Cerro El Colorado, El Mirador, Selva Baja Caducifolia con *Plumeria rubra, Amphipterygium, Bursera excelsa, Comocladia engleriana, Manihot chlorosticta, Hechtia, Agave,* etc., en suelos anaranjados derivados de roca metamórfica, 12 Sep 1983, *E. J. Lott 1863* (Holotype: MEXU; isotypes: CAS, ENCB, F, MICH, MO, US).

PARATYPES: Mexico. JALISCO. Mpio. La Huerta: same locality as type, 12 Jun 1982, *S. H. Bullock 1174 and 1175* (MEXU); 5 Dec 1982, *E. J. Lott and T. Wendt 1621* (MEXU); 6 Aug 1982, *E. J. Lott 1789* (MEXU); 1 Jul 1982, *E. J. Lott and O. Téllez V. 1140* (MEXU); 29 May 1982, *E. J. Lott 1088* (MEXU); 14 Dec 1976, *J. A. Solís Magallanes 414* (MEXU); Cerro de la Punta de la Virgen, Rancho El Milagro, en acantilado, 29 Oct 1971, *L. A. Pérez J. 532*

(MEXU); Rancho El Paraíso, a ca. 4 km al se. de la Estación de Biología Chamela, 24 Aug 1982, *E. J. Lott and J. A. Solís Magallanes 1219* (MEXU); same locality, 28 Oct 1981, *E. J. Lott and J. A. Solís Magallanes 646.*

Range. Known only from the Estación de Biología Chamela and surrounding area.

Habitat. On rocky prominences from near sea level to ca. 150–200 m, in tropical deciduous forest with *Thevetia ovata, Euphorbia schlechtendalii, Gossypium aridum, Croton* spp., and the species mentioned in the type citation.

Jatropha bullockii belongs to sect. *Platyphyllae* Dehgan & Webster [Subgenus *Curcas* (Adans.) Pax] by virtue of its 3–5-lobed petiolate leaves, relatively large, foliaceous calyx lobes in the female flower, monoecious inflorescences, 3 bifid stigmas, and trilocular fruits. It lacks the typically either glandular-margined, peltate, or cordate and tomentulose leaves of the section, although in some members of the section the leaves are glandular only in the seedling (Dehgan and Webster 1979). The seedlings are as yet unknown in *J. bullockii.* It further differs in its 8 stamens and ecarinate mature capsules, although the immature capsules are somewhat abruptly angled.

Of the species of sect. *Platyphyllae* whose characteristics are well known, *J. bullockii* seems most closely related to *J. moranii* Dehgan & Webster from the Cape region of Baja California. *Jatropha bullockii* differs from *J. moranii* in its larger habit, eglandular leaves with only occasional scattered hairs near the base, corolla tube pilose within, pale pink petals, and 8 stamens. The two species have in common estipulate, 5-lobate leaves, eglandular bracts, and entire, eglandular sepals that are more or less foliaceous in the female flower (Dehgan and Webster 1978).

Another species apparently related to *J. bullockii* is *J. fremontioides* Standl., a poorly-known species of the Isthmus of Tehuantepec. Dehgan and Webster (1979) placed the latter in sect. *Neopauciflorae,* characterized by bilocular fruits, short or stout petioles, and conspicuous, dissected stipules. However, according to the type description (Standley 1940), *J. fremontioides* has trilocular fruits, as do the collections of this species at MEXU (*Matuda 2203, R. M. King 212*). The two species have in common petiolate, eglandular leaves, stipules absent or not evident, monoecious, much-reduced inflorescences with sessile staminate flowers, corolla pilose within, biseriate stamens and trilocular fruits. *Jatropha bullockii* differs from *J. fremontioides* in its glabrous, more acute leaves, longer petioles, and 8 stamens. Dehgan and Webster (1979, p. 20) note that *J. fremontioides* "is monoecious, but inflorescences occur as short, subsessile groups of flowers in the leaf axils with no clear distinction between the exact location of pistillate or staminate flowers." Because the inflorescence structure is important in determining relationships in *Jatropha,* I hesitate to state that *J. bullockii* is more closely related to *J. fremontioides* until better material of the latter is available. *Jatropha fremontioides* might best be accommodated in sect. *Platyphyllae* with *J. bullockii* and *J. moranii* upon further study.

It is a pleasure to dedicate this new species to Dr. Stephen H. Bullock, research scientist at Estación de Biología Chamela, for his contributions toward the understanding of the flora of Chamela, particularly its plant reproductive biology.

ACKNOWLEDGMENTS

I thank Elvia Esparza for the illustrations, and D. H. Lorence, T. Wendt, and F. Chiang for their critical comments.

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NOTES AND NEWS

OBSERVATIONS OF HAUSTORIA AND HOST PREFERENCE IN *Cordylanthus maritimus* SUBSP. *maritimus* (SCROPHULARIACEAE) AT MUGU LAGOON.—The genus *Cordylanthus* (tribe Euphrasieae) includes some 35 species indigenous to western North America. One species in this genus, *Cordylanthus maritimus,* has been divided into three subspecies on the basis of geographical and, to a lesser extent, morphological characteristics. The subspecies of haustorial study in this note and the southernmost in distribution is *Cordylanthus maritimus* subsp. *maritimus,* salt marsh bird's beak. At one time this plant was a common component of coastal salt marshes in California but is currently found in only five locations from Santa Barbara County southward to Baja. This subspecies can be found April through October in dense, nearly monotypic stands within the salt marsh vegetation in the western arm of Mugu Lagoon (Ventura County, California).

The ability of plants within the genus *Cordylanthus* to continue to grow and flower during hot, dry summer months warranted scientific speculation as to the parasitic potential of the genus. Piehl first verified parasitism in *Cordylanthus* in 1966 and Chuang and Heckard found haustorial connections between *Cordylanthus maritimus* and *Helianthus annuus* in 1971. No previous haustorial work has been done with *Cordylanthus maritimus* subsp. *maritimus.* It was therefore postulated that this subspecies might also produce haustoria to draw water and/or nutrients from surrounding marsh plants through root associations. Although these connections were shown to be non-essential for *Cordylanthus* species in greenhouse culture (Chuang and Heckard, Amer. J. Bot. 58:218–228. 1971), natural environmental conditions found in salt marshes, such as low soil nutrient availability and soil moisture stress (either through elevated soil salinities or high moisture tension), could possibly "justify" the need for these haustorial connections.

At Mugu Lagoon, salt marsh bird's beak can be found growing with a variety of plant species. Commonly associated species include: *Salicornia virginica, Jaumea carnosa, Frankenia grandifolia, Limonium californica, Cressa truxillensis,* and *Distichlis spicata.* Host preference between *Cordylanthus maritimus* and *Distichlis spicata* has been suggested by Chuang and Heckard (1971) and at Mugu Lagoon, *Distichlis spicata* is the only species always associated with salt marsh bird's beak. Less common associates include: *Lasthenia chrysostoma, Monanthochloe littoralis, Cuscuta salina, Scirpus robustus, Juncus acutus, Typha latifolia, Atriplex patula hastata, Triglochin concinnum* and *Polypogon monspeliensis.*

Hosts were investigated in both the laboratory and field to determine the extent of host species specificity in salt marsh bird's beak. For the laboratory studies, host plants were collected in the field for establishment in clay pots. Salt marsh bird's beak seeds (collected the previous year at Mugu Lagoon) were planted with these hosts once they were growing successfully. The salt marsh bird's beak seedlings were thinned to three per host pot upon germination. The hosts and salt marsh bird's beak were grown together until the senescence of the salt marsh bird's beak. The soils and plants were then carefully examined for haustorial connections. In field studies, potential host plants and adjacent salt marsh bird's beak were removed with their root zones intact and the soils and plants examined for haustorial connections. Salt marsh bird's beak was also grown by itself in pots to determine whether or not the subspecies is an obligate or facultative parasite.

Salt marsh bird's beak was found to be a facultative parasite, capable of growing with or without haustorial connections to other plant species. In the laboratory studies, small lateral haustorial connections were verified between salt marsh bird's beak and *Distichlis spicata, Polypogon monspeliensis, Salicornia virginica, Jaumea carnosa* and *Helianthus annuus.* Field connections were verified with *Distichlis spicata, Frankenia grandifolia, Scirpus robustus* and *Typha latifolia.* Salt marsh bird's beak also formed haustoria with members of its own subspecies in the lab and field indicating that it

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is capable of intraspecific as well as interspecific parasitism. No haustorial connections were found with *Frankenia grandifolia* in the lab or with *Triglochin concinnum, Monanthochloe littoralis* or *Cressa truxillensis* in the field despite association with all four species in the field. The fact that *Helianthus annuus* was also an effective host indicates a lack of host specificity. The possibility exists therefore that salt marsh bird's beak distribution is a function of a strong habitat preference rather than a host preference in *Cordylanthus maritimus* subsp. *maritimus* as is indicated with *Cordylanthus maritimus* (Chuang and Heckard 1971).

There was no observable increase in vigor in the laboratory specimens associated with hosts and therefore the type of benefit to salt marsh bird's beak from these hosts is still uncertain. Chlorophyll is present in salt marsh bird's beak as is often the case in parasites that utilize many small, lateral (often ephemeral) haustoria. These parasites require a certain degree of photosynthetic efficiency to carry them through early development and search for hosts. The presence of chlorophyll may also help to bridge periods without hosts (Kuijt, *The Biology of Parasitic Flowering Plants,* Univ. California Press, 1969).

Parasitism undoubtedly permits salt marsh bird's beak to flourish in the hot, dry conditions of summer when most other annuals have completed their life cycles. This mechanism has likely been of considerable importance in successfully equipping *Cordylanthus maritimus* subsp. *maritimus* for survival in western North America.— JULIE M. VANDERWIER and JUDITH C. NEWMAN, Natural Resources Management Office, Pacific Missile Test Center, Point Mugu, CA 93042. (Received 28 Oct 1983; accepted 12 Jan 1984.)

STORAGE OF *Sisyrinchium* (IRIDACEAE) POLLEN.—An important aspect of biosystematic research is interspecific hybridization. In my study of *Sisyrinchium* sect. *Bermudiana* (Iridaceae), plants were grown under nearly identical conditions but it was impossible to promote simultaneous flowering. It was necessary, then, to store pollen until stigmas became receptive. Deep-freezing has been used successfully for long-term storage of crop pollen (Nath and Anderson, Cryobiology 12:81–83. 1975; Barnabas and Rajke, Ann. Bot. 48:861–864. 1981) and studies in the Orchidaceae and a few other taxa (Meeyot and Kamemoto, Amer. Orchid Soc. Bull. 38:388–393. 1969; Löve and Löve, Plant Chromosomes. 1975) have shown that binucleate pollen can remain viable for several months if stored at 0–8°C with a desiccant. Although *Sisyrinchium* and other members of Iridaceae have binucleate pollen (Brewbaker, Amer. J. Bot. 54:1069–1083. 1967), such viability data were unavailable for this genus.

My objective in this study was to ascertain the length of time *Sisyrinchium* pollen (binucleate) would remain viable, when stored at 5°C.

Dehiscing anthers were dissected from numerous flowers of *Sisyrinchium montanum* E. L. Greene, placed in screw-capped glass vials, and stored at 5°C. Pollen from anthers stored for 2, 10, 15, 30, and 60 days, and from newly dehiscent anthers of *S. montanum,* were placed on sterile media consisting of 2% agar and 15% sucrose (Rodionenko and Burova, Bot. Zhurn. [Moscow and Leningrad] 55:300–302. 1970) and incubated at 25°C for 24 h. The samples were then examined with a light microscope and the number of pollen tubes was recorded. Three trials were made from each storage treatment, and the fresh pollen was used as a control for all treatments.

TABLE 1. VIABILITY OF STORED POLLEN OF *Sisyrinchium* AS ASCERTAINED BY GERMINATION TESTS. *600 grains examined per sample (200/trial).

Number of days in storage at 5°C	Total number of pollen grains germinating*	Mean germination
0	579	96.5% (96–97.5)
2	579	96.5% (95–97.5)
10	581	96.8% (95–99)
15	513	85.5% (84–87.5)
30	440	73.3% (70–76)
60	264	44.0% (38–49)

Pollen remained strongly viable through 10 days; thereafter, germination decreased with continued storage (Table 1). For short-term pollen storage, a desiccant is not necessary.—ANITA F. CHOLEWA, Department of Biological Science, University of Idaho, Moscow 83843. (Received 21 Oct 1983; accepted 14 Feb 1984.)

INFLUENCE OF SLOPE ASPECT ON POSTFIRE REPRODUCTION OF *Encelia farinosa* (ASTERACEAE).—Chaparral shrub species regenerate rapidly after fire by vegetative sprouting from root crowns, or germinating from dormant seed (Hanes, Ecol. Monogr. 41:27–52. 1971; Keeley and Zedler, Amer. Midl. Naturalist 99:142–161. 1978; Howe and Carothers, S. Calif. Acad. Sci. 79:5–13. 1980; Keeley and Keeley, Amer. J. Bot. 68:524–530. 1981). The proportion of sprouts and seedlings produced by the different sprouting species following fire varies (Keeley and Zedler 1978; Keeley and Keeley 1981; Westman et al., *in* Margaris and Mooney, eds., Components of productivity of Mediterranean-climate regions. 1981). Hanes (1971) found that the amount of sprouting following fire varies with slope aspect. The percentage of sprouts was greater on coastal north-facing slopes than on the other coastal exposures due to differences in irradiation and available moisture. Also, the fraction of shrubs derived from seedlings was lowest on the coastal north-facing slopes. Seedlings appear to have an advantage on xeric south-facing slopes when compared with sprouters. Hanes (1971) reported sprouting in 43% of southern California chaparral species but did not observe any for *Encelia farinosa.*

Encelia farinosa, which is very abundant on dry slopes of creosote bush scrub and coastal sage scrub communities of southern California (Munz, A flora of southern California. 1974), regenerates following fire as a sprouter (Westman et al. 1981). Little is known about the fire response of *E. farinosa.* The purpose of this project was to locate an area in which *E. farinosa* occurred and to study the regeneration of this species with respect to slope aspect. It was anticipated that there would be a significant difference in the amount of sprouts and seedlings of *E. farinosa* on different slope exposures following fire, particularly between the mesic north-facing slopes and the more xeric south-facing slopes.

Approximately 15 ha of coastal sage scrub located in the hills south of Loma Linda, California burned in a wildfire on 15 June 1981. Species of the burned plants could be identified from standing dead stems. Nearly all of the *E. farinosa* growing in this

TABLE 1. MEAN POINT TO PLANT DISTANCE ($\bar{d}$ IN METERS) AND MEAN DENSITY OF PREBURN AND POSTBURN *Encelia farinosa* ON DIFFERENT SLOPE ASPECTS IN LOMA LINDA, CALIFORNIA.

	$\bar{d}$		Density (no. /ha)	
Slope aspect	Preburn	Postburn (1.5 yr)	Preburn	Postburn (1.5 yr)
North	6.49 ± 5.25	32.38 ± 7.87	237	<10
South	2.03 ± 1.24	2.28 ± 1.76	2422	1924
East	2.01 ± 1.30	1.46 ± 1.21	2456	4695
West	2.15 ± 1.46	1.50 ± 1.03	2171	4444

area was topkilled. Pure stands of *E. farinosa* were situated on exposures facing east, west, and south.

Sampling was begun in October 1981 using the point-quarter method (Cox, Laboratory manual of general ecology. 1980). Different 30° slope exposures were sampled within the burn area to obtain the preburn density of *E. farinosa.* Dead plants were measured and the percentage of these that had sprouted from root crowns was noted. Comparisons were then made for the amount of sprouting *E. farinosa* between the different slope aspects. Eleven, 13, 46, and 18 points were measured on the north, south, east, and west exposures respectively, from transects running perpendicular to slope aspect. Several slopes of the same aspect were added together to obtain a total for that direction. East-facing slopes predominated in this area, so there is an unequally large number of points taken on the eastern exposure. No seedlings of *E. farinosa* were present at this time.

In February 1983, point-quarter sampling was repeated on the same slopes measured in October 1981 to obtain the density of regenerated *E. farinosa* from both sprouts and one-year-old seedlings. On each of the four slope aspects 30 points were measured. Due to the extremely low density on north-facing slopes, when plants were not encountered within 35 m from the point, a ">35 meters" was recorded. Statistical comparisons were made between sprouting and seedling populations of north, south, east, and west exposures using the chi-square contingency analysis (Cox 1980).

The preburn *Encelia* densities for south, east, and west exposures were virtually identical, but density was extremely low on the preburn north-facing slopes (Table 1). *Salvia mellifera* was most common on this slope face. Postburn *Encelia* densities for east and west exposures show a 91% and 105% increase when compared with preburn densities for the same aspects (Table 1). The postburn south-facing slopes had recovered 79% of the preburn *Encelia* density. The greatest reduction in postburn *Encelia* density was seen on the north-facing slopes where only 4% of the preburn plants had recovered.

The percentage of topkilled *E. farinosa* that sprouted from plants measured in October 1981 is presented in Table 2. There was a significantly higher percentage of sprouting observed on the north exposure when compared to the percentage of sprouting on the south, east, and west exposures ($p < 0.01$). Percentage of sprouting on north-facing slopes was over 4 times that of east and west exposures, and over 7 times that of southern exposure.

Numerous seedlings of *Encelia* were found in the postburn exposures in February 1983. The proportion of *Encelia* sprouts and seedlings found on the east and west exposures was almost identical with 93% of the plants being seedlings (Table 2). An even higher proportion of *Encelia* seedlings was seen on the southern aspect which was composed of 96% seedlings. Only 23% of the *Encelia* on the northern exposure were seedlings. This proportion of sprouts and seedlings was significantly different ($p < 0.01$) when compared to sprouts and seedlings on south, east, and west exposures.

TABLE 2. PERCENTAGE OF TOPKILLED *Encelia farinosa* SPROUTING IN OCTOBER 1981 AND PERCENTAGE OF REGENERATED *E. farinosa* PRODUCED BY SPROUTS (SPROUTS/SPROUTS AND SEEDLINGS) IN FEBRUARY 1983 ON DIFFERENT SLOPE ASPECTS.

	October 1981		February 1983	
Slope aspect	n	% sprouting	n	% sprouts
North	44	29.6	13	77.0
South	52	3.9	120	4.2
East	184	7.1	120	7.5
West	72	8.3	120	6.7

The percentages of seedlings on the south, east, and west exposures were 4 times that of the northern aspect. Numerous seedlings of *S. mellifera* were observed on north-facing postburn slopes in February 1983.

Hanes (1971) previously reported *Encelia farinosa* as a nonsprouter. However, it is apparent that sprouting does occur and varies with slope aspect. He proposed that sprouters may have an advantage on mesic sites (north exposure) when compared with more xeric sites (south exposure) because of lower fire temperature and less shrub death due to cooler and moister conditions. Since death of shrubs above ground would be greater on the xeric southern exposure, reproduction would then be more advantageous by seeding versus sprouting (Hanes 1971, Howe and Carothers 1980). Although the postburn density of *Encelia* on the south exposure was less than that observed on east and west exposures, the fraction of seedlings was higher.

Encelia farinosa could be categorized as a weakly-sprouting species because only 4–30% of the topkilled shrubs in this study regenerated by crown sprouting, compared to 12–100% in sprouting chaparral species reported by Keeley and Keeley (1981). However, unlike chaparral, the percentage of topkilled shrubs that sprout in coastal sage scrub varies greatly with fire intensity (Westman, Ecology 62:170–184. 1981a; Westman, USDA For. Serv. Gen. Techn. Rep. PSW-58. 1981b; Westman et al. 1981). More intense fires suppress shrub sprouting, whereas more frequent fires favor shrub sprouting by lowering fuel loads and fire intensities (Westman 1981a). *Salvia mellifera,* which is known to sprout (Westman 1981a; Westman et al. 1981; Gray, Madroño 30:43–49. 1983), was not sprouting in this particular burn. This indicates that fire intensity was severe enough that levels of sprouting *E. farinosa* could have been higher than 30% had fire intensity been less.

Survival of *E. farinosa* on all slope aspects of coastal sage scrub communities is a result of its drought tolerance and its ability to recover from fire. However, the likelihood of recovery from sprouts is greater on the cooler more mesic sites, and less on the hotter more xeric sites.—BRADFORD D. MARTIN, Department of Biology, Loma Linda University, Loma Linda, CA 92350. (Received 11 May 1983; accepted 27 Dec 1983.)

Ipomopsis pinnata (POLEMONIACEAE) IN THE UNITED STATES.—Examination of herbarium specimens (GH, NMC, NY, US) indicates that *Gilia campylantha* Woot. & Standl. is conspecific with the Mexican species *Ipomopsis pinnata* (Cav.) V. Grant.

A new collection of was made ca. 25 km n. of the type locality of *Gilia campylantha*:

New Mexico. Hidalgo Co., Animas Peak (T31S R19W S29), 2460 m, *Soreng and Salazar 1916,* 22 Sep 1982 (NMC, TEX). It was determined as *Ipomopsis pinnata* by V. Grant. About 100 plants were noted in openings of a Douglas fir-gambel oak community. This new collection represents the first certain record of *G. campylantha* in the United States, and it matches the type well. This taxon was previously known only from the type collection made by Mearns in the San Luis Mts. 90 years ago. Mearns' collection was made near the present international boundary, but from which side is not known. However, my recent exploration of these mountains indicates Mearns was probably working in the San Luis Mts. in Mexico when he found this species and several other taxa not known from the United States. In the relatively small, low portion of the range extending into the United States there does not appear to be suitable habitat for many of Mearns' records.

These collections of *Gilia campylantha* (now *Ipomopsis pinnata*) occur at the northern end of the range of *I. pinnata,* a western Sierra Madrean species. *Ipomopsis pinnata* was until now known only from Mexico, in the states of Durango, Hidalgo, Nuevo Leon, San Luis Potosí, Mexico, and Tlaxcala, reaching nw. Chihuahua, 260 km south of the United States border. The occurrence of disjunct populations of Mexican species in the southwestern United States is a frequent pattern.

Wooton and Standley, in describing *Gilia campylantha,* suggested that their new species was similar to "*G. glomeriflora*" Benth. (=*Ipomopsis pinnata*), but that it had a "very different calyx." No consistent difference in calyx, or vegetative features, was observed in comparisons of our specimen with the type of *G. campylantha,* and with specimens of *I. pinnata* from Mexico. Specimens of these taxa exhibit a tubular corolla (ca. 10 mm long) with an abrupt sigmoid bend in the lower half of the tube. Corolla color, as described in the literature, is white, but varies to pale violet in some herbarium collections, and in our collection was creamy and tinged with purple on the tube. In both taxa stamens have filaments shorter than, or equal to, the anthers, and are arranged in the tube from just above the ovary to near the mouth, but none are at all exserted. Styles are ca. 1–2 mm long, and stigmas are positioned adjacent to the lowest anther in the tube. Leaves are nearly all pinnately lobed. There may be abundant eglandular, multicellular hairs on the stems and leaves, or the hairs may be mostly glandular, and there is a tendency towards glabrescence in age. The singular floral morphology binds these two taxa together and distinguishes *I. pinnata* from other congeners.

IPOMOPSIS PINNATA (Cav.) V. Grant, Aliso vol. 3:357. 1956.—*Phlox pinnata* Cav., Icones 6: t. 528, 1801.

Gilia campylantha Woot. & Standl., U.S. Natl. Herb. 16:160. 1913.—TYPE: Cyn. e. side San Luis Mts., 11 Sep 1893, *E. A. Mearns 2242* (Holotype: US!; isotype: DS).—*Ipomopsis campylantha* (Woot. & Standl.) Martin & Hutchins, A Flora of New Mexico 2:1580. 1981 (without citation of protolog), *nomen nudum.*

Thanks are extended to Rupert Barneby for nomenclatural advice regarding *Ipomopsis campylantha,* and to Richard Spellenberg and Alva Day for their editorial comments.—ROBERT J. SORENG, Biology Department, New Mexico State University, Las Cruces 88003. (Received 20 Sep 1983; accepted 20 Feb 1984.)

NOTEWORTHY COLLECTIONS

CALIFORNIA

WOLFFIA GLOBOSA (Roxb.) Hartog & Plas (LEMNACEAE).—USA, CA, San Diego Co., pond s. of Lake Hodges, 5 km s. of Escondido, w. side of Hwy. I-15 (33°3′15″N, 117°4′22″W), 100 m, 14 Jan 1984, *Armstrong 1196, 1197* (RSA, SD). Forming dense colonies at surface of small pond covering approximately 0.2 ha, mixed with *Lemna minuscula,* with average combined density of 42 per cm^2 of water surface. Associated with *Azolla filiculoides, Wolffia columbiana, Scirpus californicus, Typha latifolia* and *Echinodorus berteroi.* Verified by E. Landolt, Feb 1984 (Fig. 1).

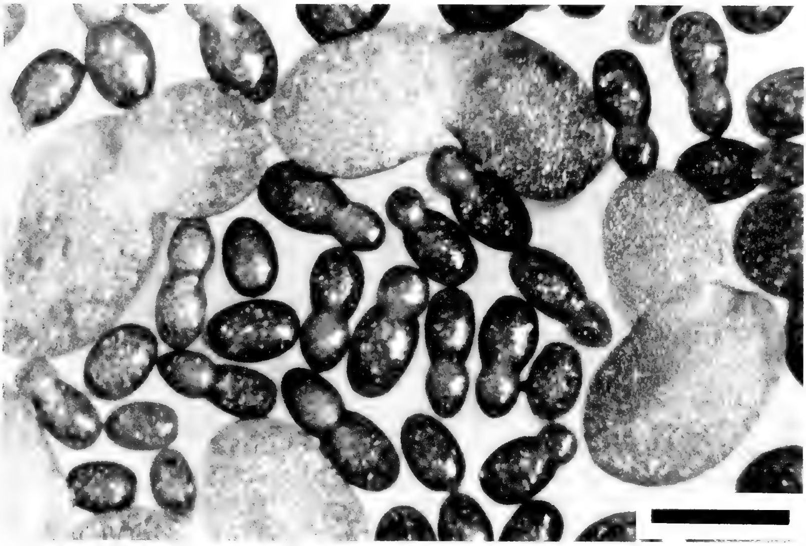

FIG. 1. Dense population of *Wolffia globosa* mixed with larger fronds of *Lemna minuscula* from pond south of Lake Hodges, San Diego Co., CA. Scale bar is 1 mm.

Previous knowledge. See Armstrong and Thorne, p. 171, this issue.

Significance. First record of *Wolffia globosa* in s. CA, a se. extension of 460 km from a slough near Minkler, Fresno Co. Three species of *Wolffia* are listed for central and northern CA: *W. borealis, W. columbiana,* and *W. globosa.* All three species have been collected in Lake Hodges, San Diego Co. They may have been introduced by migratory waterfowl, which are abundant in the area.—WAYNE P. ARMSTRONG, Palomar College, San Marcos, CA 92069.

CLAYTONIA NEVADENSIS Wats. (PORTULACACEAE).—Nevada Co., northwest flank of Mt. Lola (T18N R14E S14) at 2640 m. Small population in gravelly soil below melting snowbank. 28 Jul 1976, *Trowbridge 5845* (SFSU), *True 8063* (CAS). (Verified by J. T. Howell, CAS.)

Previous knowledge. See Chambers (Leafl. W. Bot. 19:1–8, 1963) and Ferlatte (Madroño 20:31, 1969). Relictual and disjunct in the western states.

Significance. Mt. Lola, 145 km s. of the Lassen area but 74 km n. of Freel Pk., becomes the northernmost site in the Sierra for this taxon.

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FIMBRISTYLIS AUTUMNALIS (L.) R. & S. (CYPERACEAE).—Glenn Co., w. bank of Sacramento River e. of Hwy. 45, 8 km n. of Glenn (T21N R1W S31) at 27 m. Numerous plants around edge of small pool on gravel bar. 8 Aug 1976, *Trowbridge 5757* (CAS). (Verified by J. T. Howell, CAS.)

Previous knowledge. See Kral, Sida 4:107–108, 1971.

Significance. New record for CA. Perhaps of accidental occurrence, possibly introduced by waterfowl.—BARBARA TROWBRIDGE, St. Anne's School, San Francisco, CA 94122.

ANDROSTEPHIUM BREVIFLORUM S. Watson (LILIACEAE).—San Bernardino Co., CA. hwy. 18, 1.2 km w. of jct. with US Hwy. 395 at Doby Corners, about 4 m n. of the road, 222 May 1983, *Clark 611* (CSPU). Only two individuals were seen within a radius of about 0.5 km.

Significance. This species is found in s. NV and UT, n. AZ, and sw. CO (Cronquist et al. 1977. Intermountain Flora. Vol. 6), but has been reported from CA near Needles (Abrams, Ill. Fl. Pac. St. Vol. 1), at Cronese Dry Lake in San Bernardino Co., and a location in Inyo Co. (Smith 1980. Inventory of rare and endangered vascular plants of California. Special Publ. #1, 2nd ed. CNPS). This collection represents a range extension of ca. 105 km sw. of the occurrence at Cronese Dry Lake. Although we suspect that these two individuals might be waifs, it is not inconceivable that the species is more widespread across the Mojave Desert and simply not collected.

Note. This species is incorrectly listed as *A. brevifolium* in Munz 1974. Fl. Southern California.—CURTIS CLARK, NANCY CHAREST-CLARK, DONALD L. SANDERS, and EMILIA PARRA, Biol. Sci. Dept., Calif. St. Polytechnic Univ., Pomona 91768.

NEVADA

ASTRAGALUS ENSIFORMIS M. E. Jones var. GRACILIOR Barneby (FABACEAE).—NV, Lincoln Co., Clover Mts., Cedar Wash area, 5 km s. of Julius Pk. (T7S R71E), locally common in a pinyon-juniper area, 1360 m, 17 May 1983, *Tiehm 7684* (CAS, NY, RSA, UTC) (determined by R. C. Barneby).

Significance. First record for NV. Previously known only from the Beaver Dam, Bull Run, and Pine Valley Mts. in adjacent Washington Co., UT.

ASTRAGALUS PULSIFERAE A. Gray var. SUKSDORFII (Howell) Barneby (FABACEAE).—NV, Washoe Co., Granite Range, Leadville Canyon, 1.6 km s. of the southern Leadville Road on Hwy. 34 (T37N R23E S22), growing with *Artemisia* on rocky hills of basalt rock, 1670 m, 30 Jun 1983, *Tiehm 8015* (CAS, NY, RSA, UTC) (verified by R. C. Barneby).

Significance. First record for NV. Previously known from Plumas, Lassen and Shasta Cos. CA. and Klickitat Co. WA. Range extension of over 50 km wnw. from Lassen Co.

ERIOGONUM AMPULLACEUM J. T. Howell (POLYGONACEAE).—NV, Mineral Co., Alkali Valley on the sw. side of the Wassuk Range, n. side of Alkali Lake (T5N R29E S21), growing with *Chrysothamnus* in saline areas near the lake, 2130 m, 12 Jul 1983, *Tiehm and Lavin 8143* (CAS, NY, RSA, UTC).

Significance. First record for NV. Previously thought to be endemic to Mono Co., CA, from Long Valley north to Mono Lake. Range extension of about 30 km nne. from Mono Lake.

GOODMANIA LUTEOLA (Parry) Reveal & Ertter (POLYGONACEAE).—NV, Mineral Co., Alkali Valley on the sw. side of the Wassuk Range, n. side of Alkali Lake (T5N R29E S21), growing with *Chrysothamnus* in saline areas near the lake, 2130 m, 12 Jul 1983, *Tiehm and Lavin 8140* (CAS, NY, RSA, UTC).

Significance. First record for NV. Previously thought to be endemic to CA (Brittonia 28:427–429, 1976). Range extension of over 70 km n. from the Long Valley area of Mono Co.

PHACELIA RATTANII A. Gray (HYDROPHYLLACEAE).—NV, Elko Co., s. fork of the Little Humboldt River, 5.4 km se. of the Little Humboldt Ranch (T41N R45E S7), growing in the rocks of a gorge along the river, 1520 m, 17 Jul 1983, *Tiehm and Williams 8160* (CAS, NY, RSA, UTC).

Significance. First record for NV. Previously known from CA, OR and sw. ID. Range extension of over 180 km wsw. from Three Creek in Owyhee Co., ID.—ARNOLD TIEHM, New York Botanical Garden, Bronx 10458.

NEW MEXICO

ASTRAGALUS PUNICEUS Osterh. cf. var. PUNICEUS (FABACEAE).—Harding Co. 16 km e. of Mosquero, e. slope of Tesquesquite Cr. Canyon on NM Hwy. 39, 29 May 1983, *Spellenberg 7071* (NMC, NY).

Significance. S. range extension of ca. 115 km for this variety, 240 km e. of var. *gertrudis* (Greene) Barneby. New population has even smaller flowers than those of Black Mesa, OK, plants (cf. Barneby, 1964, p. 228).

ASTRAGALUS SERICOLEUCUS A. Gray (FABACEAE).—Union Co., 4.8 km e. of central Clayton on US Hwy. 56, 26 May 1983, *Spellenberg 7053* (BYU, CAS, COLO, KANU, NMC, NY, RM); 6.4 km n. of Moses on NM Hwy. 18, 27 May 1983, *Spellenberg 7057* (NMC, TTC, UNM).

Significance. First report for NM, a range extension of 240 s. from e. CO.

ASTRAGALUS WITTMANNII BARNEBY (FABACEAE).—Colfax Co., 5.6 km n. of Springer, *Spellenberg 7020* (NMC, UNM); 19 km e. of Canadian R., 1.6 km n. of US Hwy. 56, 25 May 1983, *Spellenberg 7025* (K, KANU, NMC, NY); Harding Co., 3.2 km w. of Mills, 29 Jun 1981, *Spellenberg et al. 5991* (COLO, ISC, NMC, NY); 16 km nnw. of Mills, 2 Jul 1983, *Spellenberg et al. 6047* (NMC, UNM).

Significance. Recently described, previously known from Mora Co., near Levy, and from s. of Springer. New collections indicate species to be frequent on Greenhorn Limestone along Canadian R. Cyn. from Springer nearly to Roy, and should be removed from Federal consideration as "endangered."

EVAX PROLIFERA Nutt. (ASTERACEAE).—Union Co., vic. Clapham (Sec. 8, T22N, R33E), 27 May 1983, *Spellenberg 7065* (NMC, KANU).

Significance. First report for NM, w. range extension from n. cent. TX and w. OK.

PARTHENIUM ALPINUM (Nutt.) T. & G. var. ALPINUM (ASTERACEAE).—Harding Co., 26 km ne. of Roy, s. side of Carrizo Cr., on white caliche exposed in prairie, 29 May 1983, *Spellenberg 7074* (KANU, NMC, NY, UNM).

Significance. First report for NM, s. range extension of 730 km from var. *alpinum* in e. cent. WY, and 250 km from var. *tetraneuris* (Barneby) Rollins in s. cent. CO.—RICHARD SPELLENBERG, Dept. of Biology, New Mexico State Univ., Las Cruces 88003.

REVIEW

Agaves of Continental North America. By HOWARD SCOTT GENTRY. The University of Arizona Press, Tucson. 670 pp.

This book is obviously a labor of love, destined to become an indispensable reference. Aimed at professional botanists and interested laymen, Gentry's writing style is very readable and engaging. The first chapter, aptly titled "The Man-Agave Symbiosis," is a review of *Agave* ethnobotany including archaeological evidence, historical records, and recent commercial data. A long relationship between humans and agaves is evident, with many opportunities for feed-back influencing evolution in both *Agave* and regional cultures.

The taxonomic sections are introduced with an overview of the taxonomic history and general morphological trends in the genus. Although little attention is given to the relationship of *Agave* to other taxa in the Liliales, the history of the genus and its specialists seems well documented. Gentry's broad experience is evident in his discussions of organ morphologies and their taxonomic utility, and his inclusion of sections dealing with pollination biology and preparation of herbarium specimens is praiseworthy.

Species descriptions are thorough; in addition to morphological characterization, attention is given to habitat, geographical distribution, pollination, and ethnobotanical attributes. For many species fiber quality and sapogenin content are presented to indicate taxa with commercial potential. Good drawings and photographs are plentiful. There are lucid explanations for Gentry's taxonomic decisions with no hesitation in pointing out many unresolved problems. It is evident that Gentry has invested an enormous amount of labor in attempting to base his descriptions on field collected material, in designating types, and in tackling a nomenclatural morass full of poor descriptions and inadequate herbarium material. There are problems inherent in wide-ranging species complexes that show appreciable intra-populational variation, and further complications have been introduced through hybridization and horticultural dispersal. Linking names based on single clones in European gardens with natural populations has not always been possible, but Gentry has accomplished some successful resolutions as in *Agave kewensis* and *A. geminiflora.* Taxonomic criteria are almost entirely morphological; taxon delineations generally reflect gaps in the correlated variation of flower, inflorescence, and leaf characteristics. In some cases, as in the *Marginatae* group, species are defined largely on the basis of growth habit and leaf morphology. Gentry's species concepts are flexible. For example, in the *Rigidae* group many taxa are submerged under *A. angustifolia,* whereas the closely allied *A. tequilana* is distinguished, with the note that ". . . the commercial trade with this important economic plant will profit by the maintenance of a simple binomial." In several cases Gentry considers his taxonomy to be provisional due to a lack of data, and he urges future workers to correct these deficiencies.

There are minor editorial flaws, but they don't detract from the book's value. In a few instances a species name used in one part of the book is reduced to synonymy elsewhere, and a few passages from introductory chapters are repeated in the taxonomic section. Unfortunately there are serious difficulties in some keys due to apparent internal contradictions, with exceptional taxa being ignored. Acknowledging this, Gentry remarks ". . . several key pathways may need to be explored. All is relative." Serious users will be advised to note exceptions as they are discovered at pertinent spots in the key to reduce confusion. To some extent identification problems are alleviated by the inclusion of separate keys for specific geographical areas, such as the Chihuahuan Desert, Arizona, etc. In working through the keys one gets a sense of the difficulties Gentry must have encountered in trying to impose order upon the taxonomically intractable *Agave.*

MADROÑO, Vol. 31, No. 3, pp. 194–195, 30 July 1984

In *Agaves of Continental North America* we have the legacy of a dedicated researcher. This is clearly a product of decades of work and a depth of field experience not often seen in grant-oriented academicians. Gentry's book provides a secure foundation recommended to anyone interested in *Agave.*—Tony L. Burgess, Herbarium, Univ. Arizona, Tucson 85721.

Editor's Note

In addition to expressions of pleasure and approval from Madroño readers at having Volume 30 of this journal dedicated to Reid Moran, there have been various queries and comments. In response to these, the Editor states that the photograph of Reid facing the Dedication was taken on the road to Corral de Sam, Sierra San Pedro Mártir, Baja California, México, by Robert F. Thorne on 15 Aug 1967. The plant in the photograph is *Haplopappus arborescens* subsp. *peninsularis.* Reid's "I found it there then" contribution may be found in Vol. 16 under *Cneoridium dumosum.* And finally, the Clausen with whom Reid studied at Cornell was Robert, *not* Jens Clausen of Carnegie Institution of Washington at Stanford.

Reid Moran has been not only an indefatigable and meticulous collector, but also he has made uniquely valuable contributions to our knowledge of Crassulaceae. In addition to his many published papers on members of this family, as well as those on phyteographical and historical subjects, his photographic essay titled "The Stonecrop Family," which displayed form and variation in Crassulaceae, was exhibited at the San Diego Natural History Museum and then went on to a three-year tour in the Travelling Exhibition Section of the Smithsonian Institution.

Despite rumors to the contrary, when time permits, Reid is continuing his work on various aspects of Baja California Botany.

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OFFSHOOT VARIABILITY IN *YUCCA WHIPPLEI* SUBSP. *PERCURSA* (AGAVACEAE)

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Abstract

Seed of *Yucca whipplei* Torr. subsp. *percursa* Haines was collected in Refugio Canyon, Santa Barbara County, California. Seeds from a single capsule were planted in pots annually in a lath house at the University of California, Riverside. Two-, 3- and 4-year-old plants were dug up and examined for lateral vegetative shoots, and these were collected and photographed. Three- and 4-year-old plants had various types of offshoots, including rosettes, rhizomes, and many forms of intermediates, which are described morphologically. Rosettes and rhizomes occurred on the same individual. This evidence suggests that lateral vegetative branches may not be suitable characters for subspecies delineations.

Haines (1941) and Webber (1953) used both vegetative characters and the habit of the inflorescence to separate the intraspecific taxa of *Yucca whipplei.* Haines dividied the species into four "growth-forms." These included the solitary form that produces no offshoots of any type (*Y. whipplei* subsp. *parishii* Haines, and *Y. whipplei* subsp. *whipplei*); two "caespitose" forms that have rosette offshoots either before (*Y. whipplei* subsp. *caespitosa* Haines) or after flowering of the parent axis (*Y. whipplei* subsp. *intermedia* Haines); and a rhizomatous form that reproduces clonally by underground rhizomes (*Y. whipplei* subsp. *percursa*). Descriptions of the offshoot types are scanty and morphologically inaccurate. Haines stated that the habits correlate with geographical locations of the species in southern California and with characteristics of the inflorescences.

I became interested in the species as a tool to understand the relationship of primary and secondary growth in monocotyledons with true secondary growth. A secondary thickening meristem occurs in all members of the Agavaceae (Tomlinson and Zimmermann 1969; DeMason 1983, Diggle and DeMason 1983a,b). I was especially interested in the structure of the rhizome and the transition from rhizomatous growth to rosette shoots. At the time, the literature lacked even the barest morphological descriptions of the offshoot characteristics. This study has two goals: (1) to recount the surprising vegetative variability encountered; and (2) to provide morphologically accurate descriptions of the types of vegetative shoots in this subspecies.

Madroño, Vol. 31, No. 4, pp. 197–202, 9 November 1984

MATERIALS AND METHODS

Seed of *Yucca whipplei* subsp. *percursa* was collected in Refugio Canyon, Santa Barbara County, California, from a single parent. The seeds from a single capsule were soaked in water for 48 hr and planted in pots. Plants were germinated either in the greenhouse in spring (March or April) or in a growth chamber at 20°C day/12°C nights under 8-hr days. Once established, seedlings were transplanted and moved to the lathhouse. Two- and 3-year-old plants were uprooted and checked for rhizomes first in June 1982; they were then replanted and uprooted again in June 1983. All vegetative branches were removed, examined, and photographed before dissecting and fixing specimens for future anatomical studies. No plant had yet flowered.

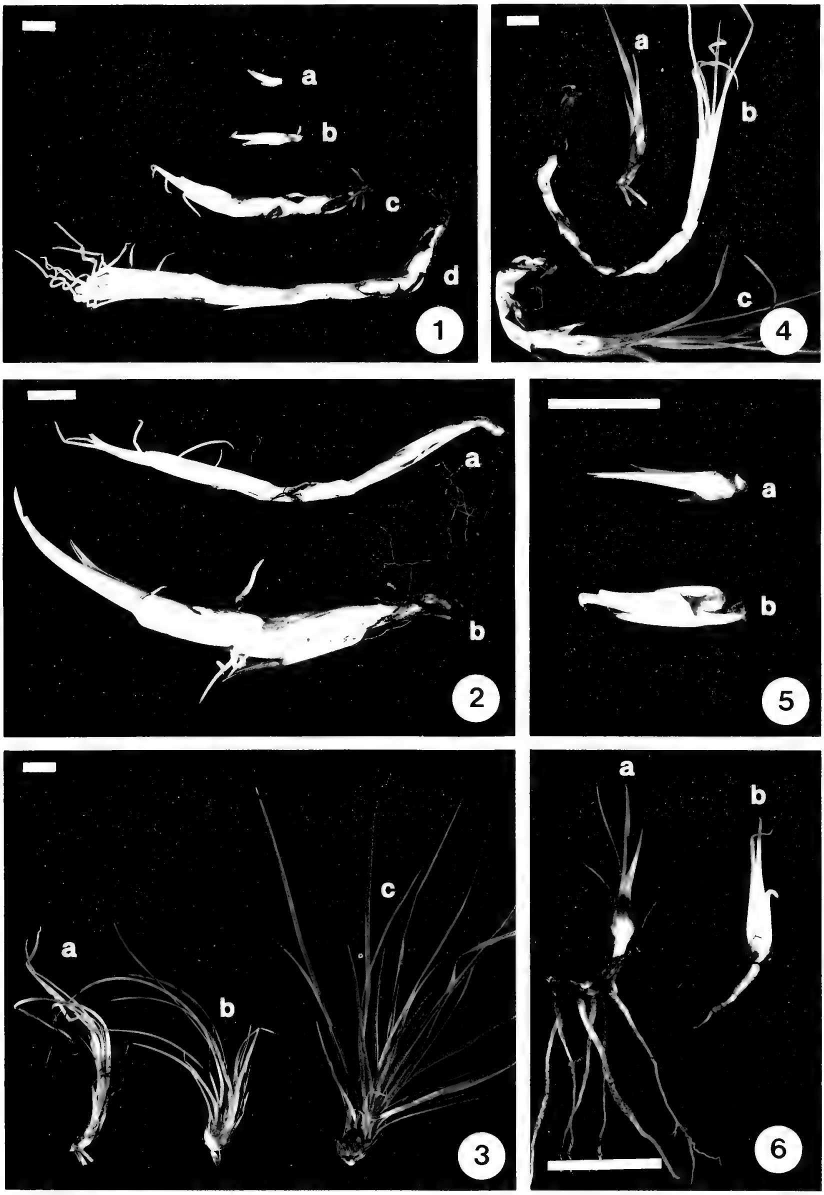
RESULTS AND DISCUSSION

Many different types of lateral branches were found on 3- and 4-year-old plants (Figs. 1–6); however, none was found on 2-year-olds. These lateral branches are considered to be rhizomes, rhizomes with terminal rosettes, rosettes, and many types of intermediates between typical rhizomes and rosettes. In 1983, 10% (4 of 39) of 3-year-old plants and 30% (7 of 23) of 4-year-old plants examined had lateral shoots. The types of lateral shoots are described below.

Rhizomes. Rhizomes ranging from 1–25 cm long were found on both 3- and 4-year-old plants (Figs. 1, 2, 4). Generally, rhizomes are attached to the parent plant stem in the root zone or below the root zone. They are achlorophyllous, have elongated internodes, and bear scale leaves. Scale leaves cover the stem and have bluntly pointed tips (Figs. 1a–d, 4b–c). Initially, rhizomes grow either vertically or obliquely down in the pots and only later curve toward the horizontal. The nodes are swollen. No branching was seen on any rhizome, although occasional axillary buds were observed.

A considerable amount of variability occurs in rhizomes. They differ in stem thickness from very thick (2.5 cm) (Figs. 2b, 4c) to thin (0.8 cm) (Figs. 2a, 4b). The leaves vary from typical scale leaves (Fig. 1c) to long pointed achlorophyllous leaves (Fig. 2a–b). Many rhizomes had terminated in rosette shoots. These had green, stiff, strap-shaped leaves when they were above the ground surface (Figs. 4a, c; 6a), or soft achlorophyllous leaves when they occurred below the soil level (Figs. 1d, 4b).

Haines (1941) described the rhizomes of *Y. whipplei* subsp. *percursa* as being "1 inch in diameter, 2.6 or more feet in length producing new individuals from terminal buds . . . ." No other information is given on the morphology of the rhizome. Certainly the rhizome can reach a diameter of ca. 2.5 cm (Figs. 2b, 4c), but most rhizomes observed in this study were considerably less robust.



FIGS. 1–6. Lateral branching in *Y. whipplei* subsp. *percursa*. 1. Developmental series of typical rhizomes. 2. Thin-stemmed (a) and thick-stemmed (b) rhizome. 3. Rosette shoots. 4. Transformation to rosette shoots. 5. Young rosette shoot (a) and young rhizome (b) from same parent plant. 6. Rosette attached to thin rhizome (a) and sessile rosette (b). Scale bar = 3 cm.

Simpson (1975) stated that rhizomes in the four sections of *Yucca* are distinctive. He studied *Yucca brevifolia* Engelm. in the section *Clistocarpa.* The rhizomes in the var. *herbertii* (Webber) Munz of the Joshua Tree are narrow and bear "firm imbricated, bluntly pointed scales" when young, but become secondarily thickened and covered by periderm when old. He observed branching and axillary buds associated with scale leaves. The rhizomes in *Y. whipplei* (sect. *Hesperoyucca*) are rather similar to those described by Simpson, although I have not observed periderm formation or branching. Rhizomes in the other two sections are quite different, and were described by Simpson (1975).

True rosette shoots. Rosette shoots, like rhizomes, are quite variable in their morphology. True rosette shoots are attached directly to the parent shoot without any intermediate rhizome or any elongated internodes (Figs. 5a, 3b–c). These rosettes bear green, stiff, pointed leaves from inception; the leaves demonstrate the same homoblastic series of short-juvenile to long-adult leaves as do the seedlings during early development. The axis, like that of seedlings, is a short, thickened, upright stem. The major difference between seedling and rosette shoots is that the rosette shoots have a spiral phyllotaxis from inception, whereas the seedlings initially have a distichous phyllotaxis that changes gradually to the spiral of the adult *Yucca.* These sessile rosettes are initiated on the parent plant stem at the upper portion of the root zone and at approximately soil level. Usually, they are small compared to the parent plant, but one of the 3-year-old plants in 1982 had three rosettes almost as large as the parent plant itself (Fig. 3c). When both a rhizome and a rosette occur on the same parent plant (Fig. 5a–b), the rosette is attached above the rhizome on the stem. The rosettes grow upward from inception.

Haines (1941) named two subspecies with the caespitose habit. His subsp. *intermedia* is described as having axillary branching after it is mature, so that only one flowering stalk is produced per cluster in one season. His subsp. *caespitosa* has branching early, so that several branches often flower in one season. The individuals with rosettes in this study usually fitted the description of subsp. *intermedia* because the rosette shoots were generally much smaller than the parent axis. However, one plant fit the description of subsp. *caespitosa* because the three axillary rosettes were almost as large as that of the parent plant.

Intermediate rosettes. Not all rosettes were sessile on the parent plant. Some rosette shoots had, at their base, distinct, thin-stemmed and long-internoded rhizomes that bore adventitious roots (Fig. 6a). These rhizomes also had small membranous scale leaves. A distinct bulbous rosette terminated the shoot. Other rosettes had green leaves, which are characteristic of rosettes; however, dissection showed that the basal internodes were elongated (Fig. 3a). Also, some shoots showed a gradual change over several elongated internodes, from scale leaves on long internodes to green leaves on rosette shoots (Fig. 4a). Haines (1941) and Webber (1953) included no detailed information on the morphology of the rosette shoots of the two subspecies.

CONCLUSIONS

Most of the seedlings had no lateral vegetative branching at all. Among those that did, plants ranged from having all offshoots typical of the subsp. *percursa* (that is, only rhizomes were produced) to those with both rhizomes and lateral rosettes, to those that had only rosettes. Lateral rosettes were usually much smaller than those of the parent plant; however, one plant had three lateral rosettes similar in size to the parent axis. This variability covers the entire range seen in this species.

There are at least two possible explanations for this amount of variation in sibling plants grown in a common garden: (1) the seeds resulted from natural hybridization in the field; and (2) the variation in the species *Y. whipplei* is greater than appreciated earlier. I feel that the first possibility is unlikely. Subspecies *percursa* occurs in three fairly isolated populations in the mountains of San Rafael and Santa Ynez, and in the Santa Lucia Mountains from Santa Barbara to Monterey County (Haines 1941). Because the closest population of another subspecies is of subsp. *caespitosa,* which occurs from San Bernardino County along the western border of the Mojave Desert to Walker Pass (a distance of about 100 miles), it is unlikely that these seedlings are the result of natural hybridization. I feel the second explanation is more likely because the plants described here have been grown in pots, making it easy to uproot and observe the growth patterns of many more plants than can be excavated carefully in the field (Haines 1941).

In recent studies of the genus *Yucca,* authors have remarked on the large amount of variability in vegetative characters compared to the very stable floral and fruit characters (McKelvey 1938; Haines 1941; Webber 1953, 1960; Simpson 1975). For this reason, vegetative characters have been used to identify not only species within the genus, but also forms, varieties, and subspecies within the species. If vegetative characters are going to be used taxonomically, it is necessary to have detailed and morphologically accurate descriptions of the forms observed. Results from this study suggest that the variation within one subspecies of *Y. whipplei,* with respect to the types of lateral branching produced, is much greater than previously thought; and furthermore, it is possible that characteristics of branching are not taxonomically reliable. Future revisions of *Y.*

whipplei and possibly other species within the genus should include detailed observations of offshoots and studies of plants grown in a common garden.

ACKNOWLEDGMENTS

I thank Drs. Jon and Sterling Keeley and Janet Lee for collecting the seed used in this study. I also thank Dr. Norman Ellstrand for reading the manuscript and James Stillman for cultivating the plants. This study was funded by a grant from the National Science Foundation (PCM-8021422). The growth chambers were purchased with monies from PHS/BRSC # 2 S07 RR07010-15.

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(Received 28 Sept 1983; accepted 22 Mar 1984.)

A RE-EVALUATION OF *PHYSARIA DIDYMOCARPA* VAR. *INTEGRIFOLIA* (CRUCIFERAE)

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Abstract

Specific status is given to *Physaria didymocarpa* var. *integrifolia* and a new variety, **P. integrifolia** var. **monticola,** is described. This new variety is known from the mountains of western Wyoming and eastern Idaho.

Rollins (1939) considered *Physaria didymocarpa* (Hook.) Gray to be remarkably uniform in the northern part of its range. He also commented that *P. didymocarpa* var. *integrifolia* Rollins from west-central Wyoming showed certain transitional stages to its southern analogue, *P. acutifolia* Rydb. (as *P. australis* (Payson) Rollins). Then Rollins (1983), while discussing several evolutionary trends in *Physaria,* pointed out that the thin, inflated silique valves are better adapted for wind dispersal than the heavier-walled, less inflated ones. In doing so, he made note that this trend can be seen between and even within species. His example for within a species was, "Over most of the geographic range of the species, populations of *P. didymocarpa* (Hook.) Gray have siliques with heavy-walled valves, but var. *integrifolia* Rollins, which is restricted to western Wyoming and eastern Idaho, has thin, highly inflated valves." In addition to observations by Rollins, recent field, herbarium, and laboratory studies by the author can now justify specific separation of *P. didymocarpa* var *integrifolia* from the more northern var. *didymocarpa. Physaria didymocarpa* var. *didymocarpa* and var. *lanata* A. Nels. have dentate leaves and spreading trichome branches on the siliques, whereas var. *integrifolia* has entire leaves and appressed trichome branches on the siliques. Scanning electron micrographs show highly branched trichomes with a distinct central umbo in var. *integrifolia* as compared to less branched trichomes lacking a distinct umbo in var. *didymocarpa* and *lanata* (Rollins and Banerjee 1975). I therefore elevate *P. didymocarpa* var. *integrifolia* to specific status.

Physaria integrifolia (Rollins) Lichvar, stat. nov.—Based on *Physaria didymocarpa* (Hook.) Gray var. *integrifolia* Rollins, Rhodora 41:407. 1939. Type: WY, Lincoln Co.: Grand Canyon of the Snake River, 8 Jul 1932, *L. Williams 809* (GH).

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Rollins (1981) discussed the infrequent occurrence of a retoños root system in only two species of *Physaria, P. brassicoides* Rydb. and *P. alpina* Rollins. This type of branching root system gives rise to rosettes that emerge several centimeters from the main plant. In western Wyoming and eastern Idaho, there is an undescribed taxon that commonly displays this unusual character. It is closely related to *P. integrifolia* in leaf shape, but it has other distinguishing characters.

Physaria integrifolia (Rollins) Lichvar var. **monticola** Lichvar, var. nov. (Fig. 1).

Radix primaria divisa; folia radicalia 1.5–3.5 × 0.5–1.5 cm; inflorescentia fructifera foliis (2–)4–6(–9) cm longior.

Perennial with an underground branching root system or rarely a simple tap root, caespitose, silvery-stellate throughout; caudex mostly branched, sometimes simple; radical leaves entire, oblanceolate to obovate, rounded to acute at apex, the blade 1.5–3.5 cm long, 0.5–1.5 cm wide, abruptly tapered to a slender petiole, (1–)2.5–4.5 cm long; inflorescence compact to elongate in fruit and exceeding leaves by (2–)4–6(–9) cm; sepals erect, pubescent, 5–6 mm long, ca. 2 mm wide; petals yellow, spathulate, 8–10 mm long, 3–4 mm wide; siliques didymous, inflated at maturity, with deep apical and basal sinuses, 1–2.5 cm wide, 1.1–2.1 cm long; valves suborbicular with an elliptical orifice; styles 5–8 mm long; replum linear to oblong, not constricted, 3–5 mm long, ca. 2 mm wide; ovules 4(3–6) in each loculus; seeds elliptic, 3–4 mm long, 2–3 mm wide.

TYPE: USA, WY, Lincoln Co.: Wyoming Range e. of Soda Lake (T32N R115W S12 NE¼), 2469 m elev., 8 Jul 1981. Rocky calcareous slope, associated with *Artemisia tridentata, Penstemon humilis,* and *Ipomopsis aggregata. Robert W. Lichvar 4586* (Holotype: RM; isotypes: to be distributed).

PARATYPES: USA, WY, Lincoln Co.: Wyoming Range, Shale Cr. drainage (T30N R116W S17 SE¼), 27 Jun 1979, *L. M. and J. S. Shultz 3443* (GH); Wyoming Range, Middle Piney Lake (T30N R115W S8 NE¼), 8 Jul 1982, *Lichvar 5222* (RM); McDougal Gap (T33N R115W S8), 18 Aug 1982, *Dorn 3822* (RM); Salt River Range, Mt. Wagner (T30N R118W), 4 Aug 1979, *L. M. and J. S. Shultz 3650* (GH); Wyoming Range, Triple Pks. (T32N R115W S7), 18 Aug 1978, *J. S. Shultz 347* (RM); Wyoming Range, Wyoming Pk. (T30N R116W), 24 Aug 1978, *L. M. Shultz 2972* (GH); Salt River Range, Lake Barstow (T32N R117W S7 SE¼), 5 Aug 1979, *L. M. Shultz 3722* (GH); Salt River Range, hills e. of Afton, 28 Jun 1923, *Payson and Armstrong 3825* (RM); Sublette Co.: Wyoming Range, Cottonwood Cr. (T32N R115W S12), 26 Jun 1978, *L. M. and J. S. Shultz 2653* (RM); same location, 8 Jul 1982, *Lichvar*

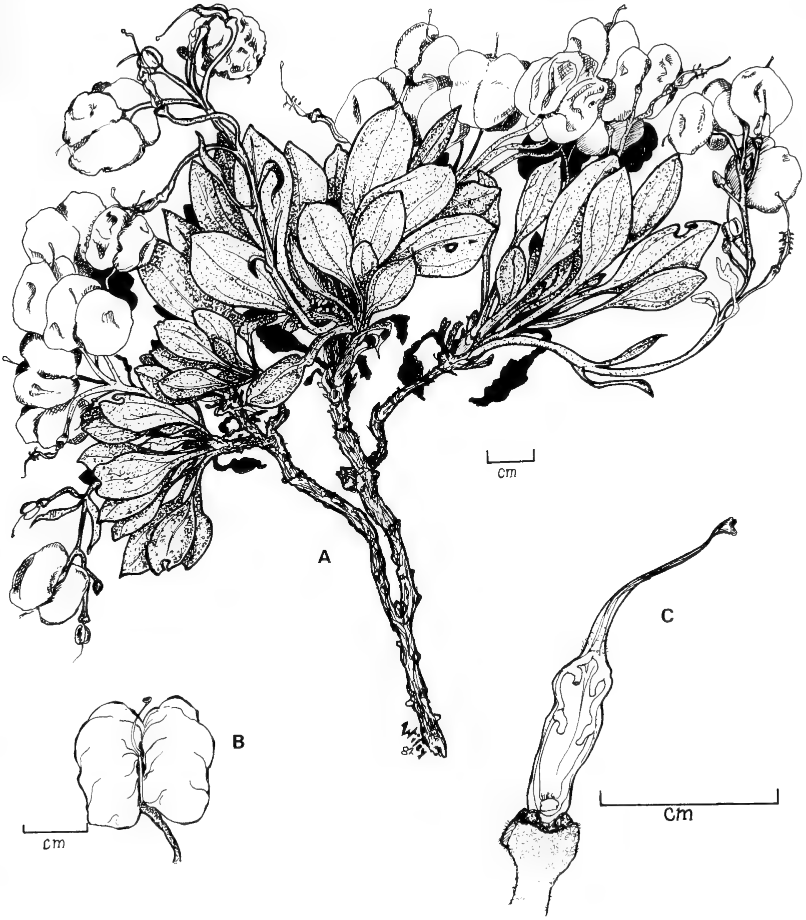
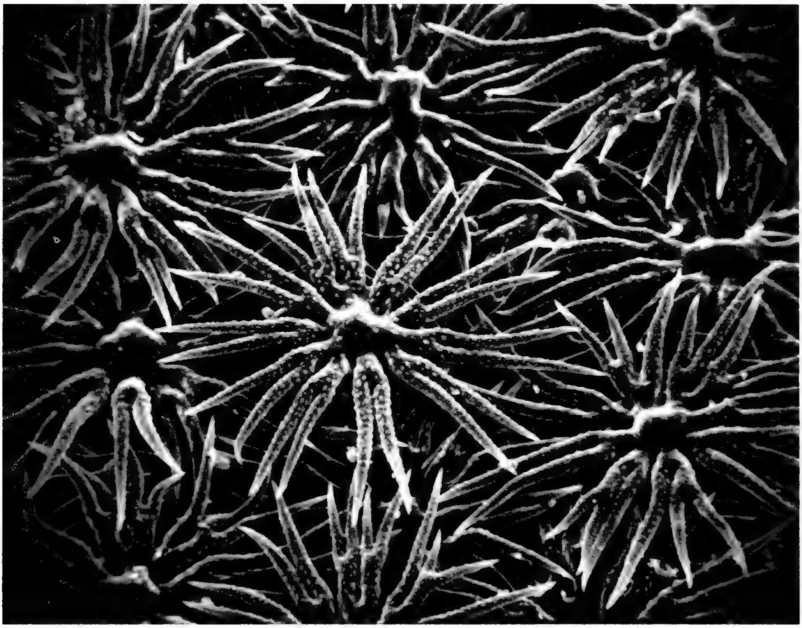


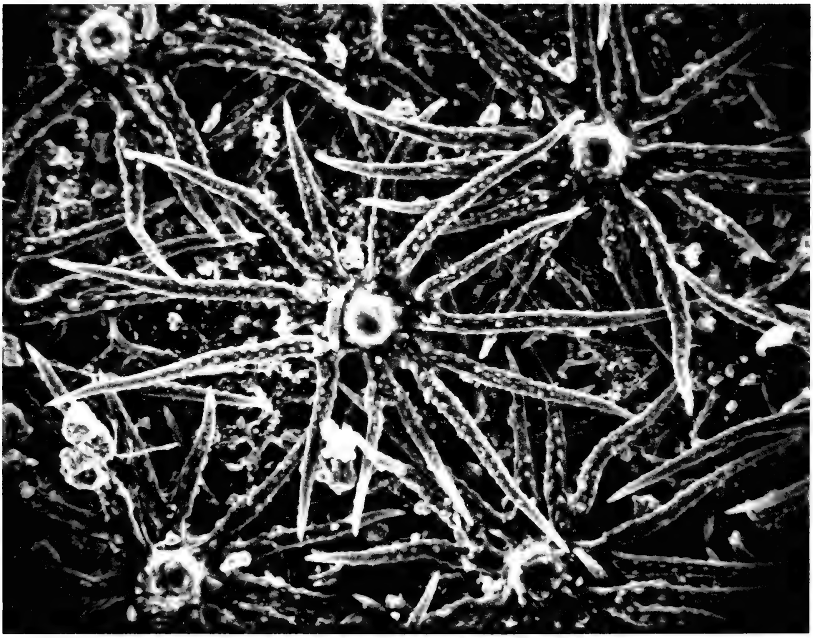
FIG. 1. *Physaria integrifolia* var. *monticola* (from the type). A. Habit. B. Silique. C. Replum.

5223 (RM); Teton Co.: Sheep Mtn. ca. 14 mi ne. of Jackson, 30 Jul 1957, *Beaman and Stone 1490* (GH); IDAHO, Bonneville Co.: Caribou Range, 9 air mi s. of Palisades Dam (T2S R45E S31), 22 Jul 1971, *Holmgren and Marttala 5584* (GH).

In the key to the Wyoming species of *Physaria* (Lichvar 1983), *P. integrifolia* var. *monticola* would key to *P. didymocarpa* var. *integrifolia,* from which it differs as follows:

1. Inflorescence exceeding leaves in fruit by (6–)8–14 cm, leaf blades 4–6 cm long, petioles 4–8 cm long, root system mostly simple . . . . *P. integrifolia* var. *integrifolia*





FIGS. 2–3. Leaf trichomes of *Physaria integrifolia*. 2. (Top) Var. *monticola* (from the type), ×190. 3. (Bottom) Var. *integrifolia* (from *Lichvar 4329*), ×150.

1. Inflorescence exceeding leaves in fruit by (2–)4–6(–9) cm, leaf blades 1.5–3.5 cm long, petioles (1–)2.5–4.5 cm long, root system usually highly branched ....*P. integrifolia* var. *monticola*

The leaf trichomes of var. *monticola* have a depressed central umbo that blends into the bases of the shanks (Fig. 2) rather than a conical umbo that is distinct from the shanks as in var. *integrifolia* (Fig. 3) (Rollins and Banerjee 1975).

Specimens of var. *monticola* commonly have a highly branched root system, but those with a simple tap root can easily be distinguished from var. *integrifolia* on leaf length and plant height (4–15 cm vs. 12–20 cm, respectively). Variety *monticola* can be distinguished easily from other entire leaved physarias as follows: smaller specimens of var. *monticola* can be separated from *P. condensata* Rollins by linear to oblong replums and rounded to acute leaf tips rather than obovate replums and acute leaf tips. Variety *monticola* differs from *P. dornii* Lichvar in that the inflorescence exceeds the leaves by (2–)4–6(–9) cm rather than 2–3 cm, the plants are loosely caespitose rather than in a condensed rosette growth form, and the replums are linear to oblong rather than obovate. Variety *monticola* differs from *P. eburniflora* Rollins in that the fruit trichomes are appressed, the leaves oblanceolate to obovate, the replum linear to oblong, and the petals yellow compared to erect fruit trichomes, nearly orbicular leaves, elliptic to obovate replum, and whitish petals in *P. eburniflora.*

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ROLE OF CHARRED WOOD IN THE GERMINATION OF THE CHAPARRAL HERBS *EMMENANTHE PENDULIFLORA* (HYDROPHYLLACEAE) AND *ERIOPHYLLUM CONFERTIFLORUM* (ASTERACEAE)

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Abstract

Germination of the chaparral herbs *Emmenanthe penduliflora* and *Eriophyllum confertiflorum* is markedly stimulated by charate (powdered charred *Adenostoma fasciculatum* wood). The active component is not activated charcoal but is water soluble. Chaparral populations of *Emmenanthe* exhibit a nearly obligate dependence upon charate for germination. *Eriophyllum*, however, is facultatively dependent upon charate; charate is largely required for germination on potting soil or mature chaparral soil, but this species germinates readily on non-soil media. Soil extracts will inhibit germination of *Eriophyllum* on filter paper but this inhibition is overcome by aqueous charate extracts. Germination of this species is also reduced 50% with 0.05 M mannitol. Germination of both species is greatly stimulated by extracts of previously heated soil, though it is uncertain whether this is due to production of charate-like compounds from organic matter or to the destruction of inhibitors. Scanning electron micrographs showed that charate-stimulated germination was not accompanied by visible changes in the seed coat.

The abundant herbaceous flora characteristic of chaparral sites after fire is in striking contrast to the depauperate herb growth in mature stands. Most of the species making up this diverse "temporary" flora have seeds that remain dormant under the chaparral canopy. The mechanisms responsible for cueing germination to the postfire environment have been the subject of controversy. It has been hypothesized that allelopathic compounds leached from the shrub canopy (McPherson and Muller 1969) or produced by microbes in the soil (Kaminsky 1981) inhibit germination of native herbs and that these inhibitors are destroyed by fire. Alternatively, Christensen and Muller (1975b) and others have hypothesized that the environmental conditions under the shrub canopy are unfavorable for herb survival; thus, many species have evolved seeds that require a stimulus from fire to cue germination to the postfire environment.

Evidence in support of either of these mechanisms is relatively limited. Allelopathic inhibition of germination was demonstrated for four species in laboratory bioassays by McPherson and Muller (1969), but only with concentrations that are probably not found in

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nature (Kaminsky 1981). Christensen and Muller (1975a) did not observe allelopathic inhibition of germination for six out of eight native species. Recent experiments (following techniques of Christensen and Muller) with 28 native herb species have likewise failed to show any "allelopathic" inhibition of germination in the vast majority of species (Keeley et al. in press).

Cues from fire that might stimulate germination are intense heat and/or chemicals produced by combustion of organic matter. Sweeney (1956) applied a variety of heat treatments to seeds of many chaparral herb species but failed to demonstrate any increased germination. McPherson and Muller (1969) and Christensen and Muller (1975a) investigated the effect of heat on seed germination and found that a few species showed significantly increased germination but others did not.

Sweeney (1956) investigated whether or not chemicals from burned wood stimulated germination and he, as well as Christensen (1973), failed to observe any enhancement of germination from wood ashes. However, Wicklow (1977) and Jones and Schlesinger (1980) found that, although wood ashes produced no effect, partially charred wood produced a highly significant increase in the germination of *Emmenanthe penduliflora* Benth. (Hydrophyllaceae). A similar response has been observed for *Eriophyllum confertiflorum* (DC.) Gray (Asteraceae) (Keeley and Keeley 1982) and several other species (Keeley et al. in press).

The purpose of this study was to examine further the charred wood enhancement of seed germination in *Emmenanthe penduliflora* and *Eriophyllum confertiflorum.* Both species are locally abundant on recent chaparral burns throughout California. *Emmenanthe* is an annual that reaches its peak abundance in the first year after fire, and on some sites it may disappear by the second year. It is rare in unburned chaparral even in openings or disturbances. *Eriophyllum* is a suffrutescent perennial. Seedling establishment is largely restricted to the first post-fire year, though *Eriophyllum* seldom dominates at this time. Flowering begins in the second postfire year, and peak dominance occurs in the third or fourth years. Unlike *Emmenanthe, Eriophyllum* commonly establishes in openings within the chaparral matrix though it never is successful under the mature canopy. Specific questions addressed were: 1) Does activated charcoal stimulate germination? 2) Is the charred wood stimulatory effect due to a water soluble compound? 3) Is this effect influenced by the germination medium? 4) How is it affected by prior soil heating? 5) Do soil microbes play a role? and 6) Is charate-stimulated germination accompanied by SEM-detectable changes in the seed coat, as is the case for heat-stimulated seed germination in *Lotus salsuginosus* and other fire-type species (J. and S. Keeley, unpubl. data).

METHODS

Emmenanthe seeds were collected in 1979 from a one-year-old burn in the Santa Monica Mountains, Ventura County, California by W. Schlesinger and were from the same seed source used in Jones and Schlesinger (1980). *Eriophyllum* seeds were collected from an open site adjacent to mature chaparral in southwestern Riverside County, California in 1980. All experiments were done between July 1981 and June 1982.

Germination was compared on different media. Petri dishes (60 × 15 mm) had either 2 sheets of 5.5-cm filter paper (Whatman #42 ashless), 15 cc of vermiculite (Terra-Lite medium), acid-washed sand (J. T. Baker), potting soil (L & L UniGrow), or chaparral soil from either a mature (25 years) stand of *Adenostoma fasciculatum* or an adjacent 2-year-old burn in the San Gabriel Mountains, Los Angeles County. All three soils were filtered through a 3-mm screen. Fifty seeds were sown per dish and n = 10 dishes per treatment. Deionized water or aqueous extracts were applied (levels given in tables) and the dishes were incubated in the dark for 21 days at 5°C followed by 14 days at 23°C. This regime was repeated twice. Germination was scored every 7 days in the light.

Charate was prepared from *Adenostoma fasciculatum* stems (<20 mm dia.) by completely charring with a torch, but not ashing, and grinding in a Wiley Mill to pass a #20-mesh screen. Previous studies (S. Keeley, unpubl. data) have shown that unheated but powdered stems have no effect on seed germination. Charate treatments received 1.0 ± 0.1 g of powdered charate.

A water extract was made by soaking 2.5 g of charate in 20 ml deionized water for 18 hr and vacuum filtering through Whatman #1 ashless filter paper. Soil extracts were made as above with a ratio of 2 cc soil: 1 ml water for the potting soil and burned soil. For the mature chaparral soil the proportion of water used to prepare soil extracts was increased 30% due to much greater absorption of water by the chaparral soil. A filter paper extract was made in a ratio of 3 sheets of 9 cm #42 Whatman-ashless: 7 ml deionized water. A combined extract of charate plus soil was made by combining double strength extract of each.

Heated mature chaparral soil was prepared by spreading soil 3–4 mm deep on trays and heating to 195°C ± 5°C for 10 min. To examine the effect of microbial by-products in these soils, sterile extracts were prepared from soil 1) immediately after heating and 2) after heating, wetting and incubating for 12 days at 23°C in the dark. Sterile extracts were prepared by vacuum filtering soil extracts, prepared as described above, through sterile 0.2-μm nitrocellulose filters.

TABLE 1. GERMINATION OF *Emmenanthe penduliflora* AND *Eriophyllum confertiflorum* ON POTTING SOIL WITH CHARATE (FROM PARTIALLY CHARRED *Adenostoma fasciculatum*) OR ACTIVATED CHARCOAL. (Each dish received 7 ml H_2O; n = 10 dishes of 50 seeds each, $^{**}p < 0.01$; means, within a row, with the same superscript letter are not different at the indicated significance level.)

	Percentage germination			
	Control	Charate	Activated charcoal	p
Emmenanthe	0^a	25	0^a	**
Eriophyllum	10^a	57	2^a	**

Osmolality of soil extracts was determined with a Wescor Vapor Pressure Osmometer.

Individual experiments were analyzed with one-way ANOVA on arcsin transformed data and significant differences between cell means were distinguished with Fisher's Least Significant Difference test.

Scanning electron micrographs were made of seeds to investigate effects of charate on the seed coats. Seeds were sown in petri dishes with 4.0 ml H_2O and with or without 0.5 g charate. After stratification for 21 days at 5°C, seeds were incubated at 23°C. SEM pictures were taken of a subsample of seeds each day during the first week. Seeds were dried in a critical point drier both with and without prior fixation in a glutaraldehyde and graded acetone series.

RESULTS

Table 1 compares germination of *Emmenanthe penduliflora* and *Eriophyllum confertiflorum* in the presence of charate, made from charred *Adenostoma fasciculatum,* and in the presence of activated charcoal. Charate produced a highly significant increase in germination whereas activated charcoal did not, and therefore it apparently is not the component of charate responsible for stimulating germination.

Emmenanthe penduliflora germination on several media, with and without charate and various extracts, is shown in Table 2. Under control conditions (i.e., without charate or extracts) germination was low although across media it was significantly greater on chaparral soil. Charate significantly increased germination on all media and this charate enhancement was greatest on chaparral soil. A water extract of charate enhanced germination as well as or better than charate applied directly. Soil extracts applied to seeds on filter paper or vermiculite had no significant effect on germination.

In contrast to *Emmenanthe, Eriophyllum confertiflorum* germi-

Table 2. *Emmenanthe penduliflora* Germination on Various Media and Treated with Charate and Aqueous Extracts of Charate and Soils. (All dishes received 7 ml of H_2O or extract; n = 10 dishes of 50 seeds each, $^{**}p < 0.01$, NS $p > 0.05$; means, within a row, with the same superscript letter and, within a column, with the same superscript number, are not different at the indicated significance level.)

	Percentage germination				
	Filter paper	Vermiculite	Potting soil	Chaparral soil	p
Control	$1^{a,1}$	5^{1}	1^{a}	10	**
Charate	18^{a}	14^{a}	11^{a}	47	**
Charate extract	54	23	9	44	**
Potting soil extract	5^{1}	8^{1}	—	—	NS
Chaparral soil extract	6^{1}	4^{1}	—	—	NS
p	**	**	**	**	

nation under control conditions was substantially greater on filter paper than other media (Table 3). This relatively high germination on filter paper (without charate) was significantly reduced with the addition of soil extracts. Charate significantly enhanced germination on all media, though a water extract of charate significantly enhanced germination only on filter paper and vermiculite.

Some of the treatments used with *Emmenanthe* (Table 2) were replicated with less moisture on filter paper, and higher moisture on other media (Table 4). Under control conditions (without charate or extracts) the additional moisture resulted in higher germination on potting soil than on chaparral soil, a reversal of the pattern observed in Table 2. From a comparison of the same media treatments in Tables 2 and 4, it is clear that altering the moisture levels can greatly magnify the charate response. Of particular interest is the observation that chaparral soil heated and cooled prior to sowing produced relatively high germination without charate. Equally surprising was the observation that neither charate nor charate extract enhanced germination on this previously heated soil.

Some of the media treatments used with *Eriophyllum* (Table 3) were also replicated with different moisture regimes (Table 5). These experiments show that once again even without charate *Eriophyllum* seeds germinate readily on filter paper but less so on other media, in particular on soils. Addition of filter paper extract reduced germination on filter paper but had no effect on soils, whereas on sand it produced a response comparable to the charate effect. In Table 3 it was noted that soil extracts reduced germination on filter paper and vermiculite. However, these soil extracts do not inhibit germination when combined with charate extract (Table 5). Heated soil extract increased germination on all media except filter paper.

An examination of the effect of different osmotic pressures on

TABLE 3. *Eriophyllum confertiflorum* GERMINATION ON VARIOUS MEDIA AND IN COMBINATION WITH AQUEOUS EXTRACTS OF CHARATE AND SOILS. (All dishes received 7 ml of H_2O or extract; n = 10 dishes of 50 seeds each, $^{**}p < 0.01$; means, within a row, with the same superscript letter and, within a column, with the same superscript number, are not different at the indicated significance level.)

	Percentage germination				
	Filter paper	Vermiculite	Potting soil	Chaparral soil	p
Control	28	$7^{a,1}$	$6^{a,1}$	$2^{a,1}$	**
Charate	55^{a}	$64^{a,2}$	56^{a}	37	**
Charate extract	70	59^{2}	$12^{a,1}$	$9^{a,1}$	**
Potting soil extract	7^{1}	1^{1}	—	—	**
Chaparral soil extract	13^{1}	2^{1}	—	—	**
p	**	**	**	**	

germination was done for species in the absence of charate. In these experiments 9 ml of water or mannitol were the only media in the petri dishes. *Emmenanthe* did not germinate under any of these conditions. *Eriophyllum* germination was 34% with water, 18% and 0% with 0.05 M and 0.15 M mannitol respectively ($p < 0.01$, LSD = 6, n = 10 dishes of 50 seeds each). Several conclusions can be drawn from these experiments. Previous tables (3 and 5) showed, under control conditions (i.e., without charate or extracts), higher *Eriophyllum* germination on filter paper than on other media. In the present experiments 34% germination with just water but no filter paper suggests there is no effect due to filter paper per se. Germination however is strongly influenced by the osmotic pressure of the medium. At 0.05 M germination was reduced 50%, possibly explaining some of the reduced germination observed with soil extracts (Tables 3 and 5), which had osmolalities between 0.04–0.05 M.

Germination of both species on mature chaparral soil and on 2-year-old-burn soil, both with and without prior soil heating, is shown in Table 6. On mature chaparral soil both species showed greatly enhanced germination when the soil was previously heated. Sterile extracts made from this heated soil produced comparable germination to the heated soil itself. However, for both species, if the soil was wetted and incubated before the sterile extract was prepared, there was a significant reduction in germination. On burn soil, germination was greater than on mature soil for both species and heating the soil prior to sowing produced higher germination. Both species showed the highest germination with sterile extracts from heated burn soil. However, if this heated soil was incubated prior to making sterile extracts, germination was reduced only for *Emmenanthe.*

For both species, SEM pictures failed to show any differences in

TABLE 4. *Emmenanthe penduliflora* GERMINATION ON ADDITIONAL MEDIA AND IN COMBINATION WITH CHARATE AND AN AQUEOUS EXTRACT OF CHARATE. (Moisture levels differed from Table 2; filter paper dishes received 4.5 ml and all other dishes received 9 ml of H_2O or extract; n = 10 dishes of 50 seeds each, $^{**}p < 0.01$; means, within a row, with the same superscript letter and, within a column, with the same superscript number, are not different at the indicated significance level.)

	Percentage germination						
	Filter paper	Vermiculite	Sand	Potting soil	Chaparral soil	Heated chaparral soil (195°C 10 min)	p
Control	0^{a}	$9^{a,b}$	2^{a}	$15^{b,c}$	1^{a}	27^{c}	**
Charate	$73^{a,1}$	$54^{b,c,1}$	$64^{a,b,1}$	$60^{a,b,1}$	47^{c}	25	**
Charate extract	87^{1}	$64^{a,1}$	$46^{a,b,1}$	$53^{a,b,1}$	15^{c}	$34^{b,c}$	**
p	**	**	**	**	**	NS	

seed coats between ungerminated controls and germinated charate treated seeds.

DISCUSSION

On soil, germination of the majority of *Emmenanthe penduliflora* and *Eriophyllum confertiflorum* seeds is stimulated by a water soluble extract of charred wood. The difference in response observed for these two species on other media suggests that the mechanism of charate stimulation may differ.

Germination under control conditions (i.e., in the absence of charate or other extracts) is distinctly different between these two species. Without charate, *Emmenanthe* germination is always very low but is consistently lower on filter paper than on soils (Wicklow 1977, Jones and Schlesinger 1980; Tables 2 and 4). *Eriophyllum* shows consistently higher control germination on non-soil media, and on certain media, germination may be as high for controls as for charate treatments on soil. It is clear that whatever is in soils that reduces *Eriophyllum* germination, it is water soluble because aqueous soil extracts applied on filter paper reduced germination to levels observed on soils.

Charate consistently enhances germination for both species regardless of media, though the magnitude of charate-stimulated germination varies with medium and moisture level. Wicklow (1977) found that *Emmenanthe* germination with charred wood was highest on potting soil and lowest on filter paper, whereas Jones and Schlesinger (1980) reported highest on filter paper and lowest on chaparral soil. In the present study *Emmenanthe* germination in the presence

TABLE 5. *Eriophyllum confertiflorum* GERMINATION ON ADDITIONAL MEDIA AND IN COMBINATION WITH VARIOUS EXTRACTS. (Moisture levels differed from Table 3; filter paper dishes received 4.5 ml and all other dishes received 9 ml of H_2O or extract; n = 10 dishes of 50 seeds each, $^{**}p < 0.01$, NS $p > 0.05$; means, within a row, with the same superscript letter and, within a column, with the same superscript number, are not different at the indicated significance level.)

	Percentage germination						
	Filter paper	Vermiculite	Sand	Potting soil	Chaparral soil	Heated chaparral soil (195°C 10 min)	p
Control	62^{1}	$26^{a,1}$	27^{a}	12^{b}	8^{b}	35	**
Filter paper extract	49^{2}	26^{1}	64^{1}	14^{a}	7^{a}	—	**
Charate extract	$75^{a,3}$	$70^{a,2}$	62^{1}	—	—	—	**
Charate extract & potting soil extract	$66^{a,1}$	$68^{a,2}$	53^{1}	—	—	—	**
Charate extract & chaparral soil extract	$73^{1,3}$	72^{2}	53^{1}	—	—	—	NS
Heated chaparral soil extract	49^{2}	39	77^{1}	—	—	—	**
p	**	**	**	NS	NS		

of charate was highest on chaparral soil and lowest on potting soil in one experiment and in another experiment highest on filter paper and lowest on chaparral soil. The only parameter that varied in these two experiments was moisture level which suggests that slight differences in experimental conditions can produce subtle differences in germination.

For both species germination was higher on soil from a two-year-old burned chaparral stand. This likely derives from residual charred wood remains in the soil. The consistently higher germination for both species on both soils when the soil was heated (but cooled prior to sowing) is possibly due to the production of a stimulant similar to what is produced in charred wood. Several observations support this. It is already known that wood need not be charred to stimulate germination: *Adenostoma* wood heated to 175°C for 10 min and powdered, produces significantly greater germination for both of these species over unheated powdered wood (S. Keeley, unpubl. data). It is also known that both heated lignin and cellulose are responsible for this effect (S. Keeley, unpubl. data). Thus plant litter in the soils, upon heating, may contribute to the stimulation of germination observed for both species (Table 6). That the propor-

TABLE 6. GERMINATION OF *Emmenanthe penduliflora* AND *Eriophyllum confertiflorum* ON MATURE AND BURNED CHAPARRAL SOILS WITH OR WITHOUT PRIOR HEATING OF THE SOIL (WITH 9 ml H_2O). In addition, sterile extracts of these heated soils were made, either immediately after heating or following wetting and incubating at 23°C for 12 days (4.5 ml of sterile extract were applied to petri dishes without other media; n = 10 dishes of 50 seeds each, $^{**}p < 0.01$, NS $p > 0.05$; means, within a row with the same superscript letter are not different at the indicated significance level).

	Percentage germination				
			Sterile extract of heated soil		
	Control (not heated)	Soil heated (195°C 10 min)	No incubation	Prior incubation	p
Emmenanthe					
Mature chaparral soil	0	31^a	32^a	1	**
Burned chaparral soil	6	17	74	24	**
p	**	**	**	**	
Eriophyllum					
Mature chaparral soil	9	48	58	28	**
Burned chaparral soil	28	52	72^a	68^a	**
p	**	NS	**	**	

tional increase was always greater when soil from mature chaparral (with greater plant matter) was heated is consistent with this hypothesis.

An inevitable complication in experiments using natural substrates is the interaction with microbes. This could have been a complicating factor in our experiments with natural soils. As mentioned above, heated soils stimulate germination of *Emmenanthe* and *Eriophyllum.* However, if these heated soils are incubated under conditions suitable for microbial growth, a sterile extract of this soil will inhibit germination over a sterile extract made immediately after soil heating (Table 6). Whether or not microbial toxins control germination of these species under natural conditions is unknown. Kaminsky (1981) has argued that dormancy of chaparral seeds under the mature canopy is due to just such an effect. The fact that *Emmenanthe* does not germinate in mature chaparral soil is not likely because of such toxins since it will not germinate on filter paper or other artificial substrates unless charate is applied. *Eriophyllum* seeds appear to be inhibited by natural soils, thus it is possible that microbes play a role in limiting its germination in mature chaparral.

Two mechanisms of charate-stimulated germination may be operating in these two species, though presently it is not possible to attribute conclusively one or the other to either species. 1) Charate may "bind" or deactivate an inhibitor in the soil and thus release seeds from inhibition or 2) charate may act directly on the seed either by extracting or altering an inhibitor, affecting seed coat membrane permeability or directly stimulating germination in some other way.

Chaparral populations of *Emmenanthe penduliflora* (but not desert populations, e.g., Jones and Schlesinger 1980) show a nearly obligatory dependence upon charate for germination, regardless of the medium, and thus mechanism number one seems unlikely.

Eriophyllum confertiflorum shows a facultative response to charate in that germination is most dependent upon charate when seeds are sown in soil. However, the data presented here for *Eriophyllum* are consistent with either of the two mechanisms proposed above. Consistent with mechanism number one are the following: germination without charate is consistently much higher on non-soil media, soil extracts inhibit germination and charate extract overcomes inhibition due to soil extracts. However, mechanism number two can not be ruled out for several reasons. One is that charate increases germination on both soils and artificial media. Higher germination on artificial media in the absence of charate can be explained as the result of an inhibitor within the *Eriophyllum* seed that is easily leached out in deionized water but not in soil solutions with their higher osmotic pressures. Observations consistent with this interpretation are: the strong inhibition of germination by mannitol, the reduction of germination on filter paper with the addition of soil extracts and even with the addition of filter paper extract.

Emmenanthe penduliflora and *Eriophyllum confertiflorum* seedlings are abundant in recently burned chaparral stands. Previous studies have shown that heat per se has no stimulatory effect on germination of either species (Sweeney 1956, Keeley and Keeley 1982, Keeley et al. in press). On the natural soils the bulk of the seed pool of each species requires contact with a water soluble product from charred wood. This product is presumably most abundant immediately after fire, as is germination of *Emmenanthe* and *Eriophyllum.* With time, charred fragments are very likely leached of this product accounting for the reduced establishment of these species in older burns. This may account for the distribution of annual species such as *Emmenanthe penduliflora* (and other charate dependent species such as *Phacelia* spp.) in older burns. In the first year after fire these herbs are locally widespread, but in subsequent years the few that are present are commonly clumped around the charred remains of shrubs (J. and S. Keeley, pers. observ.). Eventually another fire will be required for additional seedling establishment.

Perennial species such as *Eriophyllum confertiflorum* dominate burned sites for several years after fire, though largely from seedlings established the first year after fire (Keeley et al. 1981). *Eriophyllum* germination is much more dependent upon charred wood on soils than on artificial media, suggesting that at least for part of the seed pool, the charred wood product may overcome some inhibitory component of soils. As the shrub canopy returns, the bulk of the seed pool remains dormant until the next fire. However, away from the shrub canopy, soils apparently are less inhibitory since *Eriophyllum* (unlike *Emmenanthe*) commonly establishes in gaps within the chaparral matrix.

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CHARACTERISTICS OF MIXED EVERGREEN FOREST IN THE SONOMA MOUNTAINS OF CALIFORNIA

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ABSTRACT

Ten stands of mixed evergreen forest were sampled at 16 locations using belt transects to estimate density and basal area of overstory tree species, and small quadrats to estimate cover of understory species. Physical environmental variables were measured at each quadrat. Ordination based on overstory composition showed four distinct clusters, but that based on understory composition showed little differentiation. The overstory types included *Pseudotsuga*-hardwood and mixed hardwood phases, thus incorporating both north and south extremes of this wide-ranging forest type. No correlation was found between overstory or understory composition and measured site characteristics.

The mixed evergreen forest of California is a poorly defined and little-studied vegetation type covering large areas of the lower montane zone of the state. The type, in part, was probably first recognized by Cooper (1922) as his "broad-sclerophyll formation," which ranged from southern Oregon to northern Baja California. Cooper defined this formation primarily as being dominated by broad-sclerophyll trees (*Quercus, Lithocarpus, Arbutus,* and *Umbellularia*), with a small coniferous component (*Pinus* or *Pseudotsuga*) in its transitional limits in the North Coast Ranges and at its upper limits in the Sierra Nevada and Transverse Ranges. Munz and Keck (1949, 1950) were the first to define explicitly a Mixed Evergreen Forest Community on the basis of indicator dominants including a variety of broad-leaved evergreen trees (*Quercus, Lithocarpus, Arbutus, Umbellularia*), two broad-leaved deciduous trees (*Acer macrophyllum* and *Quercus kelloggii*), the conifer *Pseudotsuga menziesii,* and a variety of shrubs. Whittaker (1960) suggested a more restricted definition, to include only those forests with shared dominance between coniferous and broad-leaved evergreen trees. He recognized the type as transitional between sclerophyll vegetation and the montane and coastal coniferous forests, but argued for its being considered a formation in itself. Sawyer et al. (1977) have dealt most extensively with the community, and they used a broader definition. They rec-

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ognized mixed evergreen forest as typified by closed stands of broad-leaved sclerophyll dominants with a minor to significant conifer component. Their treatment also recognized two divisions of the type: the *Pseudotsuga*-hardwood forest, and the mixed hardwood forest. Barnhart (1978) adopted a similarly broad definition, viewing the mixed evergreen forest of the southern North Coast Ranges (especially in Sonoma County) as a series of associations ranging from mesic conifer-hardwood forest to more xeric hardwood woodland. For the present, we define "mixed evergreen forest" as any stand dominated by a mixture of coniferous and broad-leaved evergreen trees, or dominated by a mixture of broad-leaved evergreen trees with at least a small coniferous component.

The literature pertaining to mixed evergreen forests has been synthesized recently by Sawyer et al. (1977). A few published quantitative accounts of the community exist (e.g., Campbell 1980, Waring and Major 1964, Wells 1962, Whittaker 1960), but these deal with only the distributional limits of the community. No accounts are available of mixed evergreen forest—nor of many other communities—in the Coast Ranges between San Francisco and the Mendocino area. As part of a study of tree spatial patterning (Wainwright 1982, Wainwright and Pollock unpubl. data), we sampled several stands of mixed evergreen forest in the Sonoma Mountains. Our purpose was to characterize quantitatively the mixed evergreen forests found in that small but representative and central area.

METHODS

Study site. The study was carried out at Annadel State Park, located at the north end of the Sonoma Mountains, Sonoma County, California (Fig. 1). These mountains are low (maximum elevation ca. 650 m), with a north-south trend. The range is dominated by Pliocene Sonoma Volcanics overlying older sediments (Jenkins 1951). Climatic data have been recorded at two nearby stations: Santa Rosa, ca. 12 km west northwest of the park, and Sonoma, ca. 18 km southeast of the park (U.S. Weather Bureau 1964). Both stations show the Mediterranean-type precipitation pattern typical of most of California (Fig. 2). Though total annual precipitation is low (710–770 mm/yr), winter rainfall is abundant, averaging more than 150 mm in January. Temperatures are hot in summer (July mean daily maximum 28–29°C) and mild in winter (January mean daily minimum 2–3°C). The highest and lowest temperatures on record are 44°C and −9°C (for Santa Rosa). The area has a significant amount of frost: mean number of days with minimum temperature below 0°C is 47–48. The climate of the study site is expected to be generally similar to that of these stations, with some differences due to local topography.

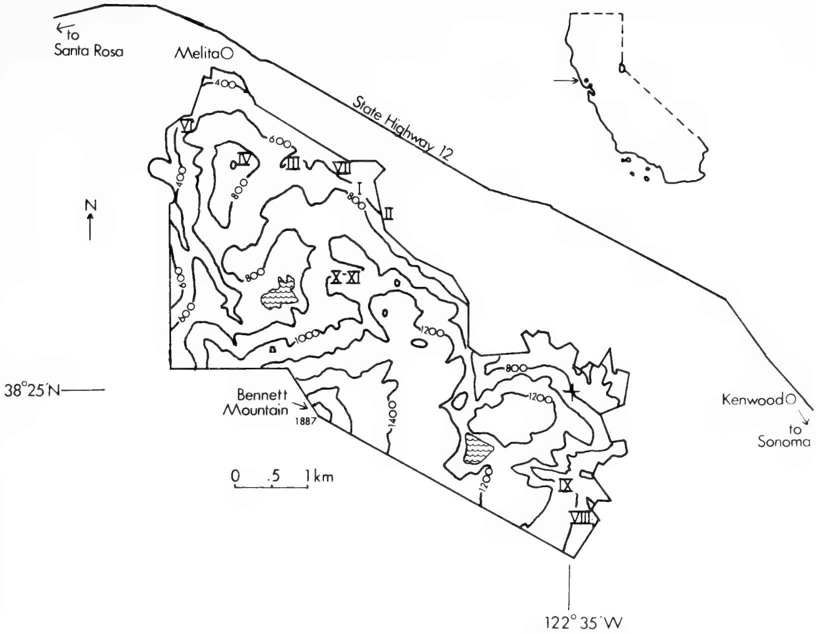

FIG. 1. Map of Annadel State Park. Roman numerals show approximate locations of sample stands. Elevations are in feet. Arrow and dot on inset map of California show location of the Sonoma Mountains.

The vegetation of Annadel is a complex mosaic of types including (using the nomenclature of Munz and Keck 1950) mixed evergreen forest, northern oak woodland, coastal prairie, valley grassland, chaparral, and freshwater marsh. Evergreen forest is generally restricted to the northerly slopes or tops of hills. South slopes are typically dominated by chaparral or grassland, and valley bottoms by oak woodland or grassland. Oak woodland also occupies many north slopes, particularly at higher elevations. Some of the oak-dominated communities on Bennett Mountain have been described by Tunison (1973), and his work is the only available description of vegetation in the park.

Little is known of the ecological history of the park. However, the recent human history of the park and its surroundings is well known, and has some ecological relevance. Prior to European settlement in the early 19th century, the area was inhabited by the Southern Pomo tribe of Native Americans. Annadel contains two small village sites, an obsidian quarry, and several work sites dating from this period (Wright 1975). Futini (1976) chronicled the history since that time. From the 1830s to the 1870s the park area apparently was used

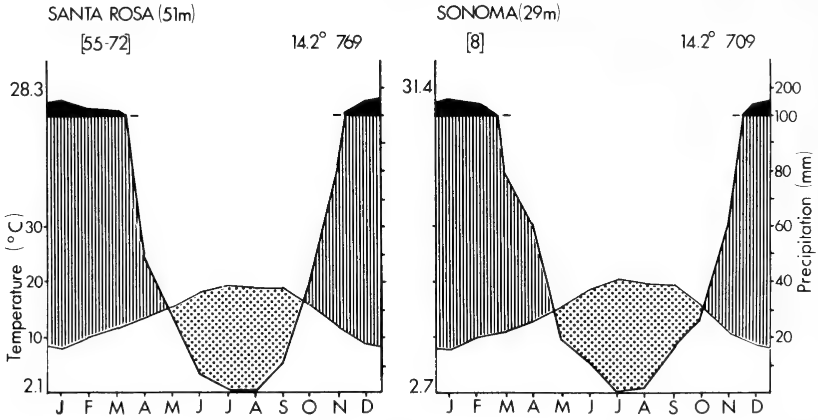

FIG. 2. Climate diagrams (after Walter 1979) for two nearby weather stations. Mean monthly precipitation (note scale change above 100 mm) and mean monthly temperature are given. Elevation follows station name. Duration of observations in years is in brackets below the station name (for Santa Rosa, first figure is for temperature, second for precipitation). Mean annual temperature and mean annual precipitation are at upper right. Along left margin, lowermost figure is mean daily minimum temperature for coldest month, uppermost is mean daily maximum temperature for hottest month. Period of relative drought is indicated by dot shading; relatively humid season is indicated by vertical shading. Data from U.S. Weather Bureau, 1964.

primarily for cattle grazing, with some quarrying of basalt. From 1870 to about 1920, quarrying for cobblestones and other building materials was the dominant business in the area, and several quarry sites are still apparent in the park. During this period, many of the hardwoods in the park area were cut for firewood. Around 1930, cattle ranching returned and continued as the dominant activity until the state park was established in the 1970s.

Field methods. Methods were chosen to serve two purposes: this vegetation description and a spatial pattern analysis of the tree dominants (Wainwright 1982; Wainwright and Pollock, unpubl. data). Ten forest stands were subjectively selected to reflect the ranges of canopy species composition and habitat (slope and aspect) for mixed evergreen forest at Annadel. Selections were restricted to stands of such size and uniformity that a variable-length transect up to 100 m long could be established without crossing any major transition in overstory composition. Accessibility was also a significant factor.

Mixed evergreen forest is typically composed of two layers: a usually dense tree overstory and a more-or-less sparse shrub and herb understory. These layers were treated separately in the data collection and analysis.

Trees were sampled using 5-m wide variable-length transects. From a randomly selected starting point within a given stand, a line was established approximately parallel to slope contours. Species, breast-height diameter (dbh), and distance along the line were recorded for each tree stem taller than 1 m that was encountered within 2.5 m on either side of the line. Each tree stem with no above-ground connection to another was counted as an individual, even though two or more nearby stems were sometimes clearly of the same genet. Stems with an above-ground connection were recorded as parts of the same individual. Transects were continued until either 132 trees had been recorded or a distinct change in overstory composition was reached. (The 132-tree limit was chosen for statistical reasons relating to the spatial pattern analysis.)

Understory plants were sampled using a 1 m^2 square-shaped quadrat laid at 20-m intervals (10 m in transect "1a") along the center line of each transect. In each quadrat, cover was estimated for each species of vascular plant, and for mosses as a group. At each quadrat, environmental factors (aspect, slope, estimated crown closure, and soil surface pH) were recorded, and soil samples were collected for the A horizon (usually ca. 6 cm deep). These samples were later analyzed for color, texture, and consistence and compared with descriptions of mapped soil units of the area (Soil Conservation Service 1972) to determine the soil type present.

Transects were replicated in some stands, for a total of 16 transects. (In one additional transect, "2b," only overstory data were collected.) Species nomenclature follows Munz (1973).

Analytical methods. To classify the stands, overstory and understory were treated separately. For the overstory, similarities of the 17 samples were calculated using Motyka's modification of Sorensen's index of similarity (IS) as described in Mueller-Dombois and Ellenberg (1974). Calculations were made based both on stem density and percent stem cover. These similarities were visually displayed as a two-dimensional ordination, using comparative stand ordination (Bray and Curtis 1957). Three ordinations were done: one based on stem density, one based on percent stem cover, and a composite using the average of the two IS values. From these results, samples were placed into groups showing high within-group IS values and low between-group IS values.

A similar procedure was used to classify the 16 understory samples, with the following differences: (1) the index of similarity was based on the mean percent cover of each species; and (2) the ordination had to be carried out to three dimensions to adequately represent the range of dissimilarity in understory composition.

RESULTS AND DISCUSSION

The overstory ordination based on percent stem cover and the composite ordination showed similar transect-clusterings, while that based on stem density showed little clustering. For grouping of stands,

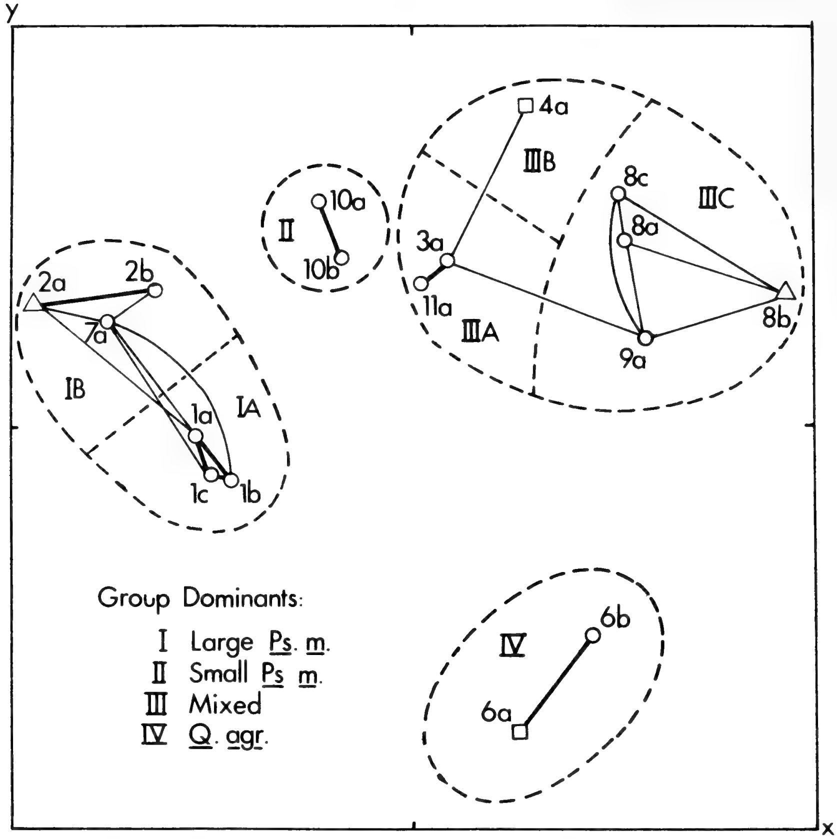

FIG. 3. Ordination of transects by overstory composition. Triangles mark endpoints of ordination on first (x) axis; squares mark endpoints on second (y) axis. Bold lines connect stands with IS values greater than 75%; light lines connect those with values between 60% and 75%. Dashed lines and Roman numerals indicate clustering as discussed in text. Arabic numerals with lower-case letters refer to individual transects.

the composite ordination (Fig. 3) was used because it shows the clearest separation of transect clusters. Four quite distinct clusters are apparent, two of which may be further subdivided.

These clusters may be typified as follows. Group I is dominated by large (30–170 cm dbh) *Pseudotsuga menziesii.* In the scheme of Sawyer et al. (1977), this group would fall under the broad heading "*Pseudotsuga*-hardwood forests," and is representative of the Klamath Mountains/North Coast Range phase of the forest type. Subgroup IA represents dense stands of *Ps. menziesii* with *Umbellularia californica* forming a sub-canopy. This type of forest is not recognized

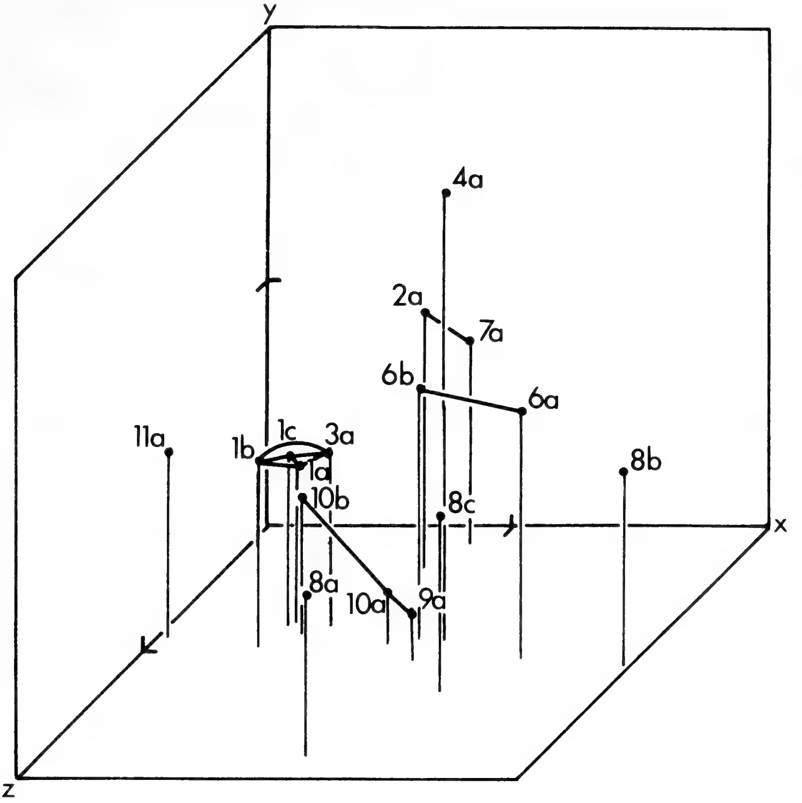

FIG. 4. Ordination of transects by understory composition. Endpoints used are: x-axis—11a and 8b; y-axis—9a and 4a; z-axis—7a and 8a. Bold lines connect points with IS greater than 50%. Numerals and letters refer to individual transects.

in the Sawyer et al. scheme, but is apparently structurally similar to their "*Pseudotsuga-Lithocarpus* forests." Subgroup IB represents open forest of almost pure *Ps. menziesii,* with a sparse mixture of broadleaf evergreens in the lower canopy layers. Group II also tends toward pure *Ps. menziesii,* but contains dense stands of small (less than 20 cm dbh) *Pseudotsuga* with significant amounts of *Umbellularia, Quercus kelloggii,* and *Quercus garryana*; this group would also fall under the "*Pseudotsuga*-hardwood" heading.

Group III is a cluster of mixed stands, each containing a significant amount of *Q. kelloggi.* Sub-group IIIA is co-dominated by *Ps. menziesii, U. californica,* and *Q. kelloggi*; IIIB is dominated by *Q. kelloggi,* with some *Ps. menziesii* and *U. californica*; IIIC is very mixed, each stand consistently containing six tree species. This group appears to be transitional between *Pseudotsuga/Umbellularia* forest

TABLE 1. TRANSECT SUMMARY. Overstory group refers to Fig. 3. Notes: 1. Dash indicates no data collected. 2. Soil types: Fo—Forward gravelly loam; Gg—Goulding clay loam; Gl—Goulding cobbly clay loam; La—Laniger loam; Sk—Spreckels loam. 3. Geological substrates: Tertiary: Tsa—andesitic to basaltic lava flows; Tsag—agglomerate with volcanic breccia and tuff breccia; Tsrp—perlitic rhyolite; Tst—pumicitic ash-flow tuff. Quaternary: QTge—fluviatile gravel, sand, silt, and clay with locally interbedded tuff (from Fox et al., 1973). 4. For overstory, upper figure is density (#/ha), lower figure is total basal area (m²/ha).

Overstory group:	I						II		III							IV	
	A			B					A		B	C					
Transect:	1a	1b	1c	7a	2a	2b	10a	10b	11a	3a	4a	8a	8b	8c	9a	6a	6b
Strip length (m)	351	275	272	99	243	328	103	100	114	142	159	59	62	73	106	149	150
No. of quadrants	23	14	14	6	13	0	6	6	6	7	8	4	4	4	6	8	8
Mean slope (%)	41	38	46	42	24	—[1]	50	38	56	60	30	39	19	40	59	24	23
Average aspect	N	NE	NE	E	N	—	N	N	N	N	NE	E	E	E	N	NE	NE
Mean pH of soil	6.5	6.5	6.6	6.3	6.2	—	6.6	6.7	—	6.6	6.6	6.9	6.5	6.9	6.5	6.5	6.4
Soil type[2]	Gl	Gl	Gl	Sk	Sk	—	Sk	Sk	Sk	Gg	Gg	La	La	La	Fo	Gg	Gg
Geological substrate[3]	Tsa	Tsa	Tsa	Tsa Tsag	Tsa QTge	Tsa QTge	Tsrp	Tsrp	Tsrp	Tsa	Tsa	Tst	Tst	Tst	Tst	Tsag	Tsag
Overstory composition[4]																	
Umbellularia californica	530	630	740	180	40	70	270	350	930	990	290	540	710	250	760	600	570
	6	8	13	0	0	1	2	2	11	10	6	6	5	2	7	0	5
Pseudotsuga menziesii	190	180	200	240	430	370	1710	1820	860	460	260	1020	130	600	320	70	
	50	78	68	76	61	43	27	17	17	6	6	3	0	9	2	0	
Quercus kelloggii				80	30	90	290	140	260	340	1050	510	620	630	340	30	80
				10	1	4	9	7	17	16	19	23	10	12	7	1	6
Heteromeles arbutifolia	10	20					40		40	30	10	440	1560	1530	470	10	50
	0	0					0		0	0	0	0	2	1	0	0	0
Quercus agrifolia	10			120	20	80						170	60	220	40	640	680
	0			2	0	1						1	1	3	1	26	17

TABLE 1. CONTINUED .

Overstory group:	I						II		III							IV	
	A			B					A		B	C					
Transect:	1a	1b	1c	7a	2a	2b	10a	10b	11a	3a	4a	8a	8b	8c	9a	6a	6b
Quercus	10			60		10	230	480	40		10			30			30
garryana	0			1		0	7	17	2		0			0			0
Arbutus					60	180	20	60				580	1230	330	280		110
menziesii					0	2	1	3				12	15	7	8		0
Sequoia		140	30						140								
sempervirens		20	3						12								
Amelanchier									40	10					280		
pallida									0	0					0		
Arctostaphylos											10						30
manzanita											0						0
Aesculus												30					
californicus												0					
Fraxinus	10																
latifolia	0																

and *Q. kelloggi* woodland. In fact, Group IIIB could be considered as strictly oak woodland, were it not for the component of small-statured *Ps. menziesii* and *U. californica.* [Tunison (1973) noted the recent increase of both of these evergreen species in oak communities, and suggested that this could result from a recent development of a closed oak canopy producing an increasingly mesic understory. He also suggested that it is likely that mixed evergreen forest will eventually replace these communities.] Group IV represents two broad-leaved stands dominated by *Quercus agrifolia* with *U. californica* sub-dominant. This would be included under the "mixed hardwood forests" by Sawyer et al., and is representative of the South Coast Range/Southern California phase of the forest type; but it again is not a species combination they mention. A similar type in the Berkeley Hills has been discussed by McBride (1974), who suggested that *U. californica* is replacing *Q. agrifolia* in oak woodlands.

The ordination based on understory similarities (IS) is shown in Fig. 4. Overall, the understory samples were quite diverse: the highest similarity was 70%, and only 10 sample-pairs (out of 120) showed greater than 50% similarity. Consequently, little clustering was observed, and no general classification of the understory was possible. Clearly, much of this diversity may result from the small size (4–23 m^2) of the samples taken. These samples are not minimal area (suggested to be 50–200 m^2 for temperate forest understories by Mueller-Dumbois and Ellenberg 1974), so the ordination represents only the most common species of each stand.

Table 1 summarizes the composition of overstory transects with species listed in order of constancy. Clear group segregations are noted by underlining. Of the overstory species, only *U. californica* occurred in every stand, although *Ps. menziesii* and *Q. garryana* occurred in all groups and subgroups.

Understory composition showed little segregation by overstory group (Wainwright 1982). Of about 60 species encountered in the understory, nine (*Rhus diversiloba, Melica torreyana, Osmorhiza chilensis, Galium californicum, Symphoricarpos mollis, Torilis arvensis, Vicia* sp., *Cynosurus echinatus,* and *Dryopteris arguta*) occurred in every overstory group and subgroup. A few species, however, clearly segregated: *R. diversiloba* and *Festuca californica* both reached their highest cover in subgroup IIIB, *Bromus diandrus* is characteristic of subgroup IB, and *Polystichum munitum* is characteristic of IA.

Table 1 also includes a summary of physical environmental factors. There are no striking correlations between any of these factors and overstory or understory composition. Several factors could be responsible for this. The area studied is quite diverse in geologic substrate and topography. The area also has a long history of human use that could locally influence vegetation. Other historical factors may also be involved.

Lack of specific information regarding human and other disturbances is a major drawback in the analysis. Clearly, the vegetation analyzed is transitional, and composition might be much different if the site had had no human usage. As was noted earlier, the park holds several abandoned quarries, which were avoided in our sampling. However, the associated impacts of wood cutting (mostly prior to 1920—Futini 1976) were unavoidable: there was evidence of past cutting of *U. californica, Q. kelloggii,* and *Sequoia sempervirens* in all stands in which they occurred. There was also evidence of past fire in some stands. The combination of known selective removal of species and unknown occurrences of other disturbances make successional interpretation of our data impossible without thorough knowledge of age-structures of the populations involved.

There is much room for further study of woodland and forest communities in the Coast Range near San Francisco Bay. First, basic descriptive work is needed, followed by study of the dynamic relationships among the various communities. While our data provide no conclusions regarding such relationships, there are indications (Barnhart 1978, McBride 1974, Tunison 1973) of a successional trend from oak woodland to mixed evergreen forest. However, as Barnhart (1978) pointed out, the diverse nature of plant communities in the region makes conclusive study of successional trends quite difficult.

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CORRELATION OF PHYSIOLOGICAL DIVERGENCE WITH REPRODUCTIVE MODE IN CHAPARRAL SHRUBS

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ABSTRACT

Transpiration rates among chaparral species were found to correlate with mode of reproduction. Species of *Ceanothus* and *Arctostaphylos* that regenerate following fire only by seedlings were found to transpire on the average 2 times the rate of stump-sprouting species.

The correlation of these two life history traits suggested that other characteristics might also diverge among species of different reproductive mode. Data from the literature for water use, photosynthesis, and growth suggest that the divergence within *Ceanothus* and *Arctostaphylos* represents a fundamental change in species life-history; seedlings of obligate-seeding species may have been selected for rapid growth, exploitative resource use, and physiological tolerance of stresses during seedling establishment. Thus, obligate seeders may have seedlings with a better potential for establishment in comparison with seedlings of stump-sprouting species.

INTRODUCTION

Arctostaphylos and *Ceanothus* are among the dominants of the California chaparral and undergo regeneration of their populations following fire. In contrast to other chaparral genera, both *Arctostaphylos* and *Ceanothus* are characterized by two divergent reproductive modes. Species with the putative ancestral mode regenerate by resprouting from underground burls and by establishing seedlings (Wells 1969; Stebbins 1974, p. 180), whereas other species reproduce only by seedings. Some work has called attention to the ecological aspects of these genera and their reproductive modes in an effort to understand how the obligate-seeding species coexist with the putative ancestral form (Keeley 1977a,b; Keeley and Keeley 1977; Keeley and Zedler 1978). One central hypothesis of this work has been that the obligate seeder mode was a response to conditions favorable for seedling establishment (Keeley 1977a, Keeley and Zedler 1978). Other investigators have concentrated on differential flower production and pollinator attraction between these reproductive modes (Carpenter and Recher 1979, Fulton and Carpenter 1979).

The establishment of individuals during the juvenile stage is extremely critical and often determines the distribution of species within natural communities (Grubb 1977, Werner 1979). Germination and establishment of seedlings is rare and limited within established

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chaparral (Christensen and Muller 1975b). Also, seeds of *Arctostaphylos* and *Ceanothus* species have dormancy mechanisms that usually restrict their germination to the first season or two following fire (Hanes 1977). This is the stage, along with density-dependent thinning within the next 10 years (Schlesinger and Gill 1978), that determines the degree of success for the obligate seeder. Selection might be expected to act differentially between these two reproductive modes at this life history stage, e.g., resulting in faster growth the first few years after fire among obligate seeders (Carpenter and Recher 1979). Because the juvenile stage is physiologically more sensitive to environmental conditions of the habitat (e.g., water stress; Schlesinger and Gill 1980), an adaptive physiological response would be critical for species with the obligate seeder mode.

This article describes divergence in a physiological characteristic, transpiration, that correlates with the established divergence in reproductive modes. Furthermore, I propose here that other aspects of growth and physiology may also diverge along with reproduction and suggest that the reproductive divergence within *Arctostaphylos* and *Ceanothus* represents an adaptive shift in the entire life-history among the derived, obligate-seeding species, rather than a change in reproductive characteristics only.

METHODS

The chaparral species in this study were collected from two sites in Marin County, California. Individuals used in the first three experiments were collected from a southeast-facing slope of a ridge off Pine Mountain. *Adenostoma fasciculatum* dominates on shallow, sandstone-derived substrates, along with *Arctostaphylos glandulosa, Ceanothus ramulosus, Heteromeles arbutifolia* and minor contributions from several other species. On adjacent shallow, serpentine-derived soil *Arctostaphylos montana* is found most abundantly along with *Ceanothus jepsonii, Adenostoma fasciculatum, Quercus durata* and minor contributions from several other species. On deeper soils, grasslands are found. Mixed sclerophyll forest species such as *Quercus agrifolia, Umbellularia californica, Arbutus menziesii* and *Pseudotsuga menziesii* sparingly occupy ravines along with chaparral on the southeast-facing slopes, but they dominate most of the northerly exposures. Mt. Tamalpais was the second site where chaparral species were collected from three adjacent, parallel, south-facing ridgetops. The first ridge was predominantly covered with *Arctostaphylos nummularia* var. *sensitiva* and *A. glandulosa* along with a shrub form of *Quercus wislizenii.* The second ridge was dominated by *Arctostaphylos canescens. Ceanothus foliosus, Arctostaphylos glandulosa* and *Adenostoma fasciculatum* were also found here. The third location was on a partially serpentine and sandstone-derived substrate and contained *Arctostaphylos montana, A. glandulosa, Adenostoma fasciculatum* and *H. arbutifolia.*

Transpiration rates of 14 different species were compared using potometers. The first two experiments were performed during the drought season for these species. Field collections were taken on 17 September 1982 and 31 August 1983. The species were inactive in terms of growth or reproduction and were under considerable water stress. The second two experiments were conducted during the growing season, collections occurring on 1–2 February 1984. At this time the *Arctostaphylos* and *Ceanothus* species were initiating flowers or the buds were swelling. Only *Adenostoma* evidenced significant current-season vegetative growth. Field-collected branches were transported to the lab with their cut-ends submerged, immediately recut, and mounted underwater into erlenmeyer flasks with distilled water. The potometers were set up in a random-block design and left for two days under greenhouse conditions for the first two experiments and one day for the latter two. Conditions in the greenhouse varied considerably between experiments although the maximum air temperature remained between 30–35°C. Experiments I and IV experienced partly cloudly days including complete morning overcast that was prolonged during experiment I. Experiments II and III were conducted on days having a brief (II) or very brief (III) morning overcast followed by sunny conditions. Water loss was determined gravimetrically once daily and transpiration rates were calculated based upon leaf area. Leaf area was determined using the method of Mahall and Schlesinger (1982) modified by using photocopies of the leaves rather than using photographic proof paper. Five replicates were used in I, III, and IV and 6 in II. Statistical analysis was performed using a group-comparison "t"-test with log-transformed data (Zar 1974).

RESULTS

Because the environmental conditions of the greenhouse differed between experiments, absolute rates cannot be directly compared (Table 1), but a significant difference in transpiration rates does exist when stump-sprouting species are compared to obligate seeders. While some overlap does occur, obligate-seeding species transpired on the average at a rate twice that of stump-sprouters. This suggests that there has been a divergence among these species in their water relations that correlates with changes in reproductive mode.

The transpiration rates showed some additional patterns. The slowest rates were observed among species usually found in sclerophyll forests rather than chaparral (e.g., *Quercus chrysolepis, Umbellularia californica, Arbutus menziesii*) even though they may have occurred in "shrub-form" within chaparral stands. Among chaparral dominants, the *Ceanothus* species consistently transpired at faster rates than the *Arctostaphylos* species despite the great variety of leaf size or shape and edaphic origin. All of the obligate-seeders transpired at several times the rate of most sprouting species with two exceptions, *Rhamnus californica* and *Adenostoma fasciculatum.*

Rhamnus was included in experiment II and transpired at a rate similar to that of *Arctostaphylos montana,* an obligate seeder. *Rhamnus californica* however, is locally more abundant in more mesic sites and seems to increase in abundance in fog-dominated sites along the coast (pers. observ.), and thus may be considered to be a plant of more mesic circumstances than typical chaparral. The transpiration rates of *Adenostoma fasciculatum* were always within the range of the obligate seeders. For *Adenostoma,* this was undoubtably a reflection of greater transpiration rates compared with other sprouters, but may also represent an overestimate to some extent due to two circumstances. One may be the method chosen to determine leaf surface area. More error can be expected when determining leaf area for small, terete needles than for larger, flat leaves. The results for each experiment were statistically significant ($p < 0.05$) even though these two species overlap in transpiration rates with obligate seeders (except for experiment IV). This could be due to the occurrence of substantial new growth on *Adenostoma* shoots while all the other species still had only previous season's leaves. In the last two experiments with *Adenostoma* branches containing new growth, the magnitude of the difference between *Adenostoma* and the other sprouters is much greater compared to the earlier experiments. Without *Adenostoma* included in the data analysis, the difference between rates of obligate seeders and sprouters is highly significant ($p < 0.005$ without *Adenostoma* for IV). *Adenostoma* will be discussed in more detail later.

DISCUSSION

The obligate seeder mode of reproduction has been suggested to be an adaptive response to fire (Jepson 1939, Wells 1969), an environmental factor that has overwhelmingly shaped many of the characteristics of chaparral vegetation (Hanes 1977). Keeley and Zedler (1978) listed three life history characteristics important with respect to fire: 1) relative ability to survive fires; 2) relative ability to establish seedlings after fire; and 3) relative longevity and competitive ability between fires. Stump-sprouting species have a higher post-fire survival rate than obligate seeders. Although survival varies by species and location, at least some percentage of the stump-sprouting population survives fire (Horton and Kraebel 1955; Hanes 1971, 1977; Keeley and Keeley 1977, 1981) compared with complete elimination of obligate seeders. Comparisons of longevity have yielded various results. Some work suggests shorter lifetimes for most obligate-seeding species (Horton and Kraebel 1955; Hanes 1971, 1977; Grant 1977, p. 272), although great relative longevity has been found for other species (Keeley 1975, Keeley and Zedler 1978).

Because obligate seeders seem to be at a disadvantage in regard to survival of individuals after fire, and, at best, neutral considering longevity, the inability to resprout in obligate seeders suggests there must be significant differences between these modes in seedling establishment. Keeley (1977a) and Keeley and Zedler (1978) proposed that the obligate seeder mode is a response to conditions advantageous to seedling establishment and showed that abundance and diversity of obligate-seeding species are positively correlated with longer intervals between fires. They suggested that these longer between-fire intervals allowed for thinning of shrubs in older stands, opening up larger gaps following fires for seedling establishment between resprouting shrubs.

There should be a differential advantage during establishment, however, among individual seedlings of obligate seeders over those of sprouting-species in order to maintain the obligate-seeding populations. It becomes necessary, therefore, to consider what characteristics would be required to convey a differential advantage at establishment. If there are no significant differences between seedlings of stump-sprouting species and obligate seeders, then seeders would be at an advantage only if they numerically dominated potential establishment sites. On the other hand, if seedlings of obligate seeders were physiologically superior with respect to establishment, then numerical dominance of buried seed reserves would not be essential. In general, greater reproductive allocation has been found among obligate seeders for numbers of flowers and nectar production (Fulton and Carpenter 1979) and seed production (Keeley 1977b). Following fires seedlings of obligate seeders have tended to be more abundant than those of stump sprouters (Horton and Kraebel 1955, Hanes 1971, Vogl and Schorr 1972, Keeley and Zedler 1978); however, these studies have investigated only a limited number of species. Keeley and Keeley (1977) found that reproductive effort in obligate seeders was not maximized early in the life history but increased with time, as in stump sprouters. In younger but mature stands (23 yr) there was no significant difference in vegetative or reproductive allocation between *Arctostaphylos glauca* (seeder) and *A. glandulosa* (sprouter). Furthermore, other comparisons between congeneric pairs in both *Arctostaphylos* and *Ceanothus* have yielded no consistent pattern between stump sprouters and obligate seeders regarding seed and fruit production, numbers of viable seeds in the soil, numbers of seedlings following fire, and post-fire seedling mortality (Keeley 1977b). Seed production may differ greatly between ecotypes and be extremely poor in obligate seeders (Vasek and Clovis 1976). Seed production has also been variable and dependent upon weather patterns in all species examined (Keeley and Keeley 1977, 1981; Baker et al. 1982). The overall impression is that some obligate-seeding species may achieve seedling dominance by numerical superiority (e.g., *Ceanothus greggii*) but that this is not a consistent characteristic of species with this reproductive mode.

Alternatively, physiological superiority may provide the potential for successful seedling establishment. Post-fire conditions for establishment are initially favorable, particularly with regard to nutrient levels (Christensen and Muller 1975a), but quickly deteriorate due to growth of fire-response herbaceous and woody species (Horton 1950, Schultz et al. 1955) as well as to temperature and drought stress as summer approaches (Ammirati 1967, Hanes 1977). Physiological characteristics influencing growth under these conditions, particularly water use and carbon gain, should differ between reproductive modes if obligate seeders have an advantage at the level of individual seedlings. Most recent summaries of physiological work on chaparral species (e.g., Hanes 1977, Poole et al. 1981, Oechel et al. 1981) have not attempted to correlate physiological processes with reproductive mode, however, but instead have concentrated on characteristics of individual species or on comparisons among vegetation of different Mediterranean-type climates. The transpiration data from this study (Table 1) suggest a divergence among these species in their water relations correlated with changes in reproductive mode. Such a remarkable coincidence leads one to consider the likelihood of an integral relationship between the two processes.

Early suggestions concerning water use by evergreen species were that water use would be moderate, soil moisture would be conserved, and species would just be entering dormancy near the end of the drought period (Specht 1972a,b). As pointed out by Poole et al. (1981), this pattern is consistent with certain species only, e.g., *Adenostoma fasciculatum, Quercus dumosa,* and *Rhus ovata* (all stump sprouters), but not with *Arctostaphylos glauca* or *Ceanothus greggii.* These two obligate seeders differ in several ways from the stump sprouters. Poole et al. (1981) suggest that "in a competitive situation, a species captures and uses more water by using water lavishly when it is available, rather than by conservatively using water. Such a pattern exists in *A. glauca* and *C. greggii.*" Also, they found both *Ceanothus greggii* and *Arctostaphylos glauca* maintained leaf conductances down to −6.0 MPa while sprouting species showed no conductance at higher levels of xylem tension (−2.0 MPa for *Rhus ovata* down to −5.0 MPa for *Adenostoma fasciculatum*). As chaparral species experienced increasing water stress during the summer drought period, Baker et al. (1982) reported *Adenostoma fascicu-*

TABLE 1. TRANSPIRATION RATES OF SELECTED SPECIES IN g H_2O/dm^2/DAY ± 1 SE. Data analyzed by group-comparison "t"-test on log-transformed data: Exp I: $p < 0.05$, $t = 2.50$, $df = 7$; Exp II: $p < 0.05$, $t = 2.68$, $df = 7$; Exp III: $p < 0.05$, $t = 2.63$, $df = 5$; Exp IV: $p < 0.10$, $t = 2.18$, $df = 6$, without *Adenostoma*: $p < 0.005$, $t = 5.24$, $df = 5$.

	Experiments			
	I	II	III	IV
Stump-sprouters				
Adenostoma fasciculatum	10.47 ± 2.11	–	26.55 ± 2.36	19.84 ± 2.46
Arctostaphylos glandulosa	4.43 ± 0.73	13.90 ± 1.88	12.34 ± 2.27	7.76 ± 1.60
Heteromeles arbutifolia	6.54 ± 0.84	9.10 ± 0.82	9.95 ± 1.22	4.84 ± 0.51
Quercus durata	4.60 ± 0.48	6.00 ± 0.78	4.14 ± 1.03	–
Arbutus menziesii	4.92 ± 0.76	–	–	–
Umbellularia californica	3.73 ± 0.50	–	–	–
Rhamnus californica	–	18.70 ± 2.59	–	–
Quercus chrysolepis	–	–	–	3.38 ± 0.41
x̄ ± 1 SE	5.78 ± 1.01	11.92 ± 2.78	13.24 ± 4.76	8.95 ± 3.75
Obligate seeders				
Arctostaphylos montana	7.68 ± 0.92	18.20 ± 2.12	23.46 ± 0.65	15.30 ± 0.92
A. nummularia var. *sensitiva*	–	–	–	14.10 ± 0.93
A. canescens	–	–	–	17.52 ± 1.04
Ceanothus jepsonii	17.01 ± 1.19	30.30 ± 3.59	48.11 ± 4.36	–
C. ramulosus	9.38 ± 1.26	41.00 ± 4.36	88.34 ± 2.04	–
C. foliosus	–	–	–	20.28 ± 2.60
x̄ ± 1 SE	11.36 ± 2.87	29.83 ± 6.58	53.30 ± 18.91	16.80 ± 1.36

latum (sprouter) and *Arctostaphylos viscida* (seeder) ceased branch elongation when midday plant water potentials fell between −2.3 to −2.7 MPa, while elongation continued in an obligate seeder, *Ceanothus cuneatus,* down to −3.5 MPa. All these characteristics suggest that obligate seeders rapidly capture limited resources and have been selected to be competitive (sensu Muller 1969; or Grime 1979, p. 8). Furthermore, they can maintain physiological activity at the low water potentials certainly experienced by establishing seedlings (Schlesinger and Gill 1980). Because the obligate-seeding species have, in general, shallower rooting systems (Hellmers et al. 1955, Kummerow et al. 1977), these characteristics might be relatively advantageous largely at the seedling stage in a comparison with stump-sprouting species.

Higher transpiration rates tend to correlate with higher photosynthetic rates. A survey of published values for photosynthetic rates (Table 2) demonstrates a predicted divergence correlating with reproductive mode, obligate seeders having rates 2–3 times greater than sprouters. This divergence is remarkable because Table 2 combines field and laboratory findings that differ in season measured and in climatic features (northern vs. southern California; xeric vs. relatively mesic). In computer simulations, Miller (1981) also found that canopy photosynthesis was greater for the obligate seeders investigated (*C. greggii* and *A. glauca*) than the stump sprouters (*A. fasciculatum* and *R. ovata*) whether considered over ground area or leaf area. These photosynthetic rates suggest faster potential growth rates in obligate seeders, a contention supported by comparing seedling height data collected over a several year period for species of both reproductive modes (Horton and Kraebel 1955).

These data taken together suggest that the divergence within *Arctostaphylos* and *Ceanothus* does not, therefore, appear to be a change in a single or several reproductive life history characters, but instead, a set of traits forming an "adaptive combination" (Oka 1983). The reproductive divergence may well represent a fundamental change in species life-history within these two genera. Horton and Kraebel's (1955) data demonstrated the more rapid growth of obligate seeders at the seedling stage and support the hypothesis that the obligate seeder mode has been selected for a suite of characteristics in addition to large numbers of seedlings, such as rapid seedling growth, exploitative resource use, and physiological tolerance of stresses typical of seedling establishment (e.g., water stress). Thus, obligate seeders should have seedlings with a better potential for establishment in comparison with seedlings of stump-sprouting species. I have focused on physiological divergence at the seedling stage because establishment is essential for obligate seeders to persist in the vegetation. Faster growth and exploitative resource use would be advantageous for establishing chaparral seedlings. Such an advantage

TABLE 2. MAXIMUM RATES OF PHOTOSYNTHESIS (nmol $CO_2/cm^2/sec$) AS REPORTED FROM PUBLICATIONS. Values listed are maximum rates unless ranges were reported, in which case upper and lower values are listed. Letters following values refer to the source publication: a—Oechel et al. 1981; b—Oechel and Lawrence 1979; c—Mahall and Schlesinger 1982; d—Mooney et al. 1975; e—Harrison et al. 1971. [1]Data was analyzed by group-comparison "t"-test using log-transformed data: $p \ll 0.001$, $t = 5.58$, $df = 22$.

	Stump-sprouter	Obligate seeder
Adenostoma fasciculatum	0.221a	
	0.417a	
	0.461a	
Ceanothus leucodermis	0.455a	
Cercocarpus betuloides	0.429a	
	0.247e	
Quercus dumosa	0.391a	
Rhus integrifolia	0.271a	
Rhus ovata	0.284a	
	0.139e	
Rhus laurina	0.325e	
Heteromeles arbutifolia	0.253d	
	0.235e	
Prunus ilicifolia	0.289e	
Arctostaphylos glauca		0.480a
		0.663a
		0.802a
Ceanothus greggii		0.480a
		0.657a
		0.543a
		0.850b
Ceanothus verrucosus		0.524a
Ceanothus megacarpus		1.300c
		1.900c
$\bar{x}$	0.315[1]	0.819[1]

may not be carried into the adult stage, however, as indicated by water use and carbon gain data over 12 month periods in mature stands (Poole et al. 1981, Oechel et al. 1981). In any case, while existing data seem to support the preceding ideas and a correlation between physiological and reproductive processes hardly seems coincidental, more data need to be collected, and on additional species, before more definitive statements can be made. Further complications may arise among species groups that have occupied xeric to more mesic habitats, or vice versa, through evolutionary time (Stebbins 1974, p. 179–181) or simply due to climatic differences in habitats.

Although obligate seeders and stump sprouters seem to constitute two distinct groups in terms of resource use and growth rates, they may also be regarded as different ends of a continuum, similar to the reproductive continuum suggested by Keeley and Zedler (1978). The middle of the continuum would consist of slower growing seeders and faster growing sprouters. In this regard, special mention should be made of *Adenostoma fasciculatum.* This species had transpiration rates within the range of the obligate seeders (Table 1), leaf conductance patterns more similar to the seeders measured than to the other sprouters in one study (Poole et al. 1981), and photosynthetic rates at the high end of the sprouters (Table 2). *Adenostoma* not only resprouts effectively following fires but also establishes large numbers of seedlings (Horton and Kraebel 1955, Vogl and Schorr 1972, Keeley and Zedler 1978). Apparently, *Adenostoma* combines characteristics of both of these syndromes (sprouter vs. seeder) along with a dimorphic seed population composed of readily germinable and dormant seeds (Stone and Juhren 1953). *Adenostoma* is clearly the dominant species of lower elevation chaparral in California (Hanes 1977) and Cooper (1922) even suggested it was the "climax" dominant of the central coast ranges. This combination of characteristics in *Adenostoma* described above may account for the flexibility required to achieve and maintain this dominance.

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FOUR NEW TAXA OF *DELPHINIUM* (RANUNCULACEAE) FROM MEXICO

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ABSTRACT

Four taxa of Mexican *Delphinium* are described. A new subsection and two new series are characterized. Also described is a previously unrecognized subspecies of *D. bicornutum* Hemsley.

Delphinium is well known as a genus with complex patterns of speciation. Previous works have resulted in a less than satisfying delimitation of taxa. Much of the confusion in these studies has resulted from the close morphological similarity between taxa and the paucity of herbarium material for many taxa. All previous work with the Mexican taxa (Hemsley 1888, Huth, 1895, Ewan 1945) has been based solely on morphological analysis of herbarium specimens. Morphological studies were completed in this work in addition to extensive field studies, and cytological and chemical examination. Field work included measurement of morphological variation in living plants, pollination biology, and ecological preferences of the taxa (Warnock 1982). Forty-four populations were studied during nearly three months of field work. Supraspecific taxa recognized here are the only such taxa validly published for *Delphinium* in North America except for the two sections published by Huth (1895) and two series in a subsection published by Ewan (1936, 1942). The taxa treated here are only distantly related to the subsection named by Ewan (1936) but are provisionally placed in Huth's section *Diedropetala.* Placement of these taxa in *Diedropetala* reflects Huth's judgement in including the taxa treated here (at least those known at the time) in the section. *Diedropetala* (sensu Huth) also contains most of the rest of the North American species of *Delphinium* along with a large number of Old World species. Further work will likely show that the taxa treated here actually belong in a yet unnamed section.

Delphinium Subsection **Wislizenana** Warnock, subsect. nov.

Herbae perennes, 2–20 dm altis, glabris vel canescentibus; radices fibrosae infime abrupte tenuiter dissectae. Folia palmatisecta; petioli inferi longiores, superi breviores. Racemus 2–80-florus; pedicelli adscendentes vel adscendentes-effusi, 0.5–8 cm longi; bractae nullae

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usque ad fere foliosae; bracteolae minutae usque ad 1.5 cm longae, oppositae vel suboppositae. Petala 4. Carpella 3(–4). Semina substriata; testae cellulae multituberculatae ceraceae, squamas plus minusve definitas formantes.

Perennial herbs, 2–20 dm tall; stems usually solitary, glabrous or puberulent, from a stout, fibrous rootstock, this abruptly dissected into many narrow, string-like segments below. Leaves palmatisect, round to semicircular, reduced upward; petioles spreading to spreading-ascending, shorter upward. Floral bracts absent to nearly leafy; bracteoles minute to 1.5 cm long, opposite or subopposite; calyx of five separate, yellow to blue or blue-purple sepals; sepal spur 9–28 mm long, apex acute to rounded; lateral and lower pair of sepals nearly identical to each other, apically rounded, basally cuneate. Petals 4, arranged in two pairs; upper pair enclosed in sepal spur, 14–37 mm long, elongated into acute, posteriorly nectariferous spurs. Stamens numerous; carpels 3(–4). Follicles glabrous to sparsely pubescent, seeds 6–21 per follicle, dark brown to black, trigonally pyramidal to crescent-shaped, appearing irregularly striate, cells of seed coat highly sculptured, possessing many short pustulate knobs, the knobs appearing to secrete waxy substances; seed coat cells aggregated into more or less well defined scales. $n = 8, 16$.

Based on *Delphinium wislizeni* Engelmann *in* Wislizenus, Memoirs of a Tour to Northern Mexico, U.S. Senate Misc. Publ. 22:106. 1848. TYPE: Mexico, Chihuahua, La Bufa Mt., above Cusihuiriachic, porphyritic rocks, 17 Sep 1846, *A. Wislizenus 159* (MO!).

Comprised of *Delphinium bicornutum* Hemsley, *D. calcar-equitis* Standley, *D. pedatisectum* Hemsley, *D. subscandens* Ewan, *D. viride* Watson, and *D. wislizeni,* subsect. *Wislizenana* is characterized by abruptly dissected fibrous roots, usually branched racemes with immediately divergent (although often later parallel) pedicels, cells of seed coat with many pustulate, apparently wax-secreting knobs and these cells more or less aggregated into scales. Taxa of subsect. *Wislizenana* are found in the Sierra Madre Occidental from Chihuahua to Michoacan, the Sierra Madre Oriental from Queretaro to Puebla, and throughout the Sierra Madre del Sur. Populations are found in oak woodlands, pine forests, and subalpine forests from 1500–3000 m.

Delphinium Series **Wislizenana** Warnock, series nov.

Caulibus 3–12 dm altis, glabris vel puberulis. Folia palmatisecta, segmentis 10–32. Bracteae parvae vel nullae; pedicelli effusi 1.5–7 cm longi; sepali calcar 14–28 mm longum. Petala supera 22–37 mm longa; petalorum inferiorum laminae unguesque plus minusve uniplanares, laminis glabris vel subglabris.

Stems 3–12 dm tall, usually solitary, glabrous to puberulent. Leaves finely palmatisect, 10–32 segments. Floral bracts small to absent;

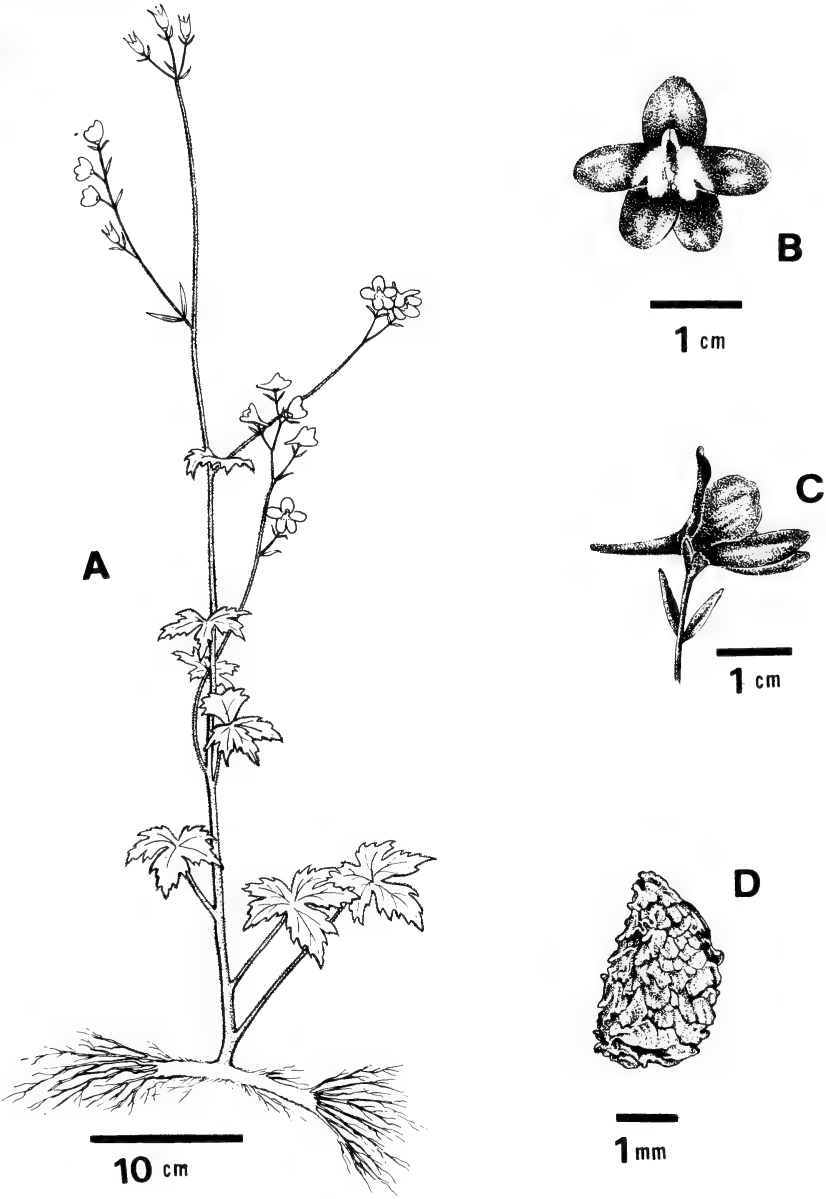

FIG. 1. Illustrations of *D. bicornutum* subsp. *oaxacanum*. A. Habit. B. Facing view of flower. C. Side view of flower. D. Seed. Scales as shown in figures.

pedicels spreading to ascending, 1.5–7 cm long; sepals dark blue or yellow, spur 14–28 mm long. Upper petals 22–37 mm long; lower petals clawed but blade nearly coplanar with claw, blade only sparsely if at all hirsute. $n = 8, 16$.

TYPE SPECIES: *Delphinium wislizeni* Engelmann.

Series *Wislizenana* includes *D. viride* and *D. wislizeni.* The series is characterized by long spurs, spreading pedicels, nearly coplanar blade and claw of lower petals, lack of pubescence on lower petals and absence of flavonol 7-rhamnosides in the leaves. Taxa of series *Wislizenana* are found in the Sierra Madre Occidental from Chihuahua to San Luis Potosi. Populations are found near springs in dry oak woodlands, in pine forests, and subalpine forests of pine and douglas fir from 1500–3000 m.

Delphinium Series **Bicornuta** Warnock, series nov.

Caulibus 2–20 dm altis; glabris vel canescentibus. Folia palmatisecta, segmentis 3–7(–14), superis parvioribus. Inflorescentia 2–80-flora, bracteae parvae usque ad foliosae; pedicelli adscendentes vel adscendentes-effusi, 0.5–8 cm longi; sepali calcar 9–25 mm longum. Petala supera 14–35 mm longa; petalorum inferiorum laminae unguesque angulo recto formantes, laminis hirsutis.

Stems 2–30 dm tall, solitary or rarely in twos or threes, glabrous to canescent. Leaf blades with fewer than 10 segments (rarely more in one species); calyx of dark blue or blue-purple sepals, spur 9–25 mm long. Upper petals 14–35 mm long; lower petals clawed, blade usually nearly perpendicular to the claw, blade adaxially hirsute to hirsute-villous. $n = 8$.

Based on *Delphinium bicornutum* Hemsley, Diagnoses plantarum novarum Mexicanarum et Centrali-Americanarum 2:17. 1879. TYPE: Mexico, Oaxaca, 1841, *A. Ghiesbreght s.n.* (K!).

Distinguished by relatively short spurs (except in *D. calcar-equitis* and *D. subscandens*), ascending pedicels, perpendicular structure of the lower petals, presence of flavonol 7-rhamnosides in leaves, and usual presence of pubescence on blades of lower petals. Series *Bicornuta* includes *D. bicornutum, D. calcar-equitis, D. pedatisectum,* and *D. subscandens.* Taxa of series *Bicornuta* are found in the Sierra Madre Occidental south from southwestern Chihuahua, in the Sierra Madre Oriental south from Queretaro and in the Sierra Madre del Sur. Populations are found in wet oak forests and pine-oak forests from 1800–3000 m.

A new taxon of *Delphinium* was discovered in the mountains of the Sierra Madre del Sur in Oaxaca. The new taxon is included in series *Bicornuta* subsect. *Wislizenana* as a second subspecies of *D. bicornutum.* Subspecies *bicornutum* is also formalized here to avoid possible future difficulties of priority.

Delphinium bicornutum Hemsley subsp. **bicornutum** stat. nov. BASIONYM: *Delphinium bicornutum* Hemsley.

Delphinium bicornutum Hemsley subsp. **oaxacanum** Warnock, subsp. nov.

Caulibus simplicibus, 6–12 dm altis; subpilosis vel pilosis. Folia basalia 4–8 cm longa, 6–12 cm lata, segmentis 3–7, canescentia; petioli 15–35 cm longis, pilosis, folia caulina 2–6 cm longa, 4–9 cm lata, segmentis 3–7, subcanescentia; petioli 0.5–8 cm longis, subpilosis. Floris 5–22; pedicelli 1.5–8 cm longis; bracteolae lanceolatae, 3–12 mm longae, 2–12 mm infra receptaculum insertae; sepali calcar 10–18 mm longum; sepala lateralia 11–16 mm longa, 5–10 mm lata; sepala infera 11–19 mm longa, 4.5–11 mm lata. Petala supera 15–25 mm longa, 2–3 mm lata, alba vel pallide azurea, ad apicem sino 0.0–1.2 mm longo; petala infera alba vel azurea, 9–14 mm longa, 2.5–4.5 mm lata, ad apicem sino 2–4 mm longo. Stamina 24–31, carpella 3; styli pallide azurei. Folliculi 12–15 mm longi, 3–4 mm lati. Semina 9–15 in quoque folliculo, 1.9–2.7 mm longa, 1–1.6 mm lata.

Stems solitary, 6–12 dm tall; puberulent to sparsely puberulent. When present, basal leaf blades 4–8 cm long, 6–12 cm wide, 3–7 segmented, variably canescent; petioles 15–35 cm long, puberulent; cauline leaf blades 2–6 cm long, 4–9 cm wide, palmatisect into 3–7 segments, sparsely canescent; petioles 0.5–8 cm long, sparsely puberulent. Flowers 5–22; pedicels 1.5–8 cm long, bracteoles subtending each flower lanceolate, 3–12 mm long, 2–12 mm below the receptacle; spur sepal 10–18 mm long; lateral sepals 11–16 mm long, 5–10 mm wide; lower sepals 11–19 mm long, 4.5–11 mm wide. Upper petals 15–25 mm long, 2–3 mm wide, apex cleft 0.0–1.2 mm deep, upper petals white near the nectary, becoming blue to dark blue or remaining white apically; lower petals white or blue, 9–14 mm long, 2.5–4.5 mm wide, blade cleft 2–4 mm deep. Stamens 24–31; carpels 3; styles blue. Pollen light yellow to yellow. Follicles 12–15 mm long, 3–4 mm wide. Seeds 9–15 per follicle, 1.9–2.7 mm long, 1–1.6 mm wide. $n = 8$.

TYPE: Mexico: Oaxaca, Municipio de Miahuatlan, 11.5 mi s. of Miahuatlan Pemex on Rt 175, s. of road; steep n.-facing slope in oak-pine woods, 19 Oct 1981, *M. J. Warnock 2536* (Holotype: TEX!; isotypes: ENCB! ILL! MEXU! MO! PSU! SHST! TEX!).

PARATYPES (all known specimens): Mexico, Oaxaca, Meratlau, San Andres, Oct 1842, *F. M. Liebmann 1035* (BM! C-5! US!); Municipio de Pochutla, Pluma Hidalgo, 10 Jan 1967, *T. MacDougall s.n.* (MEXU!); Municipio de Santa Catalina Quieri, Cerro de Quieri, 17 Jan 1964, *T. MacDougall s.n.* (MEXU!).

Delphinium bicornutum subsp. *oaxacanum* is characterized by large size of the plants (relative to most *D. b.* subsp. *bicornutum* and

D. pedatisectum), 7 or fewer leaf segments, often completely white upper and lower petals, and puberulent to canescent pubescence on stems and leaves. Root structure and seed morphology place *D. b.* subsp. *oaxacanum* in subsect. *Wislizenana.* Pedicels paralleling rachis of the inflorescence for most of their length, hirsute lower petals, nearly perpendicular parts of lower petals, and presence of flavonol 7-rhamnosides in leaves place *D. b.* subsp. *oaxacanum* in series *Bicornuta.* Short spurs and wet montane habitat ally subsp. *oaxacanum* with subsp. *bicornutum* and *D. pedatisectum* within the series. Crest and upper Pacific slopes of the Sierra Madre del Sur south of the city of Oaxaca are the principal habitat for *D. b.* subsp. *oaxacanum* Plants are found on north-facing slopes of oak-pine woodlands, at elevations of 2500–2800 m. Flowering occurs from September to January.

The subspecies is known from only four collections on steep, north-facing slopes often in ravines. Plants are found scattered under and around shrubs under oaks with occasional pines. Possibly it once was more common but it occurs in an area of intense pressure from grazing, lumbering, and marginal cultivation. The single population visited covered approximately 400 m^2 on a 50–60 degree slope between a cornfield and a road. This population contained 90–100 flowering individuals.

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NOTES AND NEWS

NOMENCLATURAL CHANGES IN *Persicaria, Polygonum,* AND *Rumex* (POLYGONACEAE).—For a revision of W. L. Jepson's Manual (Jepson, Man. fl. pls. Calif. 1925) to be published in 1993, nomenclatural changes are required to reflect new knowledge in the taxonomy of California plants and to make generic treatments internally consistent. This first installment provides nomenclatural changes in Polygonoideae.

Polygonum s.l. comprises several lineages that are morphologically coherent and distinct from one another. In North America these lineages usually have been considered subgenera or sections, but there is a growing tendency worldwide to assign them generic rank. The most intensive work on generic concepts in Polygonoideae is that of Haraldson (Symb. Bot. Upsal. 22(2):1–93. 1978). She concluded from morphology and from anatomical study of pollen, trichomes, stems, and leaves that generic recognition is warranted for most groups. Her treatment will be followed in the new Jepson's Manual; *Aconogonum, Bistorta, Fallopia, Persicaria, Polygonum s.s.,* and *Reynoutria* will be recognized.

Persicaria. Recognition of *Persicaria* is predicated upon acceptance of a recommendation by the Committee on Spermatophyta to conserve *Polygonum* L. with *P. aviculare* L. as type (see McNeill, Taxon 30:330–341. 1981). That recognition requires one nomenclatural change in the *P. amphibia* complex to conform with the results of Mitchell (Univ. Calif. Publ. Bot. 45:1–65. 1968).

Persicaria amphibia (L.) Gray var. **emersa** (Michaux) Hickman, comb. nov.—*Polygonum amphibium* L. var. *emersum* Michaux, Fl. Bor. Amer. 1:240. 1803.—TYPE: "Ad ripas fluminis Ohio."

Polygonum coccineum Muhlenb. in Willd., Enum. Pl. Hort. Berol. 1:428. 1809.—TYPE: "Pennsylvania."

Polygonum. Most or all California members of the widespread *Polygonum* subg. *Polygonum* are introduced weeds. The native, western North American taxa make up a parallel subgenus (combined below).

Polygonum L. subg. **Duravia** (S. Watson) Hickman, stat. et comb. nov.—*Polygonum* L. sect. *Duravia* S. Watson, Amer. Naturalist 7:665. 1873.—*Duravia* E. Greene, Leafl. Bot. Observ. Crit. 1:22–23. 1904.—TYPE: *Polygonum californicum* Meissner.

Subgenus *Duravia* comprises two sections: sect. *Duravia* of about five species, which is centered in northern California; and a new section (diagnosed below), which ranges broadly in western North America. Section *Duravia* is characterized by leaves that are not obviously jointed to stipule sheaths (but nevertheless fall from them) and are three-nerved, aculeate, linear, and more or less recurved. In addition, the three styles are separate, hardened, and persistent at least at the base. Members of sect. *Duravia* occupy mostly summer-dry lowland and foothill habitats.

Polygonum L. sect. **Monticola** Hickman, sect. nov.—TYPE: *Polygonum douglasii* E. Greene.

A sectione *Duravia* foliis manifeste articulatis ad stipulas, uninervibus, saltem infimis plerumque lanceolatis vel rotundatis, non aculeatis, stylis basi connatis nec induratis nec persistentibus differt.

Differing from sect. *Duravia* in its leaves, which are obviously jointed to the stipules, one-nerved, not aculeate, at least the lowest usually lanceolate to round; and its styles, which are fused at the base and neither hardened nor persistent. Members of sect. *Monticola* occupy mostly montane (but some foothill) habitats.

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The two major lineages of sect. *Monticola* (close relatives of *P. douglasii* E. Greene and of *P. polygaloides* Meissner) usually have been considered to comprise a handful of intergrading species each, but intermediates sometimes outnumber typical forms in both lineages; intergradation patterns among the extremes are highly complex. Names for the extreme forms are here combined at subspecific rank. This rank is chosen to allow continued use of well-established epithets that must be rejected at varietal rank.

Polygonum douglasii E. Greene, Bull. Calif. Acad. Sci. 1:125. 1885.—TYPE: No type was designated (protologue mentions Douglas as "perhaps its very earliest collector," but it cannot be assumed that Greene saw any Douglas material of this very common taxon); ND-G has no specimens predating publication; no Douglas specimen has been found in other herbaria; no specimen in CAS or UC shows evidence of having been used in preparation of protologue. Neotype here designated: CA, Tulare Co., Coyote Creek, 30 Jul 1904, *Culbertson 4391,* determined by Greene, distributed by C. F. Baker (Neoholotype: DS 73676!; neoisotypes should be broadly distributed).

Polygonum douglasii E. Greene subsp. **austiniae** (E. Greene) Hickman, stat. et comb. nov.—*Polygonum austiniae* E. Greene, Bull. Calif. Acad. Sci. 1:212. 1886.—*Polygonum douglasii* var. *austiniae* M. E. Jones, Contr. West. Bot. 12:75. 1908.—TYPE: "Mrs. R. M. Austin, 1884–5." ND-G has one gathering from each year. Both are from Goose Lake Valley, Modoc Co., CA. That from 1884 is labelled in Mrs. Austin's (?) hand, that from 1885 in Greene's. The latter (ND-G 14416!) is here considered holotype.

Polygonum douglasii E. Greene subsp. **johnstonii** (Munz) Hickman, stat. et comb. nov.—*Polygonum douglasii* E. Greene var. *johnstonii* Munz, Man. So. Calif. Bot. 131, 597. 1935.—TYPE: CA, San Bernardino Co., San Bernardino Mts., Fish Creek, 7600 feet, *Munz and Johnston 8506* (POM!). The type shows several features of subsp. *douglasii* but is closer to the extreme of subsp. *johnstonii* so the latter epithet can be retained at subspecific rank.

Polygonum sawatchense Small, Bull. Torrey Bot. Club 20:213. 1893.—TYPE: ". . . collected by Brandegee on the Sawatch Range, Colorado. The specimens are in the Herbarium of the California Academy of Sciences." The types are no longer at CAS and presumably were destroyed in the earthquake and fire in 1906. Other material from the Sawatch Range is intermediate to subsp. *douglasii*; no neotype is proposed.

Polygonum triandrum Coolidge, Madroño 20:266. 1970.—TYPE: ID, Blaine Co., Hyndman Peak trail, *Baker 11005* (Holotype: ID!). Plants assigned here to subsp. *johnstonii* are highly variable but show little geographic pattern and no traits that would allow segregation of reasonably well-marked taxa. All of the variant forms intergrade completely with subsp. *douglasii.*

Polygonum douglasii E. Greene subsp. **majus** (Meissner) Hickman, stat. et comb. nov.—*Polygonum coarctatum* Douglas ex Hook. f. var. *majus* Meissner in DC., Prodr. 14:101. 1856.—*Polygonum majus* Piper, Fl. Palouse Reg. 63. 1901.—TYPE: "Ad flum. Columbia (Dougl.!), in mont. Scopulosis (Geyer, n. 355!)." Lectotype here designated: *Douglas* (Columbia River, in 1830) (G-DC photo!). *Geyer* (K!) is less complete and less mature.

Polygonum douglasii E. Greene subsp. **nuttallii** (Small) Hickman, stat. et comb. nov.—*Polygonum intermedium* Nutt. ex S. Watson, Proc. Amer. Acad. Arts 17:378. 1882; not Ehrh., Beitr. Naturk. v. 178. 1791.—*Polygonum nuttallii* Small, Monogr. Polygonum 132. 1895.—TYPE: "On bluffs of the Columbia River, Oregon; C. G. Pringle, October 1881, and by Nuttall, probably in the same region." Hitchcock (Vasc. pls. Pac. NW 2:160. 1964) effectively lectotypified the name on *Nuttall.* Because this taxon will not be included in Jepson's Manual, I characterize it here. Known from northwest Oregon to British Columbia (west of the Cascade Ranges), it is uncommon, morphologically uniform, and differs from subsp. *spergulariiforme* in its broader leaves that are not reduced strongly upward, its smaller flowers and fruits, and its automatically self-pollinating habit.

Polygonum douglasii E. Greene subsp. **spergulariiforme** (Meissner ex Small) Hickman, stat. et comb. nov.—*P. coarctatum* Douglas ex Hook. f., Fl. Bor. Amer. 2:133. 1838; not Willd. ex Sprengel, Syst. Veg. 2:255. 1825.—*Polygonum spergulariiforme* Meissner ex Small, Bull. Torrey Bot. Club 19:366. 1892.—Type: "Hab. N. W. America. *Menzies. Dr Scouler.* On the sandy banks of the Columbia and its branches, and on the higher branches of the Multnomak. *Douglas.*—β. Prairies at Nusqually Bay, N. W. America. *Tolmie.*" Lectotype here designated: *Menzies* (K!). *Dr Scouler* has not been found. *Menzies, Douglas,* and *Tolmie* are mounted together on one unaccessioned sheet (K!): *Douglas* is two plants of *P. confertiflorum* Nutt. ex Piper; *Tolmie* is five plants of subsp. *spergulariiforme* that are smaller and younger than those of *Menzies.*

Polygonum coarctatum Douglas ex Hook. f. var. *minus* Meissner in DC., Prodr. 14: 101. 1856.—Type: "In Amer. arctica? (Franklin! in herb. Arnott), Oregon (Spalding.)" [Lectotype here designated: *Franklin (134/15)* GL! *Spalding* has not been found.] *Franklin* and *Tolmie* referred to above represent the same taxon, but the "β" of both protologues is assumed to be coincidental. This would be the valid name for this entity at varietal rank in *P. douglasii.* The autonym (var. *coarctatum*) derives from an illegitimate basionym.

Polygonum polygaloides Meissner subsp. **confertiflorum** (Nutt. ex Piper) Hickman, stat. et comb. nov.—*Polygonum confertiflorum* Nutt. ex Piper, Contr. U.S. Natl. Herb. 11:228. 1906.—Type: "Columbia Plains. Collected by Nuttall. Type in the Gray Herbarium" (GH!).

Polygonum imbricatum Nutt. ex S. Watson, Amer. Naturalist 7:665. 1873; not Raf., Fl. Telluriana. 1837.—*Polygonum watsonii* Small, Monogr. Polygonum 138. 1895.—*Polygonum imbricatum* Nutt. ex S. Watson var. *watsonii* (Small) Jepson, Man. fl. pls. Calif. 290. 1923, nom. illegit. (based on the same type as the species).—Type: no type was designated. *Nuttall,* "R. Mts—N. Calif" (GH!) is the only available Nuttall specimen that can be assumed to have been seen by Watson. It is considered here to be the holotype. It fits best into subsp. *confertiflorum* but is intermediate in some ways to subspp. *esotericum* and *polygaloides.*

Polygonum polygaloides Meissner subsp. **esotericum** (Wheeler) Hickman, stat. et comb. nov.—*Polygonum esotericum* Wheeler, Rhodora 40:310. 1938.—Type: CA, Modoc Co., Devils Garden, seasonally submerged adobe, 25 Aug 1935, *Wheeler 3918* (Holotype: GH!).

Polygonum polygaloides Meissner subsp. **kelloggii** (E. Greene) Hickman, stat. et comb. nov.—*Polygonum kelloggii* E. Greene, Fl. Fran. 134. 1891.—Type: only "State survey . . . n. 6005" [*Brewer*], which has not been located, is mentioned in protologue, apparently without intent to consider it the type, but (CA, Nevada Co.) "Near Donner Lake," *Kellogg s.n.,* in 1870 (ND-G!) is labelled "type!" in Greene's hand. It is here considered holotype. Akenes of *Kellogg* are somewhat striate and to that extent intermediate to subsp. *confertiflorum.*

Rumex. Members of the *Rumex salicifolius* complex are highly variable and are differentiated by only one or a few characters that vary within plants (mostly of the completely mature valves). The forms intergrade completely. Few specimens can be taken as "typical" material, and the latest monographer (Rechinger, Field Mus. Nat. Hist., Bot. Ser. 17(1):1–151. 1937) was unable to identify a substantial proportion of the material he saw because it is not completely mature. Names for the extreme forms not yet so combined are reduced here to varietal rank to achieve uniformity of treatment (without invoking two infraspecific ranks) with the fewest possible name changes.

Rumex salicifolius J. A. Weinm. var. **lacustris** (E. Greene) Hickman, stat. et comb. nov.—*Rumex lacustris* E. Greene, Erythea 3:63. 1895.—TYPE: *Baker and Nutting,* in 1894, CA, Lassen Co., Silver Lake.

Rumex salicifolius J. A. Weinm. var. **transitorius** (Rech. f.) Hickman, stat. et comb. nov.—*Rumex transitorius* Rech. f., Repert. Spec. Nov. Regni Veg. 40:296. 1936.—TYPE: no type was designated. Lectotype here designated: CA, Humboldt Co., immediate vicinity of Eureka, 20 Jun 1901, *Tracy 1157* (UC!). This specimen was cited among others in protologue and was the source of Rechinger's habit illustration (1937, op. cit.).

Rumex salicifolius J. A. Weinm. var. **triangulivalvis** (Danser) Hickman, stat. et comb. nov.—*Rumex salicifolius* J. A. Weinm. subsp. *triangulivalvis* Danser, Ned. Kruidk. Arch. 1925:415. 1926.—*Rumex triangulivalvis* Rech. f., Repert. Spec. Nov. Regni Veg. 40:297. 1936.—TYPE: no type was designated; the illustration fixes application of the name.

I thank B. Ertter, L. R. Heckard, J. McNeill, Guy Nesom, D. H. Nicolson, P. C. Silva, A. R. Smith, and J. L. Strother for critical advice.—JAMES C. HICKMAN, Botany Department, Univ. California, Berkeley 94720. (Received 15 Dec 1983; accepted 13 Apr 1984.)

HETEROSTYLY IN *Salvia brandegei* (LAMIACEAE).—Epling (Ann. Missouri Bot. Gard. 27:259–263, 1940) recognized that *Salvia brandegei* Munz is dimorphic in stamen length. The following report confirms not only stamen dimorphism, but also heterostyly, as defined by Ganders (New Zealand J. Bot. 17:607–635, 1979).

Salvia brandegei is one of the rarest and least known *Salvia* species of the sect. *Audibertia* (Neisess, Evolution, Systematics, and Terpene Relationships of *Salvia* Section *Audibertia,* Ph.D. Diss., Univ. California, Riverside, 1983). It is endemic to coastal bluffs and seaward canyons, occurring only on Santa Rosa Island (Santa Barbara Co., California) and a 40 km strip of northwestern Baja California coastline from Punta Santo Tomas south to Punta Cabras.

Specimens of *S. brandegei* were collected at Punta Cabras and grown under uniform garden conditions at the University of California, Riverside. Two distinct floral morphs

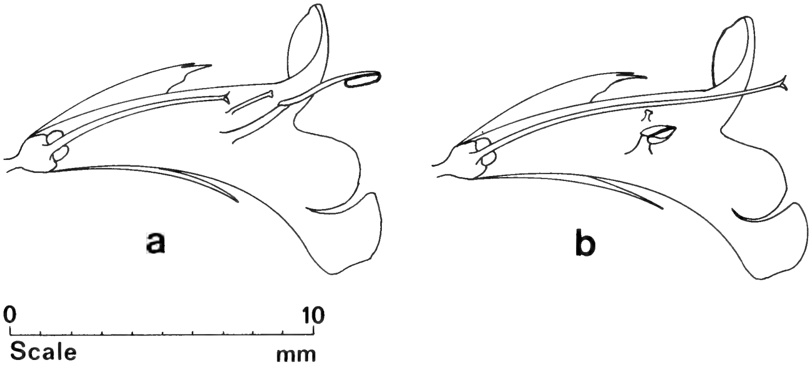

FIG. 1. Bisected pin and thrum forms of *Salvia brandegei,* showing differences in style, stamens and sterile staminoids. Scale bar = 1 cm. a. Thrum form; style included, stamen exerted. b. Pin form; style exerted, stamen included.

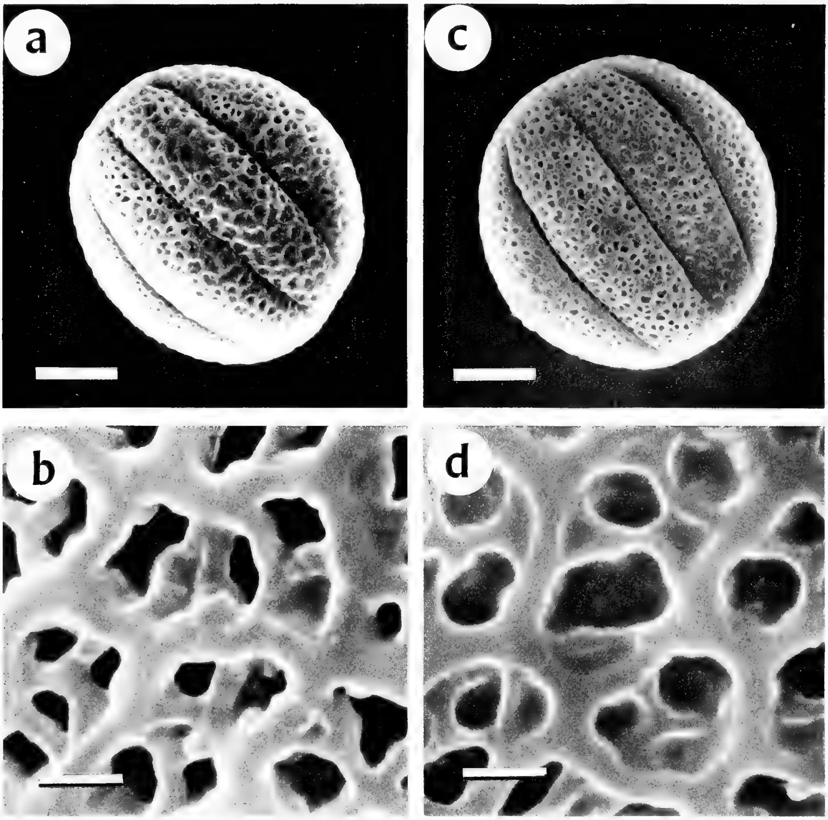

FIG. 2. *Salvia brandegei* microspores. a. Pin; scale bar = 1 μm. b. Pin exine detail; scale bar = 10 μm. c. Thrum; scale bar = 1 μm. d. Thrum exine detail; scale bar = 10 μm.

were observed (Fig. 1), one with stamens included in the throat and style exerted (pin form), and the other with stamens exerted and style included (thrum form). This observation corresponds with all voucher specimens observed in major Southern California herbaria (SD, UCR, RSA, LA, SBBG).

Pollen of both floral types was examined for exine structural differences with a JEOL JSM-35 scanning electron microscope (freshly mounted with double-sticky tape and gold coated by a Technics Hummer V sputter-coater). There was no apparent difference in external morphology (Fig. 2). Because differences in pollen size often occur in heterostylous species (Ganders 1979; Anderson, Taxon 22:537–542, 1973), relative size of the pin and thrum pollen was measured. Light microscopic images were projected through a drawing tube onto a Hewlett-Packard 9111 A graphics tablet. The outline of each image was traced and areas were calculated using a linked Hewlett-Packard 85 computer (program for area and distance provided by HP). Over fifty microspores of each floral type were measured and analysis of variance revealed no significant difference in mean area ($p < 0.05$).

Male fertility was tested following the FDA method (J. Heslop-Harrison and Y.

Heslop-Harrison, Stain Techn. 45:115–120, 1970). Both pin and thrum forms produced viable pollen (over 40% in all counts).

Segregated pin and thrum plants were self- and cross-pollinated in both directions. Seed was set in all cases, showing both floral morphs to be female fertile and self-compatible. The potential for natural selfing was examined by maintaining mixed and segregated pin and thrum plants in an open garden. The mixed group set an average of 0.27 seeds per flower (n = 200), whereas the segregated groups yielded no seed at all. This suggests that the mechanical characteristics of *S. brandegei* floral morphology discourage selfing in wild populations, despite the fact that the species is self-compatible.

Heterostyly is known in only 24 angiosperm families (Ganders 1979) and has not previously been reported in the Lamiaceae. It is rarely found in self-compatible species and, except for an unsubstantiated report by Darwin from the Verbenaceae (The Different Forms of Flowers on Plants of the Same Species, 1877, John Murray, London), the occurrence of heterostyly in *S. brandegei* is the first substantiated case for any zygomorphic dicotyledonous plant.—KURT R. NEISESS, Department of Botany, University of Texas, Austin, 78712. (Received 25 Nov 1983; accepted 16 Apr 1984.)

NOTEWORTHY COLLECTIONS

MONTANA

ALLIUM PARVUM Kell. (LILIACEAE).—Ravalli Co., open slopes, Painted Rock's cliffs, W. Fork Bitterroot River, 1710 m, 15 Jun 1975, *J. Cory 1447* (MONTU); steep w.-facing slope above E. Fork Bitterroot River just s. of Spring Gulch Cmpg. (T1N R20W S7), 1330 m, 22 May 1983, *Lesica and Moore 2582* (MONTU, ID). (*Lesica and Moore 2582* verified by D. Henderson, ID.)

Significance. First record for MT.

ASTRAGALUS CERAMICUS var. APUS Barneby (FABACEAE).—Beaverhead Co., Centennial Valley, blowout areas in sandhills 40 km ne. of Monida (T13S R2W S23), 2010 m, 11 Jul 1983, *Lesica 2716* (MONTU, NY). (Verified by R. C. Barneby, NY.)

Significance. First record for MT.

ASTRAGALUS CHAMAELEUCE Gray (FABACEAE).—Carbon Co., dry flats 1 km ne. of Gyp. Springs 16 km n. of Cowley, WY (T9S R27E S33), 1370 m, 18 Jun 1983, *Lesica 2623* (MONTU, NY). (Verified by R. C. Barneby, NY.)

Significance. First record for MT.

ASTRAGALUS MOLYBDENUS Barneby (FABACEAE).—Teton Co., E. Front mountains, Mount Wright (T26N R10 W S25), 2240 m. Dense growth in horizontal strips on mostly stabilized slide. 23 Jul 1982, *Lackschewitz and Ramsden 10062* (MONTU, NY). (Collection det. by R. Barneby, NY.)

Significance. Previously known only in the high southern Rocky Mts. of Colorado, roughly 960 air-km to the s.

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ATHYSANUS PUSILLUS (Hook.) Greene (BRASSICACEAE).—Ravalli Co., Bitterroot Mts., n. side of Blodgett Canyon, 5.6 km wnw. of Hamilton (T6N R21W S16 sw.¼), sparse, at the base of cliff, 1341 m, 25 Apr 1981, *Vincent 355* (MRC). (Verified by P. Stickney, MRC); Blodgett Canyon, above parking lot below rock cliffs (T6N R21W S16 sw.¼), locally common, on granitic ledges, aspect 190, overall slope 70%, ledge slope 10%, 1400 m, 24 May 1983, *Pierce and Vincent 1158* (MONTU).
Significance. First report from MT.

CAREX AMPLIFOLIA Boot. (CYPERACEAE).—Sanders Co., Vermillion Road, nw. of Thompson Falls in moist area of Roe Gulch, ca. 4 km upstream from Clark Fork River (T24N R31W S12 nw.¼ of sw.¼), 763 m, *Thuja plicata-Betula occidentalis* habitat in Douglas-fir/Ponderosa pine forest, 10 Aug 1978, *Ramsden 268* (MONTU, NY). (Confirmed by A. Cronquist, NY.)
Significance. First report from MT.

CAREX INCURVIFORMIS Mack. (CYPERACEAE).—Teton Co., E. Front mountains, above "Our Lake" (T24N R9W S18), 2285 m, 12 Jul 1981, *Lackschewitz 9606* (AK, MONTU, NY). (Verified by A. Cronquist, D. Murray, NY.)
Significance. Second record from MT, ca. 230 km n. of first known occurrence in the Anaconda-Pintlar Mts.

CAREX LIVIDA (Wahl.) Willd. (CYPERACEAE).—Teton Co., open fen w. of Pine Butte, 40 km w. of Choteau (T24N R7W S18), 1400 m, 24 Jul 1982, *Lesica 2316* (MONTU, NY). (Verified by A. Cronquist, NY.)
Significance. Second record for MT and the Northern Rocky Mtn. region.

CIRSIUM SUBNIVEUM Rydb. (ASTERACEAE).—Madison Co., slope of Ruby Mountain Ridge above Laurin Canyon (T6S R5W S9 sw.¼), 2600 m, open places in subalpine forest, 21 Aug 1982, *Lackschewitz and Rosentreter 10282* (MONTU, NY). (Det. by A. Cronquist, NY.)
Significance. First report for MT.

DRABA PORSILDII G. A. Mulligan (BRASSICACEAE).—Carbon Co., Beartooth Mts., steep n.-facing slope along Hwy. 212, 16 km sw. of Red Lodge (T9S R19E S17), 2750 m, 2 Jul 1981, *Lesica 1496* (MONTU, DAO); Beartooth Mts., ridge 1 km e. of Silverrun Pk. (T8S R18E S20), 3550 m, 15 Aug 1981, *Lesica 1786* (MONTU, DAO). (Det. by G. A. Mulligan, DAO.)
Significance. First record for contiguous U.S., an extension of ca. 800 km s. from Alta.

ERIGERON ASPERUGINEUS (Eat.) Gray (ASTERACEAE).—Beaverhead Co., Lima Peaks, steep w.-facing slope of Mt. Garfield, 16 km s. of Lima (T15S R9W S13), 2690 m, 11 Aug 1983, *Lesica 2794* (MONTU, NY). (Verified by A. Cronquist, NY.)
Significance. First record for MT.

IDAHOA SCAPIGERA (Hook.) Nels. & Macbr. (BRASSICACEAE).—Ravalli Co., Bitterroot Mts., Blodgett Canyon, above parking lot below rock cliffs (T6N R21W S16 sw.¼), locally common, on granitic ledges, aspect 190, overall slope 70%, ledge slope 10%, 1400 m, 3 Jun 1983, *Pierce, Lackschewitz, Vincent and Bradley 1164* (MONTU).
Significance. First record for MT.

JUNCUS ACUMINATUS Michx. (JUNCACEAE).—Teton Co., pond e. of Pine Butte, 40 km w. of Choteau (T24N R7W S17), 1370 m, 26 Jul 1982, *Lesica 2337* (MONTU, NY). (Det. by A. Cronquist, NY and F. J. Hermann, WIS.)
Significance. First record for MT.

LOMATIUM GEYERI (S. Wats.) Coult. & Rose (APIACEAE).—Lincoln Co., rock ledges at Yaak Falls, 19 km n. of Troy (T33N R33W S4), 730 m, 2 Jun 1982, *Lesica 1941* (MONTU, CA). (Det. by L. Constance, CA.)

Significance. First record for MT.

MACHAERANTHERA COMMIXTA Greene (ASTERACEAE).—Madison Co., crest of Ruby Mtn. ridge above Laurin Canyon (T6S R5W S9 sw.¼), 2700 m, near krummholz of *Pinus albicaulis* and in association with *Poa interior* and *Townsendia montana,* 21 Aug 1982, *Lackschewitz and Rosentreter 10291* (MONTU, NY). (Det. by A. Cronquist, NY.)

Significance. First report from MT.

OENOTHERA PALLIDA Lindl. var. IDAHOENSIS Munz. (ONAGRACEAE).—Beaverhead Co., Centennial Valley, blowout areas in sandhills 40 km ne. of Monida (T13S R2W S23), 2010 m, 11 Jul 1983, *Lesica 2713* (MONTU, NY). (Verified by A. Cronquist, NY.)

Significance. First record for MT.

OROBANCHE CORYMBOSA (Rydb.) Ferris (OROBANCHACEAE).—Beaverhead Co., Big Hole Valley, Big Hole National Battlefield, steppe s. of siege area (T2S, R17W, S23), 1920 m, 3 Aug 1980, *Pierce 981* (MONTU). (Verified by L. R. Heckard, JERS.)

Significance. First record for MT.

PENSTEMON PAYETTENSIS Nels. & Macbr. (SCROPHULARIACEAE).—Ravalli Co., Jew Mtn., 5 km e. of Painted Rock Reservoir (T2S R19E S8), 1670 and 1820 m, 9 Jul 1976, *Cory 1640* (ID, MONTU, NY, WTU). (Verified by D. Henderson, ID and N. Holmgren, NY.)

Significance. First report for MT.

PHIPPSIA ALGIDA R. Br. (POACEAE).—Carbon Co., Beartooth Mts. wet gravel bars below snowbank (T9S R19E S23), 2990 m, 12 Aug 1980, *Dorn 3586* (MONT); wet gravel on gentle slope of Silverrun Plateau (T8S R18E S23), 3200 m, 14 Aug 1981, *Lesica 1767* (MONTU, MONT, COLO); gravelly soil along streams on E. Rosebud Plateau (T8S R17E S2), 3510 m, 26 Aug 1983, *Lesica 2868* (MONTU). (*Lesica 1767* verified by W. A. Weber, COLO.)

Significance. First report for MT.

PLAGIOBOTHRYS LEPTOCLADUS (Greene) Johnson (BORAGINACEAE).—Phillips Co., muddy shore of pond (T22N R25E S17), 975 m, 20 Aug 1978, *Lackschewitz 8605* (MONTU, NY). (Det. by A. Cronquist, NY.)

Significance. First confirmed report from MT. (Coll. in 1874 "reportedly from Montana.")

PLANTAGO CANESCENS Adams (PLANTAGINACEAE).—Glacier Co., gently rolling glacial drift 7 km e. of Glacier Natl. Park, 23 Jul 1953, *Wright and Anderson* (MONT); Pondera Co., 8 km w. of Dupuyer on both sides of the road to Swift Reservoir, scattered colonies in dry prairie (T28N R8W S24 sw.¼), 1430 m, 13 Jul 1983, *Lackschewitz 10484* (MONTU, NY); Teton Co., grasslands 1 km n. of Bowman Range, 40 km w. of Choteau (T24N R7W S3), 1490 m, 24 Jun 1982, *Lesica 2097* (MONTU, NY); 26 Jul 1982, *Lesica 2350* (MONTU, NY). (Collections deposited at NY, verified by A. Cronquist, NY.)

Significance. Second report for MT and contiguous U.S. First record (*Umbach 377* MONT, NY) was questioned (Hitchcock et al., Vascular Plants of the Pacific Northwest Part 4, p. 443, 1959).

POTENTILLA BREVIFOLIA Nutt. (ROSACEAE).—Madison Co., Madison Range, steep slope s. of Expedition Pass, 30 km nw. of West Yellowstone (T10S R2E S15), 3080 m, 17 Aug 1983, *Lesica and DeBolt 2842* (MONTU, NY). (Verified by A. Cronquist, NY.)

Significance. First report for MT, an extension of ca. 130 km n. from the Teton Range, ID-WY.

SAXIFRAGA CHRYSANTHA Gray (SAXIFRAGACEAE).—Stillwater Co., Beartooth Mts., alpine fellfield 3 km ne. of Granite Pk., 22 km ne. of Cooke City (T7S R16E S29), 3570 m, 31 Aug 1973, *M. C. Stickney 9* (NRC); Carbon Co., Beartooth Mts., tundra on s.-facing slope 1 km se. of Silverrun Pk. (T8S R18E S20), 3600 m, 15 Aug 1981, *Lesica 1778* (MONTU, MONT); gravelly soil on the e. Rosebud Plateau (T8S R17E S2), 3540 m, 26 Aug 1983, *Lesica 2872* (MONTU).

Significance. First report for MT.—KLAUS H. LACKSCHEWITZ, PETER LESICA, JOHN PIERCE, Dept. Botany, Univ. Montana, Missoula 59812, JACULYN K. CORY, SW581 Westside Rd., Hamilton, MT 59840 and DAVID RAMSDEN, 7075 Hale, Plano, IL 60545.

UTAH

DRABA INCERTA Pays. (BRASSICACEAE).—Cache Co., crest of Bear River Range, ridge sw. of Boss Canyon, ca. 3066 m (T14N R3E S31), e.-facing slope, growing on soils derived from Laketown Dolomite, with *Pteryxia hendersonii* and *Astragalus kentrophyta*; 28 Jun 1981, *Neely 461* (UTC). Doubletop Mtn., Bear River Range (T14N R3E S7), ca. 3256 m, w.-facing slope below summit on rocky dolomitic soils, rare, with *Pteryxia hendersonii* and *Draba oligosperma*; 24 Jul 1982, *Neely and Carpenter 1042* (UTC, BYR).

Significance. These collections represent a range extension of ca. 140 km e. of the only other known collection in Utah. The first was made in 1928 by W. Cottam (BYR, in flower only) in the Raft River Mts., Box Elder Co. This recent collection site is ca. 230 km from the nearest known site at Hall's Mtn. in the Wind River Mts., WY and ca. 330 km from a known collection site at Gunsight Pk. in the Lemhi Range, ID.—ELIZABETH E. NEELY, Forestry Sciences Laboratory, 860 N 1200 E, Logan, UT 84321 and ALAN T. CARPENTER, Dept. of Range Science, Utah State University, Logan 84322.

WYOMING

OXYTROPIS PODOCARPA Gray (FABACEAE).—Sublette Co., Wind River Mts., saddle northwest of Hall's Mtn. (T33N R6W S32), exposed nw.-facing slope at ca. 3900 m, on rocky granitic soils, growing in small patches, with *Draba crassa, Chaenactis alpina* and *Astragalus alpinus*; 18 Aug 1982, *Neely and Carpenter 1078* (UTC, WYAC).

Significance. This is the second collection of this species in WY. The first was made by F. Tweedy (NY) in Aug 1897 on Yount's Pk., Park Co. in the Absaroka Mts. on volcanic soils. This collection represents a range extension of ca. 100 km se. of the only other known collection in WY.—ELIZABETH E. NEELY, Forestry Sciences Laboratory, 860 N 1200 E, Logan, UT 84321 and ALAN T. CARPENTER, Dept. of Range Science, Utah State University, Logan 84322.

REVIEWS

The Sunflower Family (Asteraceae) of British Columbia. Vol. I—Senecioneae. GEORGE W. DOUGLAS. British Columbia Provincial Museum. No. 23 Occasional Papers Series. $6.00.

This is the first of an intended 5 volumes on the Asteraceae of British Columbia, which the author hopes to complete in another 7 or 8 years. After some introductory matter (including illustrations) on the family in general, the author proceeds to the taxonomic treatment of the Senecioneae, with keys, descriptions, commentary, illustrations, and dot-maps. The 9 genera and 55 species are arranged alphabetically. The taxonomy is in general harmonious with the views of some other recent authors dealing with adjacent or more inclusive areas, but the author does not hesitate to strike out on his own when he considers it necessary. The drawings are handsome and accurate. An extensive bibliography and rather full synonymy are given at the end, but without direct citation of the places and dates of publication of the names. I was a bit taken aback to see my 1955 treatment of composites in Vascular Plants of the Pacific Northwest lauded as a pioneering work. I had thought that my own predecessors were the pioneers.

It is de rigueur for a reviewer to point out some minor errors, slyly implying that *he* would have done a better and more careful job, and indeed I could quibble about a few details in this work. Having been on the other side of the fence a few times, I will not now reach through to nip off a morsel or so. Instead I will congratulate the author on a good job well done. I trust that his estimate of the time required for completion will not prove to be as optimistic as some of my own have been.—ARTHUR CRONQUIST, New York Botanical Garden.

Landmarks of Botanical History. By EDWARD LEE GREENE. 2 volumes: x + [v] + 1139 pp. Stanford University Press, Stanford, CA, for the Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, PA. 1983. $100. ISBN 0-8047-1075-9.

Systematic botanists, as mindful as most other scientists of the debt they owe their predecessors, are nevertheless perhaps more historically inclined than many, because the method of their study often requires reference to the writings on, and indeed, the very collections of, the plants studied by colleagues long departed. For the last half century or so, however, these fathomings have rarely had to extend back into the "nomenclatural Precambrian," that time before Linnaeus' systematization of binomials. It was not always so. Although not without precedent, there emerged out of the (then) botanically rich(er) landscape of nineteenth century California the most strident voice against Linnaeanism, at least that aspect of its ordaining that plant naming would begin with Linnaeus' *Species Plantarum* (1753). That voice was E. L. Greene's, whose nomenclatural atavisms came to naught, but whose other contributions to botany enriched in some instances, merely increased in others, the literature botanists have had to contend with. The present volumes, however, are a *tour de force.*

The *Landmarks* are just that, not a chronological account. Just as in his botanizing (including, fortunately or unfortunately, even his floristic works), Greene picked what interested him. Thus Part I of the present edition (a republication of the 1909 work, which was subtitled *A Study of Certain Epochs in the Development of the Science of Botany*) concludes with the sixteenth century "German Fathers" of botany, whereas

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Part II (published here for the first time) commences with the fifteenth century "Italian Forefathers." This is not a criticism, at all. (Those seeking a brief introduction to the history of plant classification could do worse than turn to the appropriate chapter in *Taxonomy of Vascular Plants* by George H. M. Lawrence, first Director of the Hunt Institute and initiator of this new edition.) Indeed, a strictly chronological plan has too often resulted in a book dry as dust. This one is not. Greene's approach is biographical rather than sequential. For the most part, each chapter includes an account of a life, a discussion of works, and an assessment of botanical influence. Included as subjects are both the botanically luminary and obscure, from antiquity to Tournefort.

Because of the biographical approach, it is harmonious with Greene's plan that this edition of the *Landmarks* includes chapters by Robert P. McIntosh on Greene, the man, and by Rogers McVaugh on Greene, the botanist. The work is further supplemented by Frank N. Egerton's editorial notes, introduction, bibliography, and appendixes on pre-Hellenic, medieval, and seventeenth century botanical endeavor (covering, in the form of bibliographic narrative, eras of pre-Linnaean botany not addressed by Greene). The volumes are handsome, well made, and include figures and schemes illustrating plants and principles discussed by Greene and drawn from works contemporary with the subject at hand. As a result, the volumes are evocative of books of the classical era of botany that Greene himself consulted when writing the *Landmarks.* These enhancements constitute about a third of the present edition and transform the *Landmarks* into something of a Baedeker to a goodly portion of botany past.—DALE E. JOHNSON, San Diego, CA.

Dates of publication of MADROÑO, volume 31

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No. 2, pp. 69–128:	24 April 1984
No. 3, pp. 129–195:	30 July 1984
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ANNOUNCEMENT

California Botanical Society Award for Graduate Student Research

An award of $250 will be given annually to the student member of the California Botanical Society submitting the winning proposal for thesis or dissertation research. The award is intended to help defray costs of research travel, field work, or laboratory supplies for which no other source of support exists. Each years competition will be announced in the July issue of Madroño and at the CBS Graduate Student Meeting.

Each applicant must be a student member of the California Botanical Society both in the year of submittal and during the year in which the funds are used. During the year of the award the student must be enrolled in a graduate program leading to the preparation of a thesis.

The deadline for proposals is 1 November of each year and the winner will be notified and the award made on or about 1 January of the following year. The award will be made public at the Annual Banquet in February (at which the winner will be a guest of the Society) and in the April issue of Madroño.

Proposals are to include a brief description of the project, including an assessment of its importance; the need for funds; and a summary of current support. They should not exceed six double-spaced typewritten pages. Proposals should be accompanied by an evaluative cover letter from the major adviser for the project. Five copies are to be sent to the Past President of the Society.

Proposals will be reviewed by a Committee consisting of the three elected Council members, the Second Vice President, and, as *ex officio* convener, the Past President. They will be evaluated on criteria of scientific merit and appropriateness for publication in Madroño upon completion (no contract is assumed on either side). The Committee will present a small number (usually 2–3) of the best proposals to the Council with a recommendation of one as winner. The final decision will rest with the Council.

ANNOUNCEMENT

The California Botanical Society would like to announce the following individuals who received awards at the 9th Graduate Student Meetings at California State University, Chico in April 1984.

Completed Research	Douglas Spicher Tiburon Center for Environmental Studies San Francisco State University
Work in Progress	Michael P. Cummings Department of Biological Sciences California State University, Fullerton
	Dennis E. Desjardin Department of Biological Sciences San Francisco State University

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	Jan Nachlinger Department of Biological Sciences University of Nevada, Reno
Research Proposal	F. Jay Fuller Department of Religious Studies California State University, Chico
	Victoria R. Kelly Department of Biological Sciences San Francisco State University

The Society would also like to recognize and thank Sandra Morey, the graduate students at CSU Chico, faculty and staff whose efforts made the Meetings a success.

REVIEWERS OF MANUSCRIPTS

The editor thanks all the reviewers listed below, who have generously contributed their time toward maintaining the quality of papers published in Madroño.

Irene Baker
Jim Bartel
Jerry Baskin
Bert Brehm
Kenton Chambers
H. L. Clark
Susan Conard
T. Crovello
Robert Cruden
Alva Day
Dotty Douglas
Barbara Ertter
W. J. Ferlatte
A. J. Gilmartin
J. R. Griffin
R. L. Hartman
Douglass Henderson
James Henrickson
V. L. Holland
Sterling Keeley
Job Kuijt
E. Landolt
Walter Lewis
Jack Maze
John McNeill
Richard Minnich
Duncan Porter
Peter Rowlands
J. Rzedowski
J. O. Sawyer
Rob Schlising
Carla Scheidlinger
R. J. Shaw
Richard Spellenberg
John Strother
Dean Taylor
Frank Vasek
Dieter Wasshausen
W. A. Weber
Grady Webster
Dieter Wilken
Dave Young

EDITOR'S REPORT FOR VOLUME 31

Between 1 Jul 1983 and 30 Jun 1984, 38 manuscripts were received. This represents somewhat of a decrease from the submissions of 1982–83, but the decline is not nearly as precipitous as it was last year. Nonetheless, that there was a decrease at all is troubling. From early November 1983 through the end of January 1984, almost no manuscripts were received. From Feb to Apr, 14 came in. A call for some long-outstanding revisions filled in the gap and we have had thus far no shortage of papers ready to print. Of the new submissions, 23 were articles, 8 were noteworthy collections, and 4 were notes and news. Four articles were rejected, all of which arrived in the Feb-to-Apr crunch.

Published in Volume 31 are 24 articles, 9 notes and news, 14 noteworthy collections, and 6 reviews. Total pages came to 267.

The current status of manuscripts is as follows: in review, 2; in revision, 14; accepted and awaiting publication, 23. The wait from acceptance to appearance is approximately two issues, or 6 months.

C.D. 12 Sep 1984

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INDEX TO VOLUME 31

Classified entries: major subjects, key words, and results; botanical names and plant families (new names are in **boldface**); geographical areas; reviews. Incidental references to taxa (including lists and tables) are not indexed separately. Species appearing in Noteworthy Collections appear under plant family, state, or country. Authors and articles are listed alphabetically in the Table of Contents.

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals ($18 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships ($20) include one ten-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available ($25). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Manuscripts prepared on dot matrix printers may not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren and Keuken, Index Herbariorum, 6th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted ten pages in MADROÑO each year or 20 pages over a two-year period. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $60.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

CALIFORNIA BOTANICAL SOCIETY