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N. H. Cheatham, Amazon River, 1977

For her outstanding contributions—to botany through research, teaching, and administration; to ornamental horticulture; to local and international conservation causes; and to humanitarianism and compassion wherever she is—volume 26 of MADROÑO is dedicated to MILDRED ESTHER MATHIAS. Dr. Mathias was Vice-President of the California Botanical Society in 1955 and served as Editorial Board member for MADROÑO from 1941 to 1970. She has published nearly 200 articles and books, many of them (over a 50-year span) on Umbelliferae. Her contributions to knowledge of this family, partly in an enduring collaboration with Lincoln Constance, are unexcelled. Many of her students are themselves eminent botanists and have proclaimed their debt to her. As Director of the UCLA Botanical Garden and founding force behind the Las Cruces and Lankester Botanical Gardens in Costa Rica, she has added to the beauty of our world and saved precious genetic stocks. Locally she has led and developed the University of California's Natural Land and Water Reserves System (which has set aside 26 units encompassing a great diversity of California's habitat types), the California Natural Areas Coordinating Council, the California Consortium for Significant Natural Areas, the California Conservation Council, and the Southern California Chapter of the Nature Conservancy. She was founder, teacher, Board member, and President of the Organization for Tropical Studies, which has done more to show U.S. graduate students the excitement and critical need for work in tropical botany and ecology than all other sources combined. She is an untiring and effective force in more international conservation efforts than can be specified. The scientific societies in which she has been elected President and major awards to her are too numerous to mention. Mildred, your pioneering spirit, unbelievable energy, wit, humor, warmth, and effectiveness as a leader have made the world a brighter, greener, and more compassionate place for all of us. We salute you.

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ANATOMY OF KOEBERLINIA AND CANOTIA REVISITED

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ABSTRACT

Detailed anatomical descriptions of leaves and stems are presented for *Koeberlinia* and *Canotia,* desert perennials of North America with photosynthetic old stems. *Koeberlinia* has linear subulate leaves with conical unicellular trichomes, adaxial stomata, abundant palisade mesophyll, and relatively few tannin cells; whereas *Canotia* has deltoid scales lacking trichomes and having abaxial stomata, undifferentiated mesophyll, and abundant tannin cells. Stem anatomy of these genera is also dissimilar even though both have adaptations to facilitate stem photosynthesis. Myrosin cells are present in inner cortex of *Koeberlinia.* Woods are superficially similar in vessel and fiber dimensions; however, *Canotia* has low, narrow rays with abundant resin and prismatic crystals, whereas *Koeberlinia* has higher, wider rays lacking resin and crystals, and its vessels appear to have vestured pits. Bark anatomy of these genera is fundamentally different. A previous report of secretory ducts in *Koeberlinia* is incorrect. Those features shared are judged to be convergent, and the differences are great enough to negate their classification together in the bigeneric Koeberliniaceae. A recommendation is made to reassign *Canotia* to Celastraceae and *Koeberlinia* to or near Capparaceae.

Koeberlinia and *Canotia* are xeromorphic, nonsucculent perennials of North America that have spine-tipped, aphyllous, photosynthetic old stems. Whereas Metcalfe and Chalk (1950), Benson (1957), Takhtajan (1969, 1973), and Hutchinson (1973) classify these desert plants in the bigeneric family Koeberliniaceae, most recent treatments place *Koeberlinia* in Capparoideae of Capparaceae (Melchior, 1964; Airy-Shaw, 1966, 1973; Cronquist, 1968; Thorne, 1968, 1976; Novák, 1972), separating *Canotia* from *Koeberlinia* for reassignment, presumably in or near Celastraceae. Johnston (1975) lists the known similarities between *Acanthothamnus* (Celastraceae), which also has old green stems, and *Canotia,* supporting inclusion of *Canotia* in that family. Only Metcalfe and Chalk make anatomical comparisons of *Koeberlinia* and *Canotia,* these based on scanty material and Record's (1926) wood diagnosis of *Koeberlinia* that lacks illustrations; they do not cite Record's (1938) wood description of *Canotia* and previous descriptions of *Koeberlinia* stem anatomy (Cannon, 1908; Pax and Hoffman, 1936). Moreover, Airy-Shaw (1966, 1973) has questioned their report of resin ducts in *Koeberlinia.* This study expands descriptions of and more fully illustrates vegetative anatomy of *Koeberlinia* and *Canotia* so that their relationships may be reviewed.

METHODS

Samples of *Koeberlinia spinosa* Zucc. from three disjunct populations in Cochise County, Arizona (*Gibson 3243, 3263, 3463*), *Canotia holacantha* Torr. from northern Arizona (*Burgess 5481*; *Gibson 3154*),

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and *C. wendtii* M. C. Johnst. from Chihuahua, Mexico (*Burgess 5212*) were collected and preserved in formalin-acetic acid-alcohol fixative (Johansen, 1940). Herbarium vouchers are in ARIZ. Additional wood microslides of *Koeberlinia* from California (*Gill 451, 453*: POM), provided by Dr. Sherwin Carlquist, and the original microslide of Record (1926; *Yw 8959*), loaned by the Forest Products Laboratory, Madison, were examined for wood descriptions.

Wood and bark sections were cut on a sliding microtome at 20 μm and stained with safranin. Wood macerations were prepared using Jeffrey's method (Johansen, 1940) and also stained with safranin. Measurements were made with an optical micrometer on sections except those on cell length, which were obtained from macerations. Means of cell dimensions were based on 25 measurements for each sample. Vessel pitting was observed at 1000× using an Eastman Kodak No. 11 green filter.

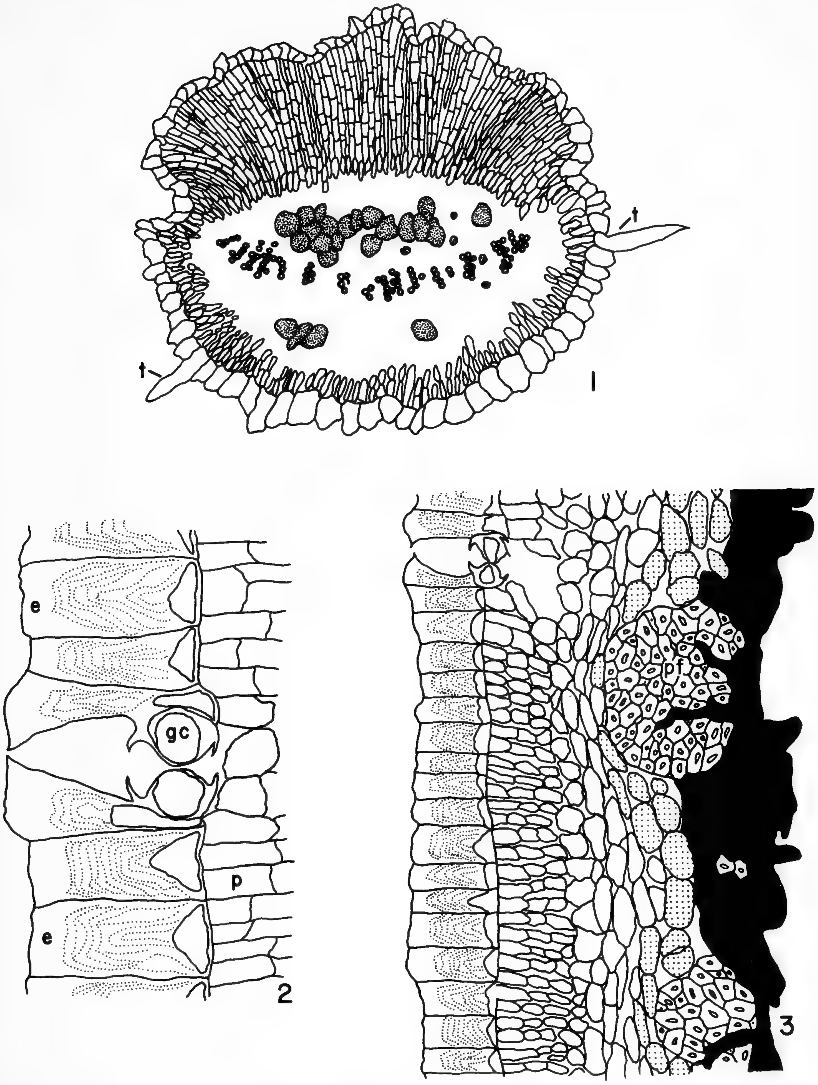
Stems and leaves were embedded in paraffin, sectioned at 10 or 15 μm, and stained with safranin and fast green. All drawings were prepared by tracing photomicrographs.

ANATOMICAL DESCRIPTIONS

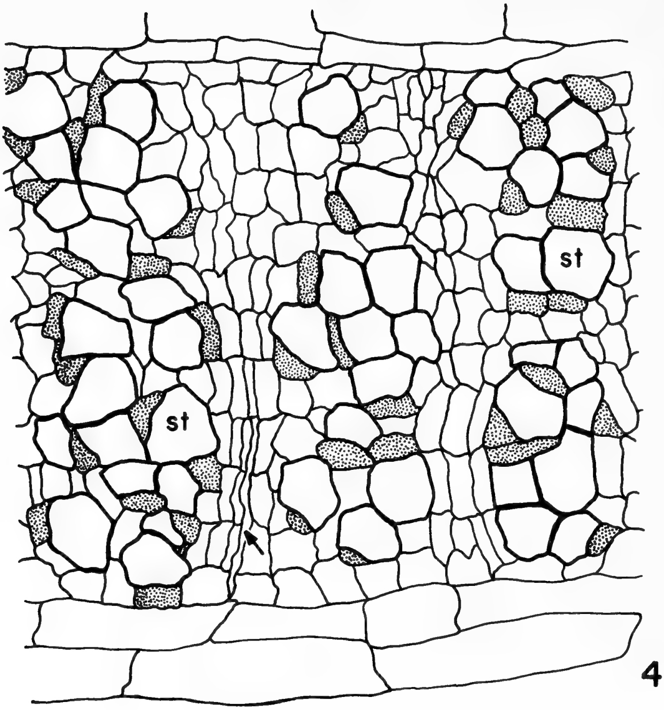
Koeberlinia

Leaves. Leaves linear-subulate, somewhat curved, 1.5–2.2 mm long, caducous, present only on very young vegetative shoots. Epidermis (Fig. 1) uniseriate; cells with markedly convex outer walls. Stomata sunken in depressions; epistomatic. Trichomes unicellular, conical with rounded tips, to 100 μm long, scattered over leaf surface. Lamina absent. Palisade chlorenchyma highly developed on adaxial side, much less so on abaxial side. Tannin cells in undifferentiated mesophyll. Primary xylem conspicuous and abundant, forming wide arc across leaf.

Green stems. Stems bright green, evenly tapering to a sharp point. Epidermis (Figs. 2, 3) uniseriate, soon becoming radially elongate with onset of secondary growth, which is precocious; outer walls excessively thickened with concentric layers of wall material (not radial as illustrated in Pax and Hoffman, 1936), impregnated with cuticle. Trichomes frequent; unicellular and conical with rounded tips; walls thickened like epidermis. Stomata anomocytic; sunken in pits when groundmass epidermis increases in length; outer and small inner ledges present. Chlorenchyma to 0.2 mm thick, palisade cells not markedly elongate. Inner cortex with *spheroidal idioblastic myrosin cells*. Sclerenchyma beneath chlorenchyma, beginning as small groups of primary phloem fibers, later forming a closed ring by differentiation of brachysclereids from parenchyma. Primary phloem with small rounded solitary crystals. Secondary phloem (Figs. 4, 5) with bands of sieve tubes and companion cells in alternation with several layers of paren-



FIGS. 1–3. *Koeberlinia spinosa.* 1. Leaf transection, showing epidermis with trichomes (t), palisade of mesophyll, tannin cells (heavy stipple) in undifferentiated ground tissue, and a wide arc of primary xylem vessels (small circles). ×100. 2. Green stem transection; outer secondary walls of epidermis (e) develop eccentrically with concentric layering, overarching stomatal guard cells (gc) with prominent ledges. Palisade (p) of cortex is not well developed. ×350. 3. Green stem transection; beneath photosynthetic tissues are myrosin cells (light stipple) and clusters of phloem fibers (pf) interconnected by brachysclereids (black), which differentiate relatively late in stem development. ×190.



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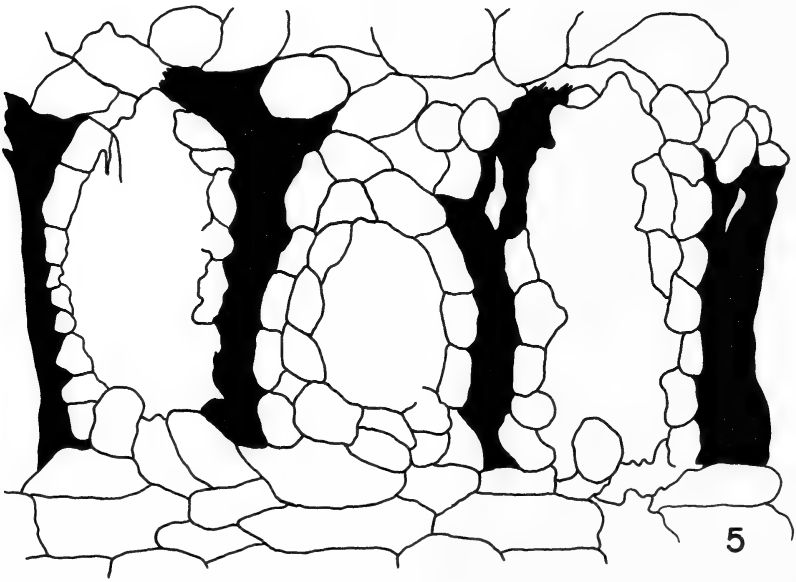

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chyma having thin walls. Sieve tube walls fairly thick; fibers absent. In outer secondary phloem, parenchyma cells enlarged and separate, forming large spaces in tissue; old bands of sieve tubes and companion cells compressed into thick, irregular band of cell wall material (Fig. 5); these spaces the "secretory (resin) canals" of Metcalfe and Chalk (1950; dried phloem also splits along these bands of parenchyma). Pith with lignified secondary walls shortly following the start of secondary growth; often with abundant prismatic to rounded solitary crystals.

Stem wood. Sapwood yellowish white, sharply defined; heartwood dense, chocolate brown. Growth rings present, usually sharply defined; wood ring-porous (Fig. 6). Pores distributed evenly throughout each growth layer; 150–175 mm^{-2} of transection. Pores circular or oval in outline. Pore diameter medium-sized to moderately small in earlywood (24–212 μm; means 43–149 μm) to very small and extremely small in latewood (means 20–49 μm). Pores mostly solitary, rarely in twos. Maximum vessel wall thickness 8 μm found in widest pores, decreasing to 1.5 μm in narrowest pores. Vessel-element length medium-sized to extremely short (68–384 μm; means 198–310 μm), longest in largest stems. Perforation plates exclusively simple; end walls nearly transverse to diagonal; tails sometimes present, especially in latewood elements. Lateral walls of vessels with numerous rows of alternate, bordered pits, 5–6 μm across; *pits inconspicuously vestured* (Fig. 8; needs SEM verification) pit aperture nearly horizontal and linear. Tertiary helical thickenings usually present. Tyloses absent but gum deposits present in some pores of heartwood. Tracheids enucleate, nonseptate, very short (means 425–588 μm), and extremely small (13–27 μm). Maximum fiber wall thickness 7.5 μm; pits abundant and conspicuous, pit diameter 4–6 μm; tertiary helical thickenings present but inconspicuous. Axial parenchyma usually abundant, apotracheal diffuse or diffuse-in-bands and scanty paratracheal; accumulating dark substance in heartwood. Rays (Figs. 6, 7) mostly multiseriate, usually 4–7 cells wide, but some biseriate and uniseriate, height 70–1200 μm; 7–9 mm^{-1}. Rays homogeneous, cells long-procumbent, lacking crystals except in very young stems where ray cells of innermost xylem have occasional solitary crystals resembling those of pith; dark substance present but not abundant in rays of heartwood, as in axial parenchyma. Storying absent.

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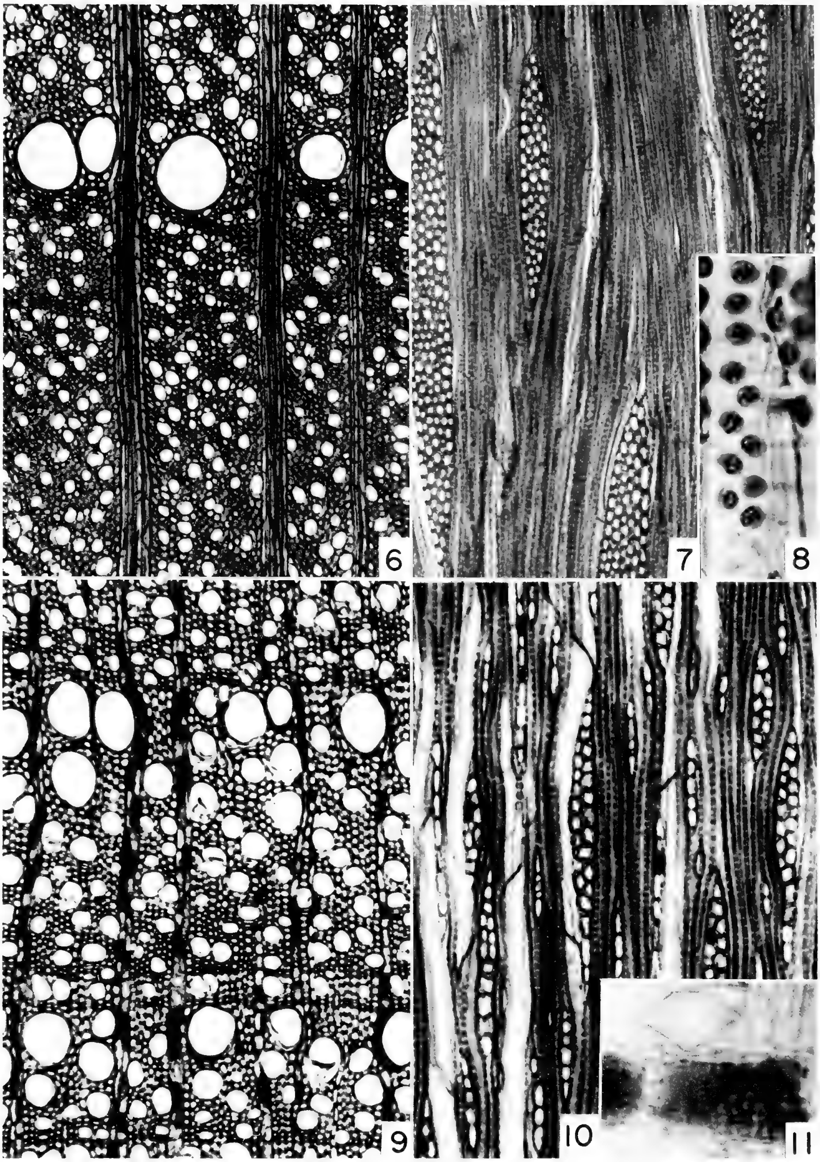
FIGS. 4–5. *Koeberlinia spinosa,* secondary phloem transections. ×500. 4. Inner conducting region composed of sieve tubes (st) having thickened walls, companion cells (heavy stipple), and parenchyma. Arrow indicates where parenchyma between growth layers has begun to split. 5. Outer region where sieve tubes and companion cells are crushed (black) and periclinal splits have developed in bands of parenchyma, resembling resin ducts but nonsecretory.



FIGS. 6–11. 6–8: *Koeberlinia spinosa,* wood. 6. Transection, showing ring porosity. ×110. 7. Tangential section. ×110. 8. Tangential section; vessel with vestured bordered pits on lateral walls. ×700. 9–11: *Canotia holacantha,* wood. 9. Transection; ring-porous wood in which vessels are abundant; dark staining cells in the narrow rays contain resin. ×110. 10. Tangential section, showing numerous low uniseriate and biseriate vascular rays often containing resin cells. ×110. 11. Radial section of same at high magnification, where resin- and crystal-bearing cells of the ray are observed. ×750.

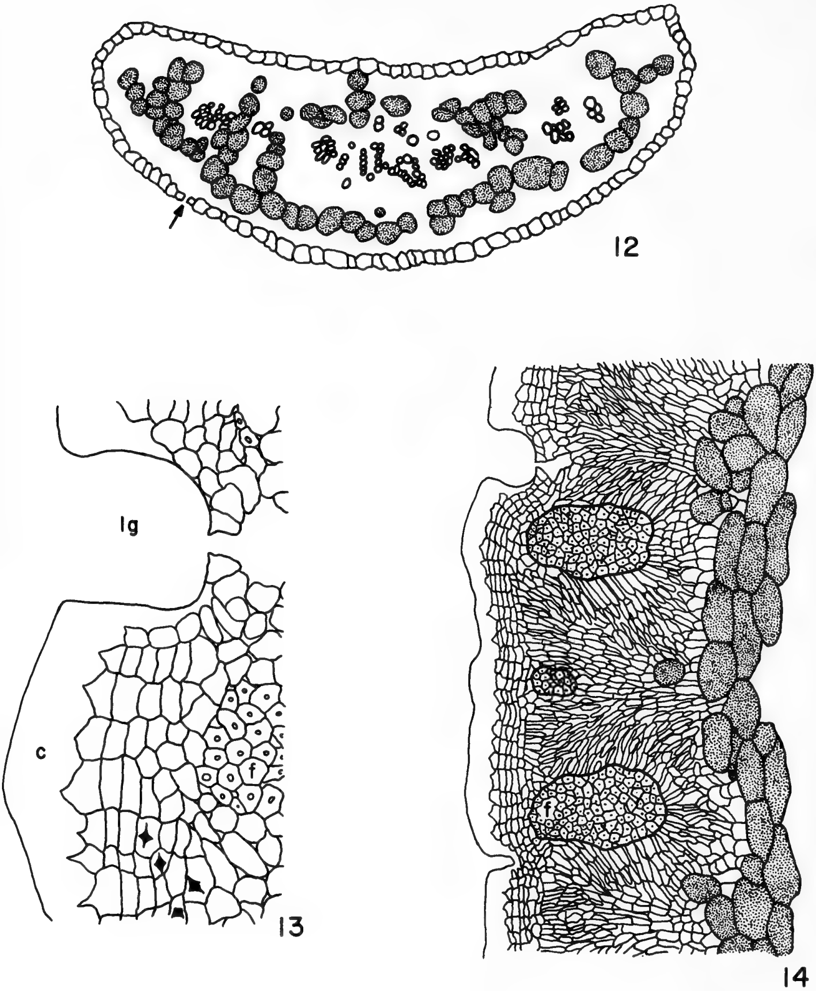
Root wood, Gibson 3243. Similar to stem wood of the stem plant except as follows: growth rings less distinct; vessel-element length and diameter slightly greater; and tracheid length greater (mean 624 μm).

Canotia

Leaves. Leaves minute caducous deltoid scales, 1–2 mm long. Epidermis (Fig. 12) uniseriate; outer wall somewhat thickened. Stomata sunken slightly; hypostomatic. Trichomes absent although multicellular glandular trichomes abundant in leaf axil, these with tannins. Lamina absent. Mesophyll undifferentiated, no palisade cells, but many interior cells having abundant tannins. Vascular tissue forming a wide arc across leaf.

Green stems. Stems pale green, to more than 1 cm diam. Epidermis (Figs. 13, 14) uniseriate at first, then dividing periclinally, even before the onset of secondary growth, to produce a multiple epidermis with 4 or more cells in a radial file; innermost cells often with solitary rhomboidal crystals; outer walls impregnated with and covered by cutin, to 45 μm thick. Trichomes as above. Stomata sunken in deep longitudinal grooves when multiple epidermis forms; outer and inner ledges present. Chlorenchyma about 250 μm thick in mature stems, palisade cells highly developed. Subepidermal clusters of thick-walled unlignified cortical fibers with minute lumina (gelatinous in *C. wendtii*), precocious in origin. Innermost chlorenchyma with solitary rhomboidal crystals. Ring of tangentially ovoid, large tannin cells beneath chlorenchyma. Primary phloem (pericyclic?) fibers present but delayed in development; thick walled. Secondary phloem axial system with broad bands of sieve tubes and parenchyma interrupted by groups or bands of bast fibers. Pith sclerified early; tannins cells very abundant; crystals uncommon.

Stem wood. Sapwood yellowish; heartwood fairly dense, somewhat purplish-brown. Growth rings of sapwood fairly distinct with the naked eye; semi-ring to ring porous (Fig. 9). Pores distributed evenly and abundant throughout each growth layer; up to 200 mm^{-2} of transection. Pores tending to be radially ovoid in earlywood and irregular in outline in latewood. Pore diameter moderately small in earlywood (23–113 μm; means 53–73 μm) to extremely small in last-formed latewood (means 22–28 μm), gradually decreasing from earlywood to latewood; mean earlywood pore diameter widest in widest growth layers, increasing also from inner to outer wood. Pores almost exclusively solitary, rarely in twos. Maximum vessel wall thickness 3 μm found in widest pores, decreasing to 1 μm in narrowest pores. Vessel-element length medium-sized to extremely short (138–723 μm; means 234–447 μm). Perforation plates exclusively simple; end walls nearly transverse (widest elements) to diagonal with long tails (narrowest elements). Lateral walls of vessels with numerous rows of alternate, bordered pits, to 6 μm across; pits not vestured; pit aperture



FIGS. 12–14. *Canotia holacantha*. 12. Leaf transection, showing epdiermis with abaxial stomate (arrow), tannin cells in undifferentiated ground tissue (heavy stipple), and a wide arc of primary xylem vessels (small circles). ×150. 13. Green stem transection; longitudinal grooves (lg) are formed by periclinal divisions of protoderm, producing a multiple epidermis that is heavily cutinized (c). Some parenchyma cells contain prismatic crystals (dark bodies); clusters of fibers (f) occur opposite multiple epidermis. ×350. 14. Green stem transection; beneath multiple epidermis palisade cells are well developed, even radiating from clusters of fibers (f). Primary phloem is enclosed by a ring of tannin cells (heavy stipple). ×100.

nearly horizontal and linear. Tertiary helical thickenings present and conspicuous in vessels. Tyloses absent. Tracheids enucleate, nonseptate, very short (means 432–825 μm), and extremely small (to 20 μm). Maximum fiber wall thickness 4.5 μm; pits abundant and conspicuous, pit diameter to 6 μm, often wider than on vessels; pit aperture diagonal; tertiary helical thickenings present but inconspicuous. Axial parenchyma apotracheal diffuse and occasionally diffuse-in-bands and scanty paratracheal; heartwood axial parenchyma usually containing abundant resin. Rays (Figs. 10, 11) uniseriate and biseriate, rarely triseriate; height 25–620 μm; up to 20 mm^{-1}. Ray heterocellular, cells mostly square to slightly procumbent; containing abundant resin in heartwood and inner sapwood, and solitary prismatic crystals throughout (Fig. 11); integumented. Storying absent.

Root wood, Burgess 5481. Similar to stem wood of the same plant except as follows: growth rings less distinct; pore diameter slightly greater because larger in earlywood and latewood; and tracheid length shorter.

Discussion

Metcalfe and Chalk (1950) correctly noted that *Koeberlinia* and *Canotia* show similar young stem structure, but the factual sources for their comparisons are not apparent; an anatomical description of *Koeberlinia* is compared with an illustration of *C. holacantha,* the structure of which is not discussed. When compared closely, one observes many differences between the two genera. *Koeberlinia* has stem vesture, a single-layered epidermis with stomata sunken in individual pits, poor development of cortical palisade, idioblastic myrosin cells in cortex, an ensheathing ring of pericyclic sclerenchyma, and no tannin cells. *Canotia* has no trichomes except in leaf axils, a multiple epidermis with stomata sunken in longitudinal grooves, prominent bundles of cortical fibers, strong development of cortical palisade, no myrosin cells, and an ensheathing ring of tannin cells. Moreover, the nature and distribution patterns of crystals in the two genera are fundamentally different. Features shared, e.g., thick cuticle, sunken stomata with ledges, and fairly wide chlorenchyma, are similarities expected from plants in which photosynthesis by old, leafless stems is the chief source of carbon assimilation for the plant, i.e., adaptations related to penetration of light, plant water status, and gaseous exchange. In fact, outer stem features of these species more closely resemble other unrelated aphyllous perennials with spine-tipped green stems than each other (Gibson, unpubl. data).

Although leaves of *Koeberlinia* and *Canotia* are ephemeral, vestigial organs, their structural designs are quite dissimilar. Their similarities include only the great amount of vascular tissues and tannins present. Both leaves resemble a midvein in structure and could have arisen convergently by a loss of marginal meristems, which are usually responsible for blade formation.

The account of Metcalfe and Chalk (1950) incorrectly characterized phloem of *Koeberlinia* as having secretory canals. These authors observed young stems from dried herbarium material and, consequently, probably observed artifactual splitting in phloem growth layers along zones of weakness in parenchyma. In bark, this splitting occurs naturally as tissues are stretched to accommodate increases in stem circumference. This splitting superficially looks like resin ducts because the openings appear to be lined with epithelium. Secondary phloem of *Koeberlinia* and *Canotia* differs significantly, especially in the banding patterns of axial elements and the abundance in *Canotia* of bast fibers, which are absent in *Koeberlinia*.

Woods of *Koeberlinia* and *Canotia* are superficially very similar in that their vessel elements and tracheids are closely comparable in dimensions and wall features, and the three species have ring-porous woods (to semi-ring-porous in *Canotia*). Nonetheless, these woods are different on the basis of the vessel pits and rays; *Koeberlinia* has vestured pits on vessels and relatively wide vascular rays whereas *Canotia* lacks vestured pits and has very numerous, low, narrow rays with abundant resin- and crystal-bearing cells. Prismatic crystals are generally absent in woods of *Koeberlinia*. Moreover, *Koeberlinia* tends to have more conspicuous and numerous axial wood parenchyma.

Woods of nonsucculent perennials from arid and semi-arid habitats typically have numerous, very short, narrow vessel elements with simple perforation plates, multiseriate alternate lateral-wall pitting, and, in many cases, tertiary helical thickenings, and the vessels characteristically occur in large groups (Webber, 1936; Carlquist, 1966, 1975, 1977). Woods of *Canotia* and *Koeberlinia* are noticeably xeromorphic except that vessel grouping is completely lacking. For desert plants, wood similarities have arisen convergently so many times that citing similarities between dimensions and wall features of axial elements from two xeromorphic taxa is unwarranted for drawing systematic conclusions.

Johnston (1975) clearly rejected the classification of *Canotia* and *Koeberlinia* in the same family, a proposal dating from Engler (1895) and Barnhart (1910), and he noted how *Canotia* fits comfortably in Celastraceae near *Acanthothamnus*. *Acanthothamnus* is unknown anatomically, so comparisons cannot be made. Nevertheless, Record (1938) concluded that woods of *Canotia* are quite typical for Celastraceae.

Given that *Koeberlinia* must be reclassified apart from *Canotia,* one must look first to Capparaceae, into which most authors have classified *Koeberlinia* on reproductive features. This anatomical study sheds new light on that placement. Species of Capparaceae, as well as Brassicaceae, have vestured pits on vessels and myrosin cells, features individually uncommon in angiosperms as a whole and quite unusual occurring together. All aspects of *Koeberlinia* stem anatomy also fit within the range of features recorded in woody Capparaceae (Metcalfe and Chalk, 1950), including crystal and sclerenchyma patterns. Therefore, assignment of *Koeberlinia* to Capparaceae is justifiable, and the significant remaining problem is to determine to which capparaceous genus *Koeberlinia* is most closely related. I expect the closest extant relative to possess normal secondary xylem, myrosin cells, and xeromorphic tendencies as well as similar design of reproductive features such as pollen (Martin and Drew, 1969). When these comparisons are completed, recognition of the monotypic Koeberliniaceae (Kearney and Peebles, 1960; Shreve and Wiggins, 1964; Correll and Johnston, 1970; Munz, 1974) will undoubtedly be judged unwarranted.

ACKNOWLEDGMENTS

I thank those who provided material for this study. I am indebted to Dr. Regis Miller, Forest Products Laboratory, Madison, who provided technical help on wood diagnoses and suggested a search for vestured pits.

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A GRAZING ECOTYPE IN A CHLOROPHYLLOUS ROOT-PARASITE, ORTHOCARPUS FAUCIBARBATUS SSP. ALBIDUS (SCROPHULARIACEAE)

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ABSTRACT

A population of unusually short *Orthocarpus faucibarbatus* ssp. *albidus* plants in a closely grazed sheep pasture on the coast of northern California was studied. Branches were gently ascending and basal instead of erect from the upper stem. Seeds from this population were grown inland where wind buffeting, salt spray, cooler temperatures, close grazing, different host plants, and limiting soil were reduced or absent. The resulting plants closely resembled the parent population in both branching form and height. Shortness in this ecotype was due mostly to shorter rather than fewer internodes. Analysis of mean internode lengths in several coastal and inland populations showed significant differences between the grazing ecotype and all ungrazed populations, and between coastal and inland populations. Because this species is shade intolerant and an obligate outcrosser, close sheep grazing is beneficial in reducing the height of associated plants, allowing greater exposure to sunlight and insect pollinators. The harsh, spiny, rosette leaves of *Eryngium armatum* afford enough protection for the lower flowers and seed capsules of this herbaceous annual to prevent its demise through overgrazing.

Orthocarpus faucibarbatus ssp. *albidus* Keck is a white-flowered, herbaceous annual that is chlorophyllous and root-parasitic on a wide range of other vascular plants (Thurman, 1965).

In June, 1962, I noticed a population of very short *O. faucibarbatus* ssp. *albidus* in a closely grazed sheep pasture, 7.7 km south of Point Arena on the northern California coast (coded "SPC" below). At that time, relatively few ungrazed plants were available to demonstrate the normal heights for this colony. This is an area that has been grazed continuously for more than 100 years (Hektner and Foin, 1977). I revisited the site early in the season in May, 1964, before the pasture was grazed closely again. The ungrazed *O. faucibarbatus* ssp. *albidus* plants in the pasture and in an ungrazed area just outside of the fence were still much shorter than members of other populations of this subspecies, even those in other coastal populations, which are generally shorter than those inland. Most of the plants also had low, gently ascending branches originating close to the ground instead of a more erect branching from the upper stem characteristic of all other populations. This type of basal branching in ungrazed plants suggested genetic variation rather than morphological plasticity or a branching response to loss of the top of the plant by grazing.

Neel and Harris (1971) reported significant height reduction in *Liquidambar* and in corn (1972) when they simulated a shaking action similar to wind buffeting. Windblown salt aerosol was reported as an important cause for the low, prostrate form of *Baccharis pilularis* dominant at low coastal sites (Clayton, 1972). However, this still does not explain why this *O. faucibarbatus* ssp. *albidus* population was so much shorter than other coastal populations exposed to these same general climatic factors.

The most noticeable difference in host plants seemed to be the abundance of *Eryngium armatum,* a member of the Umbelliferae with harsh, spiny, rosette leaves that were closely associated with many ungrazed *Orthocarpus* in the pasture. Kemp (1937) found a correlation of short strains of *Poa pratensis, Dactylis glomerata,* and *Trifolium repens* with closely grazed pastures. The natural selection of short plants that could persist among the spiny *Eryngium* leaves seemed a viable hypothesis.

Seeds from this short coastal population were planted inland in sites that were warmer, less windy, free from salt spray, ungrazed, and had different soils and host plants. The purpose of this experiment was to determine whether the observed shortness was due mainly to morphological plasticity in response to coastal environment conditions, to genetically fixed ecotypic variation, or to both.

METHODS

About 200 seeds from the short-statured populations were sown on the soil surface of a marked plot in an abandoned orchard along state highway 29 in an Inner Coast Range valley 9 km north of Napa (SPI). This site was 60 km from the coast and 56 km from the nearest coastal population.

Although no *O. faucibarbatus* ssp. *albidus* were growing there, the orchard was considered a suitable site because it supported other species of *Orthocarpus* including *O. castillejoides,* which also occurred in the sheep pasture. Both coastal and inland *O. castillejoides* have a semiprostrate form characteristic of the species. Seeds from an *O. faucibarbatus* ssp. *albidus* population (5NN) 0.8 km south of the orchard test site were sown at SPI as a standard for the suitability and performance of *O. faucibarbatus* ssp. *albidus* at the test site. Weather records showed that the test site had 40 cm less precipitation (60 cm), 27 fewer rainy days (43), and 1.3°C warmer October to May mean temperature (11.9°C) than the parent site (SPC) during this growing season (U.S. Department of Commerce, 1964, 1965).

The sown plants at SPI were observed twice during the spring of the 1965 growing season and were collected on June 5, 1965, after growth had stopped and plants were dead. Considerable plot damage by off-road vehicles just prior to collection greatly reduced the number of plants available for analysis. However, the undamaged plants appeared to be a representative sample of the population as observed earlier.

Population samples from SPC and four other coastal populations (3SG, 8NB, 2NB, JCT) collected in May, 1964, were compared with the plants grown at the inland test site, i.e., from the short coastal

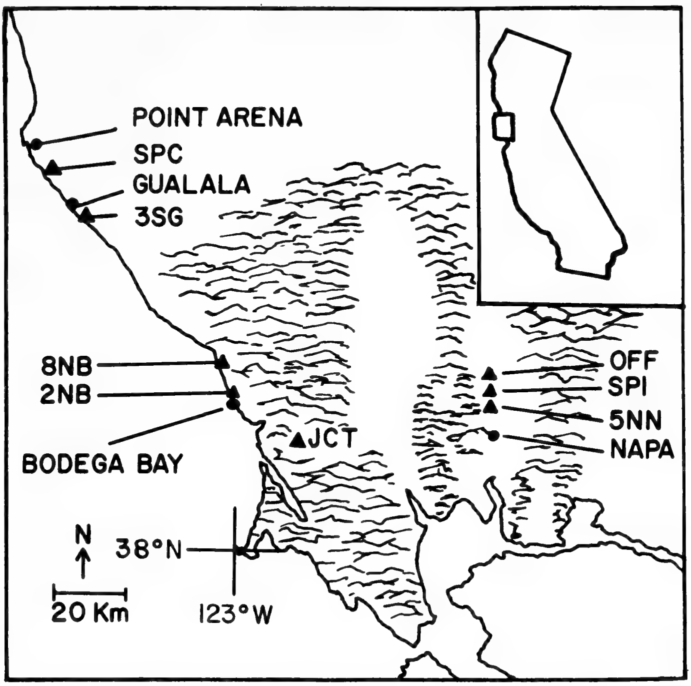

FIG. 1. Map of coastal California showing locations of the populations studied. SPC—short population in closely grazed sheep pasture 7.7 km S of Point Arena; 3SG—lightly grazed sheep range 4.8 km S of Gualala; 8NB—ungrazed roadside 12.9 km N of Bodega Bay; 2NB—ungrazed roadside 3.2 km N of Bodega Bay; JCT—lightly grazed cow pasture at junction of Dillion's Beach Rd. and Middle Rd.; 5NN—inland seed source 8 km N of Napa; SPI—seed from SPC population grown at the test site 8.9 km N of Napa; and OFF—*O. f.* ssp. *faucibarbatus* 9.7 km N of Napa.

seed source (SPI), and an inland seed source near the test site (5NN). An inland population of *O. faucibarbatus* ssp. *faucibarbatus* (OFF) from near the inland test site was also analyzed to compensate for the scarcity of *O. faucibarbatus* ssp. *albidus* plants in the inland test site. Except for flower color, the two subspecies differ little morphologically. Figure 1 shows the locations and symbols of the populations.

The number of internodes and the average internodal distance between the cotyledons and lowest flower were measured to learn whether the morphological basis of shortness was due to a reduced number of internodes, shorter internodes, or both. This is a more conservative measurement than total plant height which continues to increase as long as the plant flowers.

Two voucher specimens [*Thurman 647* (5NN) and *Thurman 711* (SPI)] are in UC. Further material is available from the author.

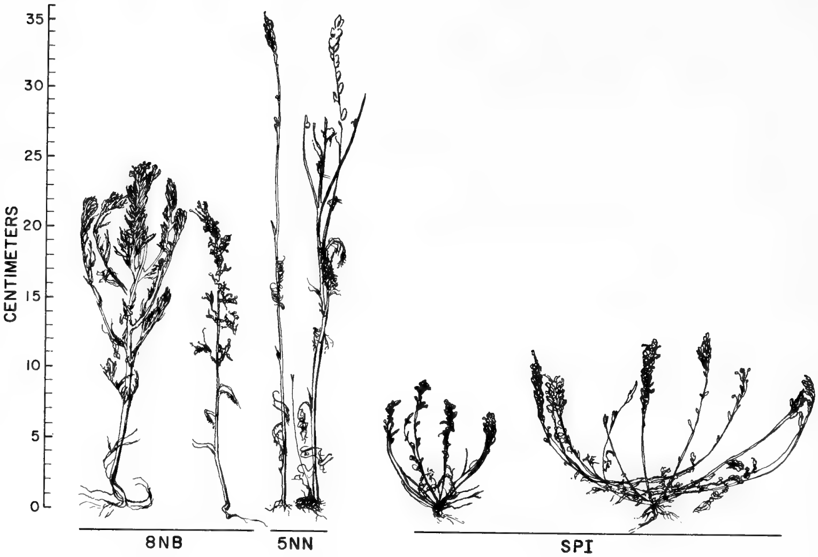

FIG. 2. Specimens of *Orthocarpus faucibarbatus* ssp. *albidus*. The left pair of plants was collected near the end of the growing season on an exposed coastal headland (8NB). The middle pair (5NN—from inland seed source) and right pair (SPI—seed from coastal sheep pasture) were harvested from the inland experimental site north of Napa at the end of the growing season.

Because variances were too heterogeneous to satisfy the assumptions for analysis of variance, the Student-Newman-Keuls test was used to determine which means were significantly different.

RESULTS

Seeds from the short, coastal sheep pasture population (SPC) when grown inland (SPI) produced plants with the same distinctive short central stem and ascending basal branches characteristic of their parent population. Figure 2 shows this growth form compared with representative plants from coastal (8NB) and inland (5NN) sites.

The mean lengths from cotyledons to lowest flower are shown in Fig. 3. The difference between SPC and the other four coastal and the two inland populations (5NN, OFF) was highly significant ($P < 0.01$). Although SPI was taller than its parent population (SPC), the difference was not significant. A highly significant difference ($P < 0.01$) was also found between the inland populations (5NN, OFF) and all others. The only other significant difference was between 2NB and 3SG ($P < 0.05$). Although 8NB had a mean height to lowest flower of 1.9 mm greater than 2NB, the smaller sample size reduced its statistical significance to slightly less than the 0.05 value.

Figure 3 shows the mean numbers and lengths of internodes, respec-

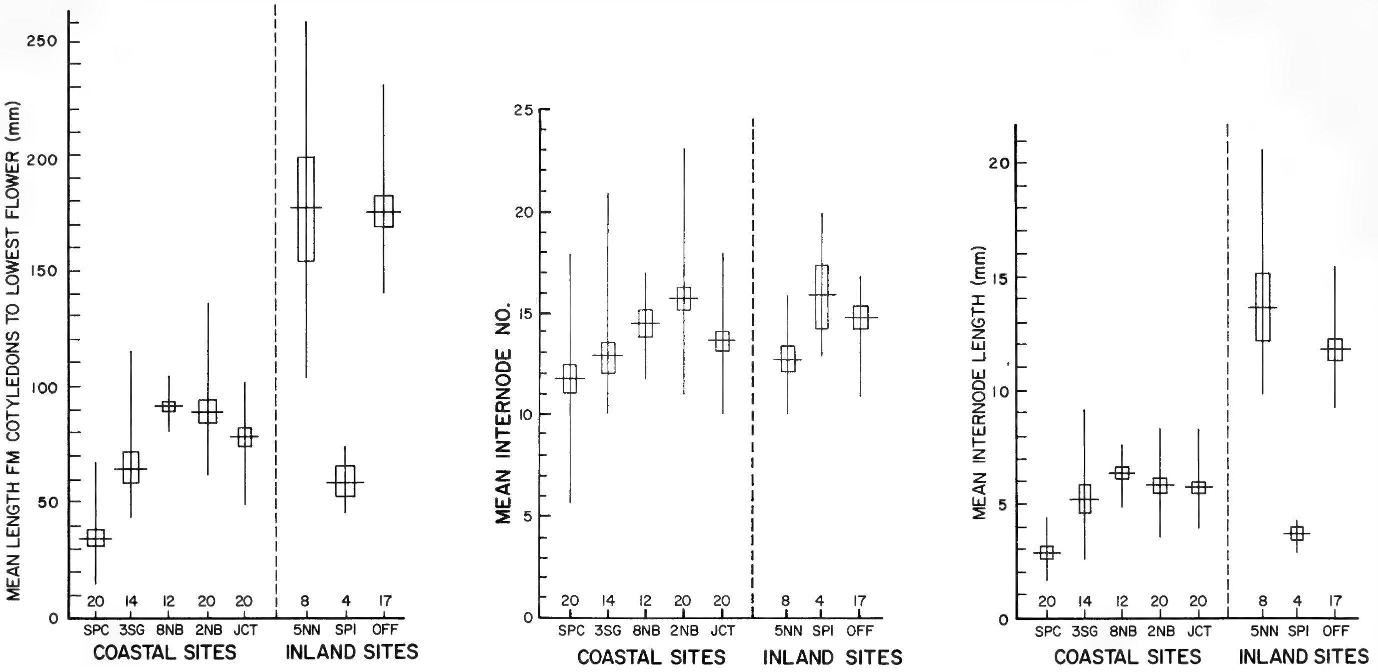

FIG. 3. Mean length of stem from cotyledons to the lowest flower, mean internode number, and mean internode length. Means shown as horizontal lines; ranges are shown as vertical lines; one standard error of the mean is shown on either side by open bars. Numbers above site designations are sample sizes.

tively, between the cotyledons and lowest flower. Mean internode lengths fall into three groups: inland (5NN, OFF), coastal (3SG, 8NB, 2 NB, JCT) and short, coastal sheep pasture, whether grown in place (SPC) or grown inland (SPI). The differences in internode lengths correspond more closely to the greater heights of the four other coastal and two inland populations than do the small differences in internode numbers. Most SPC plants had several very short basal internodes, about 3–5 mm long, a feature seldom found in other populations.

SPC differed significantly ($P < 0.05$) in internode number when compared with 2NB, 8NB, and OFF. Population 3SG was also found to differ significantly ($P < 0.05$) from 2NB in this respect.

The Student-Newman-Keuls test showed that the differences in internode lengths of 5NN and OFF and all other populations were highly significant ($P < 0.01$). The only other significant difference in internode length was between SPC and all except SPI and 3SG. The 3SG population was also in a sheep pasture but among lightly grazed bunch grasses.

Discussion

The production of the same basal, ascending branch form and short stature when seed of *O. faucibarbatus* ssp. *albidus* from the short, coastal sheep pasture (SPC) was grown under no grazing, on different soils, at higher temperature, with less wind and very little salt spray suggests a genetically fixed ecotype rather than a morphologically plastic ecophene. However, the slight increase in height of plants from SPC seed grown inland (SPI) is probably due to a plastic response to the reduced effects of coastal climatic factors.

The short coastal form (SPC) of *O. faucibarbatus* ssp. *albidus* has adaptive features similar to several Californian compositae described by Clausen and Hiesey (1958). Both *Layia jonesii* and *Hemizonia paniculata* also have marine ecotypes with shorter central stems and more spreading branches than their inland ecotypes. More extreme are *Layia platyglossa, L. chrysanthemoides,* and *Hemizonia multicaulis,* which have no central stem but only horizontal sidebranches attached to a central crown (Clausen and Hiesey, 1958). A similar response was reported in *Agrostis stolonifera* by Aston and Bradshaw (1966). Coastal climate is probably not responsible for the very short lower internodes and basal ascending branches in *O. faucibarbatus* ssp. *albidus* from SPC because the branching form of the other coastal populations is like that found in inland populations (Fig. 2).

However, the slightly shorter stature of most coastal populations is probably an adaptation to coastal conditions. Clausen and Hiesey (1958) suggest wind adaptation as a primary cause. Evidence by Neel and Harris (1971), in their studies of wind buffeting, revealed a significant reduction in number of nodes and in internode lengths in young *Liquidambar* trees when given only 30 seconds of moderate shaking daily.

They also found that corn treated similarly was 50 percent shorter and had 15 percent shorter internodes but resumed normal growth rates three days after shaking was stopped. Clayton (1972) suggested that salt aerosols in the wind are responsible for *Baccharis pilularis* being shorter (40–60 cm) on the shore than at a site one mile inland where the salt spray is less and plants are 2–3 m tall. Yet of the five coastal populations exposed to the same coastal climate, only SPC exhibited a noticeable reduction in height.

The morphological basis of shortness in coastal *O. faucibarbatus* ssp. *albidus* populations is due more to shorter internode length than to a reduced number of internodes (Fig. 3). The two populations with the greatest number of internodes are coastal (at least in origin of seed) rather than inland as expected in taller plants. In this respect, they resemble the coastal ecotypes in *Layia jonesii* and *Hemizonia paniculata* whose shortness is also due to shorter internodes (Clausen and Hiesey, 1958). Genotypes with shortening of only certain internodes have also been found. For example, Qualset et al. (1970) found short stature in a mutant of "Seneca" wheat where reduction was found only in the upper two internodes below the spike. However, a reduction of basal internodes appears to be more advantageous in *O. faucibarbatus* ssp. *albidus* by lowering the flowering branches into the spiny *Eryngium armatum* leaves, thereby reducing grazing loss.

Plant stunting, caused by small areas of unique soils such as serpentine (Kruckeberg, 1969) or an acid, podzolic soil like that underlying the pygmy forests nearby on the Mendocino coast (Jenny et al., 1969) could explain the localized nature of this phenomenon. Yet neither floristic analysis (Thurman, 1965) nor visual inspection indicated the presence of serpentine, acid, podzolic, or other unique soil condition at this site. The explanation for plants at SPC being significantly shorter than other coastal populations exposed to the same temperatures, winds, and salt spray appears to be more closely related to close grazing than to physical factors. Kemp (1937) found that short stature in *Poa pratensis, Dactylis glomerata,* and *Trifolium repens* persisted in turfs transplanted from closely grazed pastures to an experimental plot.

A second biological factor, protection by another plant from extinction due to grazing, is also suggested. Floristic analysis indicated that the persistence of *O. faucibarbatus* ssp. *albidus* easily could be due to the protection offered by *Eryngium armatum* (Umbelliferae) whose spiny, basal rosette leaves are 5–40 cm long and appeared to provide some protection from intense sheep grazing. A genotype for shortened internodes and basal, ascending branches that placed many flowers among the spiny leaves of *E. armatum* would have greater survival value because of the greater protection from sheep grazing than taller plants that branch from upper nodes. Consequently, the low form would contribute an increasingly larger proportion of seed than the taller form. These annuals usually occur in small, discrete colonies, aiding rapid establishment of adaptive variants.

The same principle may apply to the shorter 3SG population in a lightly grazed sheep pasture where the coarse, unpalatable dead stems of two perennial bunch grasses, *Anthoxanthum odoratum* and *Danthonia californica*, may provide a similar protection from grazing.

The genotype for very short internodes in a site without close grazing would be detrimental to *O. faucibarbatus* ssp. *albidus* for two reasons. First, these plants tolerate very little shading. Greenhouse and garden studies (Thurman, 1965) showed that both transplanted seedlings and plants grown from seed became pale, spindly, and even died when their host plants shaded them. Although they are hemiparasites that rarely flower without root connections to a host, they could not depend entirely upon root parasitism and required ample sunlight for their own photosynthesis. Second, these *Orthocarpus* are self-incompatible and are dependent primarily on bees to open the corolla sac and transport pollen to another plant. Flowers occurring deep in vegetation are neither as conspicuous nor as accessible as the emergent form.

Thus, the short SPC form of *O. faucibarbatus* ssp. *albidus* is dependent both upon sheep to reduce the height of taller plants that would partially obstruct both pollinators and sunlight, and upon *Eryngium armatum* to help protect flowers and seed pods. Less severe sheep grazing would probably decrease the frequency of the grazing ecotype and favor the normal type found elsewhere on the coast.

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NOTES AND NEWS

PTERIDOLOGIA, A NEW MONOGRAPH SERIES

The American Fern Society is pleased to announce a new monograph series, PTERIDOLOGIA, which will publish monographs on ferns and fern-allies. The first issue will be devoted to Dr. David Wagner's "Systematics of Polystichum in Western North America North of Mexico." It is scheduled for publication during the spring of 1979. Publication will be on an irregular schedule, beginning at a rate of one or two monographs per year. All issues will be announced several months in advance of publication.

Dr. Alan R. Smith (University of California, Berkeley) has been appointed editor of PTERIDOLOGIA, in association with Prof. Donald R. Farrar (Iowa State University, Ames), Dr. David B. Lellinger (Smithsonian Institution, Washington), and Prof. Terry R. Webster (University of Connecticut, Storrs).

The series is available to individuals and institutions on standing order at a 20% discount. Pre-publication orders for individual issues have a 10% discount. Orders should be placed with Dr. David B. Lellinger, U. S. Nat'l. Herbarium NHB-166, Smithsonian Institution, Washington, DC 20560.

ULTRAVIOLET ABSORPTION BY FLOWERS OF THE ESCHSCHOLZIOIDEAE (PAPAVERACEAE)

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ABSTRACT

Corollas of the subfamily Eschscholzioideae strongly absorb long-wave ultraviolet radiation, which likely makes them attractive as a source of food reward to foraging pollinators. Filled anthers are also absorptive, but they become reflective as they are emptied of pollen. The epidermis of both the corolla and the anthers is composed of elongated prismatic cells that may have a function in ultraviolet absorption.

The importance of ultraviolet patterns to the vision of pollinating insects has long been recognized (Lutz, 1924; Kugler, 1947, 1963, 1966; Daumer, 1958) and recently has been subjected to intensive scrutiny (Eisner et al., 1969; Ornduff and Mosquin, 1970; Horovitz and Cohen, 1972; Mulligan and Kevan, 1973; Jones and Buchmann, 1974; Guldberg and Atsatt, 1975; King and Krantz, 1975; Utech and Kawano, 1975). In summary, it has been found that food rewards in flowers are often marked by structures or patterns that absorb long-wave ultraviolet radiation, which is visible to bees and many other insects but not to humans, and at the same time reflect wavelengths of visible light. These patterns contrast in an insect's vision with other parts of the flower, or with the background (Frohlich, 1976), which reflect ultraviolet, often strongly.

In conjunction with my studies of the genus *Eschscholzia* of the Papaveraceae, I investigated the UV floral patterns of ten of the fourteen species of that genus, the monotypic *Hunnemannia fumariifolia,* and the two varieties of the monotypic *Dendromecon rigida,* which together constitute the subfamily Eschscholzioideae (Ernst, 1962). I sought to determine whether there were UV patterns that might provide visual clues to pollinating insects, and how these patterns varied within the tribe.

METHODS

Flowers of 22 populations of the 12 species were photographed in the greenhouse, field, or lab using single-lens reflex cameras with glass lenses and Kodak Tri-X film. Visible-light pictures were made with no filtration, and UV photographs with a Wratten 18A filter, which transmits only long-wave ultraviolet. Exposures were determined with a through-the-lens meter.

After preparing the corollas by the technique of Lynch and Webster (1975) for fresh pollen and coating with gold in a Polaron sputter coater, I examined the surface features with a Cambridge Stereoscan S4 scanning electron microscope, taking photographs on Kodak 4127 film.

Species examined include *Dendromecon rigida* Bentham var. *rigi-*

da, D. rigida var. *harfordii* K. Brandegee, *Eschscholzia californica* Chamisso, *E. mexicana* Greene, *E. caespitosa* Bentham, *E. parishii* Greene, *E. covillei* Greene, *E. minutiflora* Watson, *E. glyptosperma* Greene, *E. lemmonii* Greene, *E. hypecoides* Bentham, *E. lobbii* Greene, and *Hunnemannia fumariifolia* Sweet.

RESULTS

Examined corollas all strongly absorb long-wave ultraviolet radiation, appearing black in the photographs (Figs. 1–4). The species are indistinguishable on this character alone. The UV-absorbing corollas contrast strongly with backgrounds of annual grasses and forbs (Fig. 5) and reflective soils, although not so strongly with the chaparral habitats of *Dendromecon.*

Highlights on the flowers (arrow in Fig. 2) represent specular reflection from the ridged surface of the corolla, which consists of files of elongated prismatic cells (Figs. 6 and 7). This same reflection in visible light accounts for the "satiny sheen" that is a well-known feature of *Eschscholzia* flowers (Smith, 1902). Specular reflection is also apparent on the tips of the anthers in Figs. 3 and 4.

The anthers appearing reflective in Fig. 2 are empty. Anthers filled with pollen grains are hardly less absorptive than the corollas (Fig. 3). The locules of the anthers also possess a ridged epidermis.

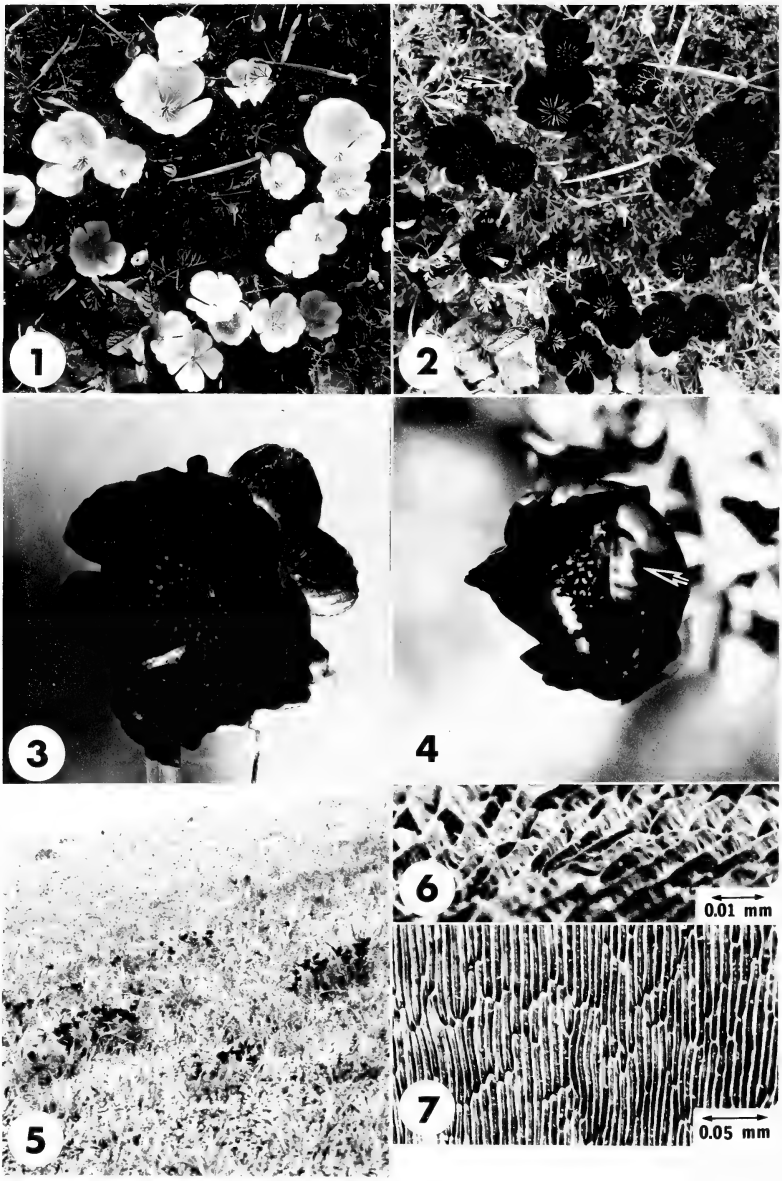
The yellow and orange pigments of the corollas are not responsible for the UV absorption. A mutant plant near Mariposa, California, with cream-colored corollas absorbed UV as strongly as the wild type.

DISCUSSION

The corollas of the Eschscholzioideae, contrasting with their backgrounds in both visible and UV wavelengths, should be quite conspicuous to pollinating insects. The strong UV absorption is a signal of food rewards, i.e., pollen. Undehisced anthers are absorptive; foraging insects break these open to remove the pollen. As the anthers are emptied, they become more reflective and presumably less attractive, the insects' attention being drawn to the floral cup, where the pollen accumulates after it leaves the anthers. The pollen grains themselves appear to be absorptive.

The epidermal ridges of the corolla are suggestive of the papillae reported by Brehm and Krell (1975) on the UV-absorptive portions of composite ray flowers. Those papillae contain UV-absorbing pigments. I do not have any evidence of specific function of the epidermal ridges in UV absorption, but it is noteworthy that the absorptive anthers also have these ridges.

The ultraviolet floral pattern appears to be constant throughout the subfamily. This is not surprising, as the flowers are constant in most other respects. The only substantial differences even among the genera are in the form of the calyx, receptacle, and stigmas. Similarity of



FIGS. 1–7. 1. *Eschscholzia californica* photographed in visible light. 2. The same plant photographed in ultraviolet light; arrow, specular reflectance (see text). 3. Ultraviolet photograph of *Hunnemannia fumariifolia*. 4. Ultraviolet photograph of *Dendromecon rigida* var. *harfordii*; arrow, honeybee (*Apis mellifera*) visiting the flower for pollen. 5. *E. californica* on a hillside of grasses near Byron, California, photographed in ultraviolet light. 6. Oblique view of the prismatic epidermal cells of *E. lemmonii*. 7. Face view of the prismatic epidermal cells of *E. lemmonii*.

floral morphology might argue for similarity of pollination syndrome, and indeed all the species studied seem to be generalists, being pollinated by a variety of insects including bees, beetles, and flies. The autogamous *E. minutiflora,* which has undergone a diminution of flower size and reduction in stamen number, retains the UV pattern of the entomophilous species.

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THREE NEW SPECIES OF CARLOWRIGHTIA (ACANTHACEAE) FROM THE CHIHUAHUAN DESERT REGION

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ABSTRACT

Carlowrightia texana, C. mexicana, and *C. lesueurii* are described, illustrated, and mapped. The new species are distinguished from *C. torreyana, C. arizonica,* and *C. mexicana* respectively.

Carlowrightia is a genus of relatively small-flowered subshrubs and suffrutescent, perennial herbs comprising about 20 species occurring from the southwestern United States to northern Costa Rica. Members of the genus have entire, linear to ovate, sessile to petiolate, opposite leaves and vestiture is uniseriate, mostly multicellular, ranging from puberulent, velutinous, hispidulous, or recurved-strigulose to stipitate-glandular on vegetative portions. Flowers are borne in axillary clusters, or more commonly in spicate to paniculate thyrses, and are subtended by leaves or reduced bracts and paired bractlets. They have 5-parted calyces, 4-parted corollas, and 2 stamens. Stamens arise from the corolla tube and have nearly parallel, equal-sized anther thecae, though these are often subequally inserted on the filaments. Corollas are usually pubescent where exposed in bud and range from nearly regular when vertical to strongly zygomorphic when horizontally oriented at anthesis. The lower corolla lobe is usually somewhat keeled and contains the anthers and style in bud. The upper spathulate, banner-like petal is actually a paired structure. It is often marked with a distinctively colored eye or radiating nerves above the point of reflexion. Lateral petal lobes are elliptical to obliquely ovate and at anthesis may be ascending, spreading, or strongly reflexed, but in bud lie inside the basal keel-like lobe and surround and enclose the upper banner-like lobe. In certain features, flowers of most species resemble papilionaceous flowers of legumes, in which the lower keel-like lobe contains the anthers and style at anthesis. However, in *Carlowrightia,* it is the upper banner-like petal, not the keel, that is the paired structure. Flowers of several species in the Chihuahuan Desert open in the morning and fall by midday. Some of these are capable of self-pollination while the anthers and style are enclosed within the keel.

Fruits of *Carlowrightia* are explosively dehiscent capsules with flattened stipes, compressed-ovoid, acuminate heads usually containing four disk-like, ovoid, smooth, muricate to tuberculate seeds; these are rounded or somewhat acute at the tip and obliquely notched at the base. Seeds may be uniform in structure (homomorphic) or heteromorphic, differing in surface markings and the development of marginal, often retrorsely barbed teeth. They rest upon subulate, upcurved retinacula that project the seeds outward as the capsule dehisces.

The genus appears to attain its greatest diversity in the desert regions of northern Mexico, where at least 13 species occur. Because previous knowledge of *Carlowrightia* has been restricted to descriptions of new taxa and regional floristic surveys, the limits and relationships of many species are poorly understood. During the senior author's preparation of a treatment of Acanthaceae for the Chihuahuan Desert Flora and in the course of the junior author's monograph of *Carlowrightia* certain distinctive novelties became apparent in the genus and are presented below.

There are two species of *Carlowrightia* common in Texas and northern Mexico that have been treated within *C. torreyana* Wasshausen. Both are low-growing perennials with broadly ovate leaves at the base and often narrowly ovate leaves above. They differ, however, in stem pubescence, position and coloration of flowers, and development of seed margins. The two species are occasionally sympatric, but remain distinguishable.

In true *C. torreyana,* based on *Schaueria parvifolia* Torrey, stem pubescence consists of both short and long, slender, erect trichomes 0.1–1 (–1.7) mm long (Fig. 4c). Flowers are usually produced on slender, terminal, stipitate-glandular spikes (Fig. 1f) and are subtended by slender, subulate bractlets. Corollas are white, except for a papillate, yellow eye surrounded by a maroon ring on the upper reflexed petal lobe, and margins of seeds are usually crenulate to denticulate, the short teeth having recurved barbs (Fig. 1h, j, k).

The new species differs from *C. torreyana* in that stem pubescence consists of stout, tapering, decurved trichomes mostly 0.1–0.5 (–1) mm long (Fig. 4a). Flowers are usually borne from the bases to the tips of the stems, with each cluster subtended by ovate, petiolate leaves (sometimes reduced to bracts above), and the inner bractlets are petiolate and narrowly ovate to lanceolate (Fig. 1a, d) rather than subulate. Corollas of this species are white with maroon nerves on each petal lobe, and the seeds have entire margins (Fig. 1b, c, e).

Carlowrightia texana Henrickson & Daniel, sp. nov.

Differt a *C. torreyana* Wasshausen caules strigosis pilis decurvis crassiusculis apicem versus angustatis, floribus axillaribus bracteolis foliosis oblongis lanceolatisve petiolatis, lobis corollae albis venis marroninis, seminibus marginibus integris.

Type: Texas, Val Verde Co.: In loose rock along route No. 163, 6

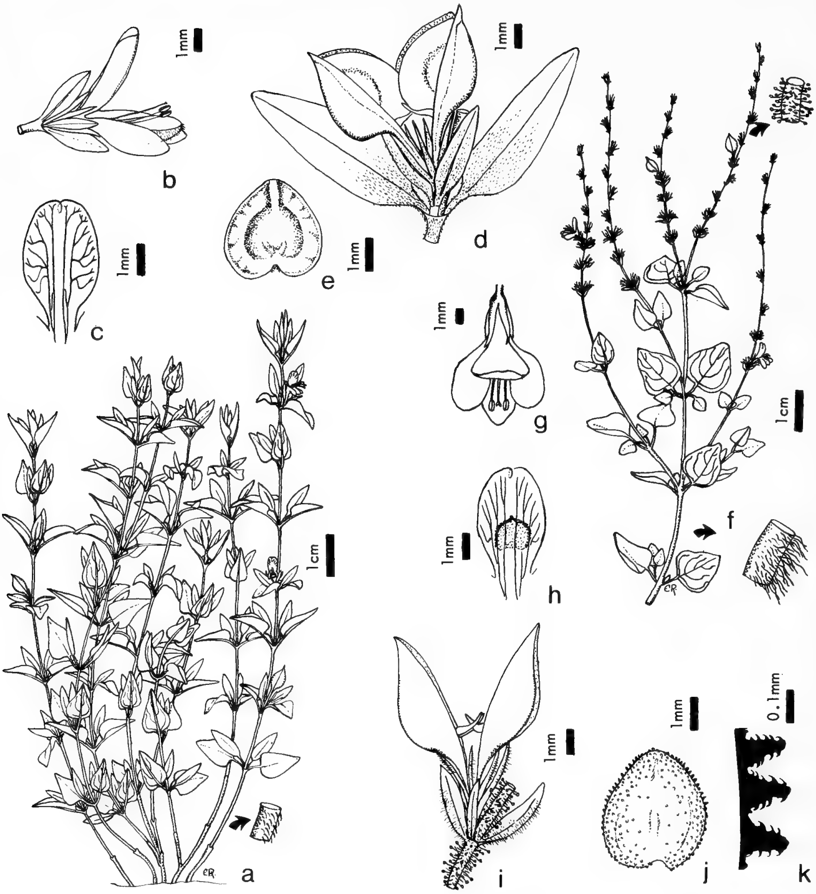

FIG. 1. *Carlowrightia texana* Henrickson & Daniel and *C. torreyana* Wasshausen. a–e: *C. texana*. a. Habit (*Warnock 6036,* LL). b. Flower, showing oblong-ovate, petiolate bracts and bractlets (*Warnock 10491,* LL). c. Upper "banner-like" corolla lobe showing venation (*Baird s.n.,* TEX). d. Open capsule showing large petiolate bracts, smaller bractlets, subulate calyx lobes, and 4 seeds situated on retinacula (*Correll & Johnston 25636,* LL). e. Seed, face view (*Correll & Johnston, 25636,* LL). f–k: *C. torreyana*. f. Habit (*Correll & Johnston 18225,* LL). g. Flower, top view showing position of lateral corolla lobes (from photograph of *Daniel 97,* MICH). h. Upper "banner-like" corolla lobe showing venation and position of papillate yellow eye (*Correll & Wasshausen 27753,* LL). i. Open capsule showing narrow bracts, bractlets, and calyx (*Warnock 21183,* TEX). j. Seed, face view, showing muricate pattern (*Warnock 11714,* TEX). k. Retrorsely-barbed denticulate seed margin (*Warnock 11714,* TEX).

mi N of Juno; flowers white, 19 June 1957, *D. S. Correll & I. M. Johnston 18254*. Holotype: LL; Isotypes: GH, NY, SMU.

Suffrutescent perennials (0.5–) 1–3 dm high from a much-branched twiggy base; stems often decumbent, erect-ascending above, scabrous

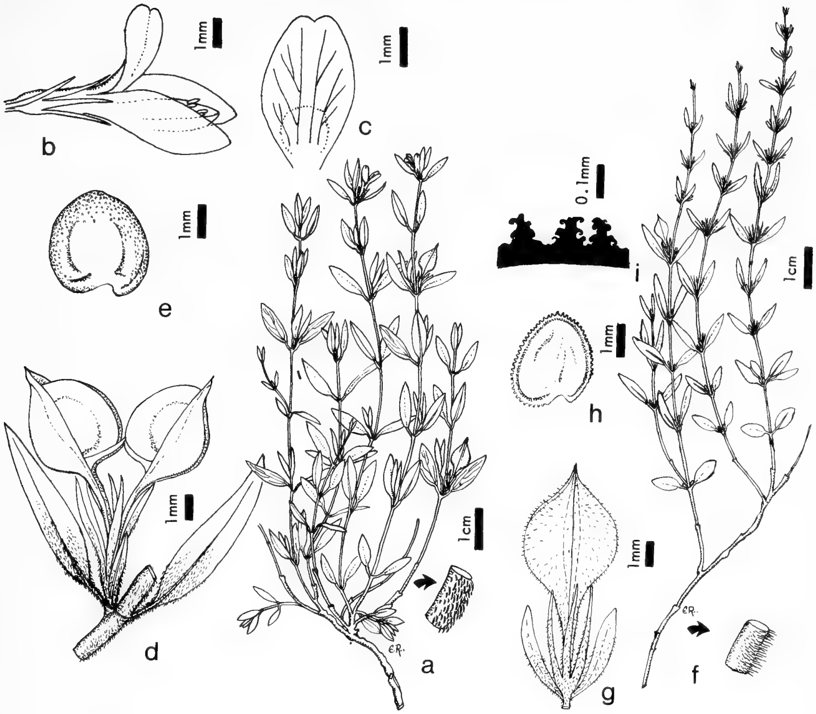

FIG. 2. *Carlowrightia mexicana* Henrickson & Daniel and *C. lesueurii* Henrickson & Daniel. a–e: *C. mexicana*. a. Habit (*Henrickson & Lee 16013,* TEX). b. Flower, lateral view (lateral corolla lobes are more reflexed at anthesis than shown) (*Wendt & Riskind 1698,* LL). c. Upper "banner-like" corolla lobe showing venation and location of papillate yellow eye (*Henrickson & Lee 16013,* TEX). d. Capsule showing large leafy bracts, smaller bractlets and calyx (*I. M. Johnston 8508,* GH). e. Seed, face view, note entire margin (*I. M. Johnston 8508,* GH). f–i: *C. lesueurii*. f. Habit. g. Mature puberulent-hispidulous capsule with bractlets, calyx. h. Seed, face view, showing denticulate margin. i. Retrorsely-barbed denticulate seed margin. (All *LeSueur 864,* TEX).

with rather coarse, strigulose, decurved, tapering trichomes 0.1–0.5 (–1) mm long. Leaves with petioles (1–) 3–7 (–20) mm long; blades broadly ovate to orbicular when larger, more oblong-ovate when reduced (2.5–) 6–16 (–42) mm long, (1.5–) 3–11 (–33) mm wide, acute to obtuse at apex, cuneate to rounded-truncate at base, entire, strigulose throughout as stems but trichomes often shorter. Flowers 1–3 in axils of (basal-) middle-upper leaves in compressed thyrses; peduncles 0–3 mm long; bracts and bractlets leafy in texture and vestiture, mostly oblong to oblong-obovate or lanceolate, (2–) 3–12 mm long, (0.7–) 1–3.5 mm wide, with petioles 1–5 mm long, occasionally stems forming elongate, eglandular, terminal, spike-like inflorescences with reduced leaves-bracts; calyx 3–5 mm long, strigulose as leaves, borne on pedicels to 1 mm long, lobes lanceolate to subulate, 2.5–4 mm long, tube 0.5–0.8 mm long; corollas zygomorphic, 6–7 mm long, white, with maroon nerves on lobes, upper lobe spathulate, reflexed, retuse, lower lobe keeled, lateral lobes oblong-obovate, 3.5–5 mm long, 2–2.8 mm wide, tube 1.5–3 mm long, 1 mm in diameter; anthers 0.5–0.9 mm long, filaments 3–4 mm long; styles 3–4.5 mm long. Capsules 7.5–11 mm long, glabrous, tan, stipes 2–3.5 mm long, heads compressed ovoid, 5.5–7.5 mm long; mature seeds black, 4.2–6 mm long, ovate, thin, smooth to muricate on sides, entire (Figs. 1a–e; 4a–b).

Rocky slopes, often disturbed areas, southern Texas across the Edwards Plateau to trans-Pecos Texas and southeastern New Mexico, Chihuahua, Coahuila, Nuevo Leon, and San Luis Potosi (Fig. 3). Flowers April–November.

While most specimens are rather uniform in leaf size, certain specimens representing extremes in variation are worthy of note. Very reduced plants, which often do not exceed 5–9 cm in height, have flowers from the base to the tip of the plant, and all leaves are reduced and bract-like, measuring 2.5–4.5 mm in length, and 1.5–2.5 mm in width. Stem pubescence, however, is recurved, bractlets tend to be petiolate and leafy in texture, and seed margins are entire. These appear to be exposed drought forms. Examples include: Texas: Kleberg Co.; Santa Gertrudis Division of King Ranch, 6 Aug 1953, *M. C. Johnston 53266.1* (TEX 3). Val Verde Co.: San Felipe Springs, 9 Jun 1963, *V. L. Cory 18921* (GH 3). Mexico: Coahuila: Saltillo, May 1898, *E. Palmer 179* (GH, US). At the other extreme, specimens may have very large, often more membranous leaf-blades to 21–42 mm long and 14–33 mm wide and more slender, sometimes straight pubescence, but otherwise they exhibit all the distinctive characters of the new species. These appear to represent shade forms. Examples include: Texas: Webb Co.: Laredo, 13 Apr 1963, *F. Mosqueda 25* (SMU, TEX). Duval Co.: San Diego, 1888, *M. B. Croft 210* (NY). Kinney Co.: Stream along hwy. 2.3 mi S of jct. of 277 and Hwy. 693, 4 Jun 1977, *T. F. Daniel 127* (MICH).

Representative Specimens: Texas: Pecos Co.: Limestone flats along US route 290, near jct. with road to Iraan, 24 mi NW of Sheffield, 7 May 1947, *R. McVaugh 8204* (F, GH, MICH, SMU, US). Webb Co.: Roadside on Hwy. 83, 13 mi NW of Webb, 16 Jul 1957, *D. S. Correll & I. M. Johnston 18108* (LL, MO, SMU). New Mexico: Eddy Co.: Carlsbad, 10 Jun 1959, *B. E. McKechnie 15* (MO). Mexico: Chihuahua: Mesas near Chihuahua, 4 Sep 1886, *C. G. Pringle 1101* (PH, UC, MO, NY). Coahuila: Roadside on Hwy. 57, 27 mi S of Monclova, 12 May 1977, *T. F. Daniel 100* (MICH). Nuevo Leon: 1 mi NE of Vallecillo on Laredo–Monterrey hwy., 10 Nov 1959, *J. Graham & M. C. Johnston 4596* (MICH, US). San Luis Potosi: Desert hill between Matehuala and Doctor Arroyo, 5.9 mi E of Hwy. 57, 16 Sep 1978, *T. F. Daniel 873* (MICH).

In contrast to the above, *Carlowrightia torreyana* must be redefined

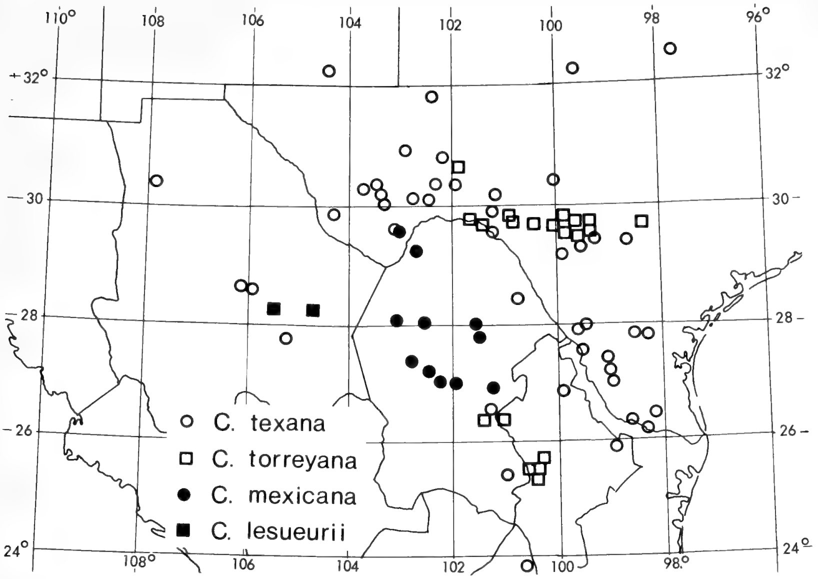

FIG. 3. Distribution of *Carlowrightia texana* Henrickson & Daniel, *C. torreyana* Wasshausen, *C. mexicana* Henrickson & Daniel, and *C. lesueurii* Henrickson & Daniel.

as follows: suffrutescent perennials 1–5 dm high; stems straggling-decumbent to ascending, strongly pubescent-villous with slender, straight to crooked trichomes (0.2–) 0.5–1 (–1.7) mm long, often with an understory of erect to decurved trichomes 0.1–0.2 mm long. Leaves with petioles 2–12 mm long; blades broadly ovate to orbicular-reniform, (6–) 10–20 (–40) mm long; (4–7) 7–13 (–27) mm wide, acute to obtuse at apex, broadly cuneate to rounded-truncate or oblique at base, pubescent throughout with slender tapering trichomes 0.2–0.6 mm long. Flowers usually 1–3 at nodes of terminal, elongate, erect to arcuate or zigzagged spikes 5–13 cm long, rachis internodes 5–25 mm long with slender glandular tipped trichomes 0.1–0.2 (–0.4) mm long and an understory of nonglandular trichomes; bracts subulate to ovate, 1–3 mm long, 0.5–1.3 mm wide, bractlets subulate, 1.2–3 mm long, 0.3–0.7 mm wide (occasionally flowers borne in axils of upper leaves but these subtended by subulate bractlets). Flowers and capsules otherwise as in *Carlowrightia texana,* but corollas 7–9 mm long, white with a papillate yellow eye surrounded by a maroon ring with radiating maroon markings on the upper reflexed petal lobe, and seed margins crenulate to denticulate with minutely barbed teeth (Figs. 1f–k; 4c–e).

Igneous-rock and limestone slopes, ledges, and plains in Texas from the Edwards Plateau to the South Texas Plains, to S Coahuila, W Nuevo Leon (Fig. 3). Flowers May–September and sporadically during other months.

Representative Specimens: Texas: Val Verde Co.: Along hwy. near mouth of Pecos River, 26 Sep 1953, *B. H. Warnock 11714* (LL, SMU). Real Co.: 2–3 mi NE of Camp Wood, 22 Jun 1963, *D. S. Correll & D. C. Wasshausen 28003* (MO, NCU, SMU, UC, US). Bandera Co.: N of Vanderpool, along Sabinal River, 23 Jun 1963, *D. S. Correll & D. C. Wasshausen 28035* (LL, NCU, SMU, US). Mexico: Coahuila: Rocky limestone valley, 23 mi SW of Monterrey, 1 Dec 1945, *B. H. Warnock & F. A. Barkley 14884m* (TEX, F, UC, US). Nuevo Leon: Mountains near Monterrey, Diente Canyon, Jul 1933, *C. H. & M. T. Muller 118* (F).

Specimens previously recognized as *Carlowrightia arizonica* Gray represent a heterogeneous group of plants. The group is taxonomically difficult, as plants are often heavily grazed and morphologically variable. During this study it was possible to distinguish a distinct new species from this complex.

Carlowrightia mexicana Henrickson & Daniel, sp. nov.

Differt a *C. arizonica* Gray corollis coloribus caryophyllaceis purpureisve lavandulisve (non albis) 5–8 (non 12–17) mm longis, foliis caulis saepe amplioribus pluribus bene distributis (non tantum infra flores limitatis), seminibus marginibus integris (non denticulatis).

TYPE: Mexico: Coahuila: ca. 30 (air) mi WNW of Cuatro Cienegas in the limestone Cañon Los Pozos, about 3–4 mi W of Rancho Cerro de la Madera along trail to Cañon Desiderio (near 27°08′N, 102°28′W), flowers blue, 1400 m, 2 May 1977, *James Henrickson & Esther Lee 16013*. Holotype: TEX; Isotypes: to be distributed.

Erect to spreading-globose, twiggy, suffrutescent perennials 1–3.5 dm high; stems ascending, moderately branched, closely strigulose with stiff, mostly decurved, tapering trichomes to 0.1 (–0.2) mm long. Leaves subsessile or with petioles 1–3 (–6) mm long, blades elliptical-lanceolate to elliptical-ovate, more ovate below, more linear-oblanceolate above, (4–) 8–17 (–29) mm long, 1–6 (–8) mm wide, ascending, acute to acuminate at apex, narrowly cuneate at base, firm, entire, sparsely to moderately short strigulose with decurved trichomes to 0.1 (0.2) mm long throughout, or only along margins and midrib beneath. Flowers axillary, 1 (2) at upper nodes, subtended by reduced, erect, linear, leaf-like bracts 2–10 mm long, 0.5–2 mm wide, bractlets subulate, 1–2 mm long, 0.2–0.4 mm wide, upper branches terminating in leafy or bracted, straight to zigzagged spikes 2–5 cm long, rachis internodes 5–15 mm long; calyx 3–5 mm long, sessile or with pedicels 0.5 mm long, lobes subulate, 2–3.5 mm long, tube 1–1.5 mm long; corollas zygomorphic, 6.5–8 mm long, pinkish to lavender-blue with yellow on base of upper spathulate, reflexed lobe, lower lobe keeled, lateral lobes elliptical 3.5–6 mm long, 1.5–2 mm wide, spreading at anthesis, tube 2–2.5 mm long, 1.5 mm in diameter, whitish; anthers 0.5–0.8 mm long, filaments 3–4 mm long; styles 4–5.5 mm long. Capsules 9–12 mm long, glabrous, tan, stipes 3–5.5 mm long, heads compressed-ovoid, 5.5–7 mm long; mature seeds black, 3.5–4.5 mm long, ovate, thin, concavo-convex, somewhat muricate on faces, margins entire (Fig. 2a–e).

Rocky flats and slopes, especially in consolidated arroyo gravel; trans-Pecos Texas (Brewster Co.) to mountains of central Coahuila (Fig. 3). Flowers April–October.

In his original description of the genus *Carlowrightia,* Gray (1878) described both *C. linearifolia* and *C. arizonica* as having rose to purple corollas. Later published descriptions indicate *C. arizonica* has cream or white corollas (Standley, 1926) with lavender or purple markings (Kearney and Peebles, 1960; Shreve and Wiggins, 1964). In contrast Wasshausen in Lundell (1966, see also Correll and Johnston, 1970) indicates the corollas of *C. arizonica* may be either white or purple. The label on Gray's type specimen of *C. arizonica* (*Palmer s. n.* 1867, GH) states "corolla yellow and deep purple." Field studies have shown that *C. arizonica* has long (12–17 mm), white corollas with a yellow eye bordered by purplish radiating lines on the upper banner-like lobe and a twiggy habit usually with a few reduced leaves subtending the flowers. Palmer's type specimen of *C. arizonica* has similar small leaves and corollas 12 mm in length, indicating that it probably had a white-flowered corolla with yellow and deep purple markings. The purple-flowered plant that has been included within *C. arizonica* represents the newly described species *C. mexicana,* which is easily separated from *C. arizonica* by its shorter, purple to blue-lavender corollas 6–8 mm long, more leafy growth habitat, and entire seed margins.

Representative Specimens: Texas: Brewster Co.: 17 mi E of Marathon, Hwy. 90, 31 Oct 1966, *D. S. Correll 34082* (LL, GH, US). Mexico: Coahuila: Sierra de la Madera, vicinity of "La Cueva" in Corte Blanco fork of Charretera Canyon, 11–15 Sep 1941, *I. M. Johnston & C. H. Muller 637* (LL, GH). Cañon de Cuervo Chico about 16 km N of Cuesta Zozaya, 27 Aug 1941, *I. M. Johnston 8508* (LL, GH 2). Cañon de San Enrique, E side Sierra de la Encantada, 5 km W of Rancho Buena Vista, 4 Sep 1941, *R. M. Stewart 1385* (GH). Sierra de Santa Rosa, S of Muzquiz, 27 Jul 1938, *E. G. Marsh 1551* (GH). Intersection of Huerfanita-Jardin Rd. N of Rancho Piedra Azul and NE of Rancho El Jardin, 27 Jul 1973, *M. C. Johnston et al. 11763c* (LL). Sierra de la Gloria, Cañon del Chilpitin, ca. 5 mi up (E) from mouth of cyn, near El Chilpitin, 7 Sep 1976, *T. Wendt & D. Riskind 1698m* (LL). El Berrendo, near Muzquiz, 13–16 Jul 1939, *S. White 1867* (MICH).

A third new species shows affinities with *C. mexicana.*

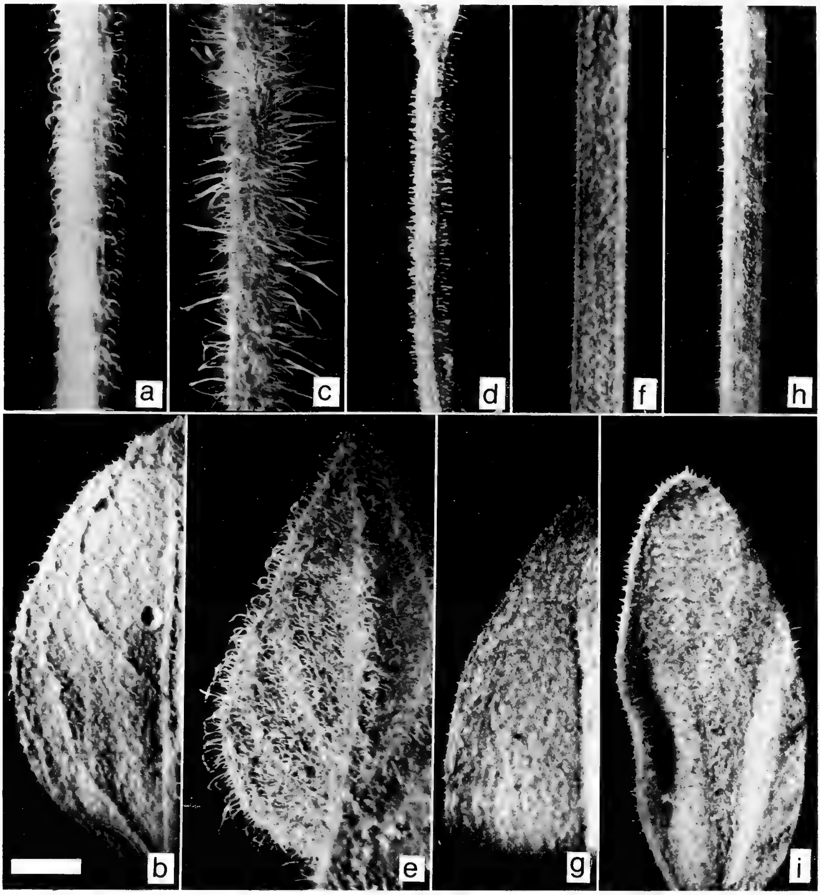

FIG. 4. Photographs of stem, inflorescence, and leaf material of Carlowrightias. a–b: *C. texana* Henrickson & Daniel. a. Stem showing decurved, tapering, white trichomes. b. Leaf, lower surface showing recurved trichomes (both *Correll 18254,* Type, LL). c–e: *C. torreyana* Wasshausen. c. Stem, showing long, straight, tapering, white trichomes. d. Inflorescence showing conspicuous gland-tipped trichomes. e. Leaf, lower surface showing long trichomes (all *Correll & Johnston 19399,* LL). f–g: *C. mexicana* Henrickson & Daniel. f. Stem with short descending trichomes. g. Leaf, upper surface showing straight trichomes (both *Henrickson & Lee 16013,* TEX). h–i: *C. lesueurii* Henrickson & Daniel. h. Stem showing small erect trichomes. i. Leaf, upper surface showing short straight trichomes (both *LeSueur 864,* TEX). White bar in b. is 1 mm long.

Carlowrightia lesueurii Henrickson & Daniel, sp. nov.

Differt a *C. mexicana* Henrickson & Daniel caulibus pilis rectis (non retrorsis), bracteolis 3.5–6 (non 1–2) mm longis, corollis 8–9 (non 5–8) mm longis, capsulis 8–8.5 (non 9–12) mm longis pubescentibus (non glabris), seminibus marginibus denticulatis (non integris).

TYPE: Mexico: Chihuahua: Meoqui, 6 Aug 1936, *Harde LeSueur 864*. Holotype: UC; Isotypes: ARIZ, UC, CAS, F, GH, MO (2), SMU (2), TEX.

Erect to spreading, suffrutescent perennials 0.5–2 dm high from a stout or tortuous, twiggy, spreading, corky base, stems closely striate, uniformly puberulent with slender, straight or slightly decurved moderately dense trichomes 0.1–0.4 mm long. Leaves with petioles 0.5–2 mm long; blades elliptical to oblong-lanceolate, oblanceolate, more obovate below, more linear-lanceolate and bract-like above, 4.2–13 mm long, 0.5–4.5 mm wide, acute to obtuse-rounded at apex, cuneate at base, entire, puberulent as stems, midnerves raised below. Flowers axillary, 1–4 at middle and upper nodes, sessile or on distinct peduncles 0.5–3 mm long, paired bractlets subulate to oblong-lanceolate, 3–7 mm long, 0.3–0.5 mm wide, puberulent as leaves; calyx 2.5–3 mm long, lobes 1.5–2.5 mm long, subulate, puberulent, tube 0.5–1 mm long; corollas 8–9 mm long, color unknown, zygomorphic, lobes narrowly obovate, 5–6 mm long, 2 mm wide, tube 2.5–3 mm long, 1 mm in diameter; anthers 0.9–1.1 mm long, filaments 3.5–4 mm long; styles 6–6.5 mm long. Capsules 8–8.5 mm long, puberulent-strigulose with trichomes 0.1–0.2 mm long, tan, stipes 2.3–3 mm long, heads compressed-ovoid, 5.5 mm long; mature seeds black, 3.5–4 mm long, faces smooth to somewhat muricate, margins with retrorsely barbed teeth 0.1–0.2 mm long.

Although known from only two collections, this is a very distinctive species of *Carlowrightia* that can be distinguished from other species by the combination of its puberulent capsules, narrow leaves, and denticulate seed margins. It appears to be most similar to *C. mexicana,* from which it can be distinguished by the longer bractlets, corollas, and anthers; and by the shorter calyx and capsules, as well as the pubescent capsules and denticulate seed margins.

Representative Specimen: Mexico: Chihuahua: Los Organos Mts., (near 26°42′N, 103°02′W), 8 Sep 1937, *Harde LeSueur 1254,* (F, TEX).

ACKNOWLEDGMENTS

We thank M. C. Johnston for Latin diagnoses and the curators of the following herbaria for loans of specimens: ARIZ, F, GH, LL, MICH, MO, NCU, NY, PH, SMU, TEX, UC, US. Illustrations were drawn by Frances Runyon.

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NOTES AND NEWS

International Register of Specialists and Current Research in Plant Systematics

The Hunt Institute for Botanical Documentation has received a grant from the U. S. National Science Foundation to produce an international register accounting for both specialists and individual research projects in systematic botany. The *Register,* to be produced in both computerized and published forms, will revive and incorporate the now dormant "Index of Current Research" previously sponsored by the American Society of Plant Taxonomists and "Register of Specialists" produced by the International Association for Plant Taxonomy. This new *Register* project is being undertaken with the endorsements and assistance of both those organizations. Financial assistance has also been received from the U. S. National Park Service, through the New York Botanical Garden.

Questionnaires and accompanying instructions (trilingual: English, French, German) will be distributed within the systematic botanical community starting in November 1978. Major means of distribution will include enclosure in individual copies of *Taxon* (first 1979 mailing) and *Systematic Botany,* and by mailing modest supplies to selected botanical institutions and academies of science. These forms have been designed to permit easy photoduplication, which is strongly encouraged. Anyone working in systematic botany (including its history, bibliography, art, and applications to structural, ecological and evolutionary botany) is urged to fill out and return a questionnaire by 31 August 1979. Those not receiving questionnaires directly should obtain them (or photocopies) from a convenient botanical institution or can request them by writing to: Hunt Institute, Attention Register, Carnegie-Mellon University, Pittsburgh, PA 15213 USA. Such direct requests should be made only if the materials are unavailable through the other channels.

The first printed edition of the *Register* will be published in spring 1980. Thereafter, with adequate continuing assistance from the botanical community and its sponsors, the Institute plans to maintain the *Register* as an active computerized data base and to produce succeeding printed editions triennially. A copy of the published *Register* will be sent without charge to each questionnaire respondent as well as to relevant institutions and governmental agencies. Reasonable special query service will be available to the public at no or minimal cost upon application to the Institute. This may involve special permutations of the data, or simply requests for up-to-date information on a given topic during the periods between successive published editions.

The utility of the *Register* to both the botanical community and the general public will depend in large measure upon its comprehensiveness. To maximize coverage, the Institute is requesting the cooperation and active assistance of botanists and their institutions on a worldwide basis.

TWO NEW SPECIES OF TUBEROUS LOMATIUMS (UMBELLIFERAE)

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ABSTRACT

Two species of tuberous lomatiums are described. *Lomatium quintuplex* is found only on Umtanum Ridge, between Ellensburg and Yakima, Washington. *Lomatium stebbinsii* is restricted to the west slope of the Sierra Nevada in Tuolumne and Calaveras counties, California. Neither species is closely related to other tuberous lomatiums.

The tuberous lomatiums constitute an easily recognized infrageneric group. This assemblage is characterized by a low, usually acaulescent habit, tuberous roots, leaves with linear segments, and fruit with an elliptical outline and narrow, thin lateral wings. The center of distribution and species diversity of this group is the Columbia River Plateau of eastern Washington and Oregon and adjacent Idaho, where it forms a conspicuous element of the early spring flora. Tuberous lomatiums typically occur in gravelly, thin soils of hillsides, ridges and scablands, and other open, windy habitats that dry up early in the growing season. It is probably in response to this environment that their distinctive features have evolved. Coulter and Rose (1888) treated the tuberous lomatiums as an infrageneric unit and Jones (1908) named them section *Cous*. Mathias (1938) and Mathias and Constance (1945) retained the group for purposes of identification but made no decision as to whether or not it is an entirely natural one.

The existence of low, acaulescent, tuberous species of *Tauschia* and *Orogenia* in the same habitats occupied by tuberous lomatiums indicates that these features may have evolved more than once in western North American Umbelliferae. These characters may also have several origins within diverse, widespread genera such as *Lomatium*. Interspecific variation in morphology and flavonoid chemistry led Brehm and French (1966) and Schlessman (1976) to hypothesize that the tuberous lomatiums are not a natural group. Recognition of two new tuberous lomatiums without close morphological affinities to any other member of the group tends to support this hypothesis.

Lomatium quintuplex Schlessman & Constance, sp. nov.

Herba perennis, acaulescens, caule conspicuo subterraneo (pseudoscapo) vaginis scariosis 2–5 vestito, e glabra ad scabridisculam varians, 1.5–3 dm alta; radix tuberosa, irregularis, usque ad 5 cm longa, 3 cm lata, 2 cm crassa; folia 3–8, ovata; lamina quinata-bipinnata, 5–12 cm longa, 2.5–6 cm lata, divisionibus ultimis e linearis ad filiformis variantes, 1–3 mm longis, minus quam 1 mm latis; petioli 2–6 cm longi, scariosis, omnino vaginatis; pedunculi 2–5, 15–20 cm longi, folia excedentes; radii fertiles 5–8, patenti-adscendentes, inequales, 2–8 cm longi; involucellum dimidiatum, bracteolis 3–5, anguste lanceolatis, 2–4 mm longis, scarioso-marginatis; petala, antherae at stylopodia citrini; pedicelli fructificantes 7–17 mm longi; fructus ellipticus, 7–9 mm longus, 3 mm latus, glabris, alis tenuibus, 0.5 mm latis; vittae pusillae, in valleculis 4–7, ad commissuras nullis (Fig. 1).

Acaulescent perennial with a prominent underground stem (pseudoscape) bearing leaves at ground level and clothed by 2–5 scarious, dilated, bladeless sheaths, glabrous to minutely scabrous, 1.5–3 dm tall; root tuberous, irregular, up to 5 cm long, 3 cm wide and 2 cm thick; leaves 3–8, ovate in general outline; blades quinately then bipinnately dissected, 5–12 cm long, 2.5–6 cm wide, the ultimate divisions linear to filiform, 1–3 mm long, less than 1 mm wide, the apices acute; petioles 2–6 cm long, sheathing throughout, the margins scarious; peduncles 2–5, 15–20 cm long, exceeding the leaves; fertile rays 5–8, spreading-ascending, unequal, 2–8 cm long; involucel dimidiate, of 3–5 narrowly lanceolate bractlets 2–4 mm long, the margins scarious; umbellets 15–20 flowered; calyx teeth obsolete; petals, anthers and stylopodia yellow; styles 1.5 mm long and spreading at maturity; pedicels 7–17 mm long in fruit; fruit dorsally compressed, elliptic in outline, 7–9 mm long, 3–4 mm wide, glabrous, the wings thin, 0.5 mm wide, vittae small, 4–7 in the intervals, absent on the commissure.

TYPE: United States: Washington: Kittitas Co., east-facing gravelly slope near the summit of North Umtanum Ridge, on west side of Interstate 82, just north of milepost 17, 17 miles (27.2 km) south of Ellensburg or 6.8 miles (10.9 km) north of bridge over Selah Creek, 695 m, with *Lewisia rediviva, Lomatium farinosum* var. *hambleniae, Eriogonum, Erigeron* and *Collomia,* 25 May 1978, *Schlessman 792* (Holotype: WTU; Isotypes: NY, UC, WS).

Distribution: Rocky, basaltic slopes of Umtanum Ridge, located between Ellensburg and Yakima, Washington, 690–970 m.

Phenology: Leaves appear in March; flowers from early April to early May; fruits mature from late April through early June.

Specimens examined: United States: Washington: Kittitas Co.: ca. 20 miles (32 km) north of Yakima, along Durr Road on Umtanum Ridge, south-facing slope, 10 April, 5 May and 7 June, 1976, *Thomas G. Nielsen s.n.* (UC, WS, WTU); 2 miles (3.2 km) north of Kittitas-Yakima county line or 17 miles (27.2 km) south of Ellensburg, just east of elevation sign on Interstate 82 at North Umtanum Ridge, 694 m, 28 April 1976, *Schlessman 236* (WTU); basaltic east-southeast-facing slope at hairpin turn in Durr Road, 7 miles (11.6 km) north of entrance to L.T. Murray game area north of Selah, Umtanum Ridge, 969 m, 15 May 1977, *Schlessman 641* (WTU); east-facing gravelly slope just below summit of ridge on west side of Interstate 82, milepost

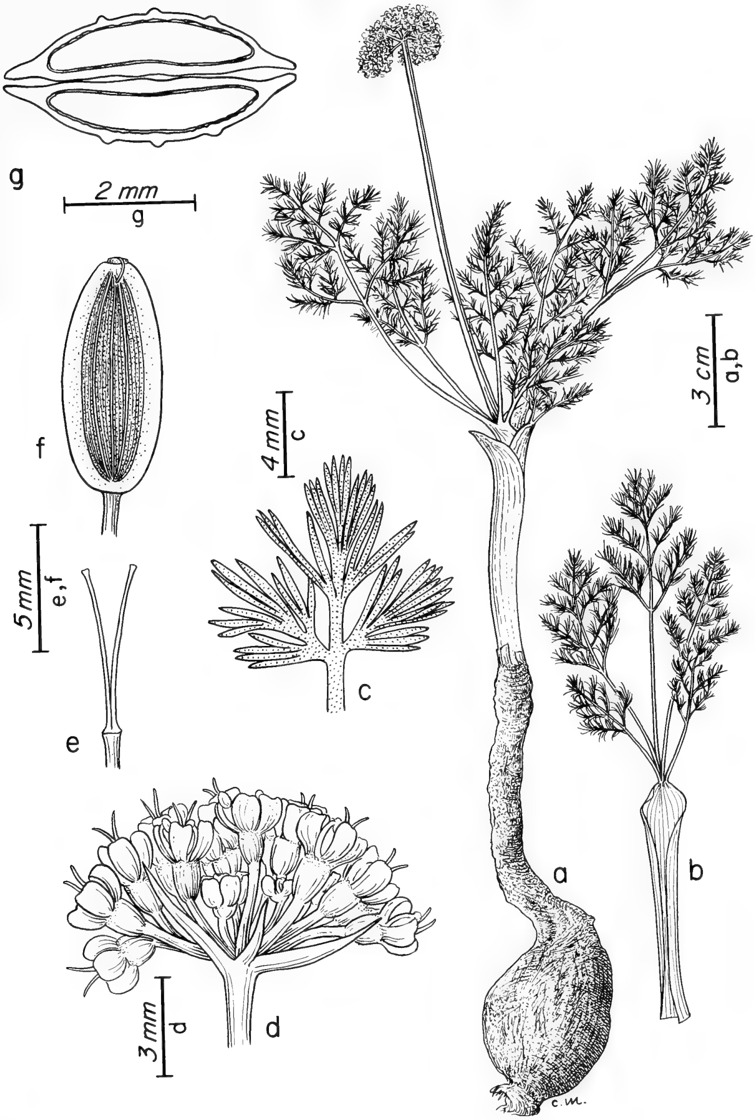

FIG. 1. *Lomatium quintuplex*. a. Habit. b. Leaf. c. Ultimate divisions of the leaves. d. Flowering umbellet. e. Carpophore. f. Dorsal view of fruit. g. Transection of fruit. a.–e. from *Thomas G. Nielsen s.n.*, f. and g. from *Schlessman 792*.

17, North Umtanum Ridge, 694 m, 14 April 1978, *Schlessman 719* (WTU); North-northeast-facing slope just below hairpin turn in Durr Road, L.T. Murray Wildlife Recreation Area, 13 miles (20.8 km) north of Selah, 915 m, 15 April 1978, *Schlessman 722* (WTU); North Um-

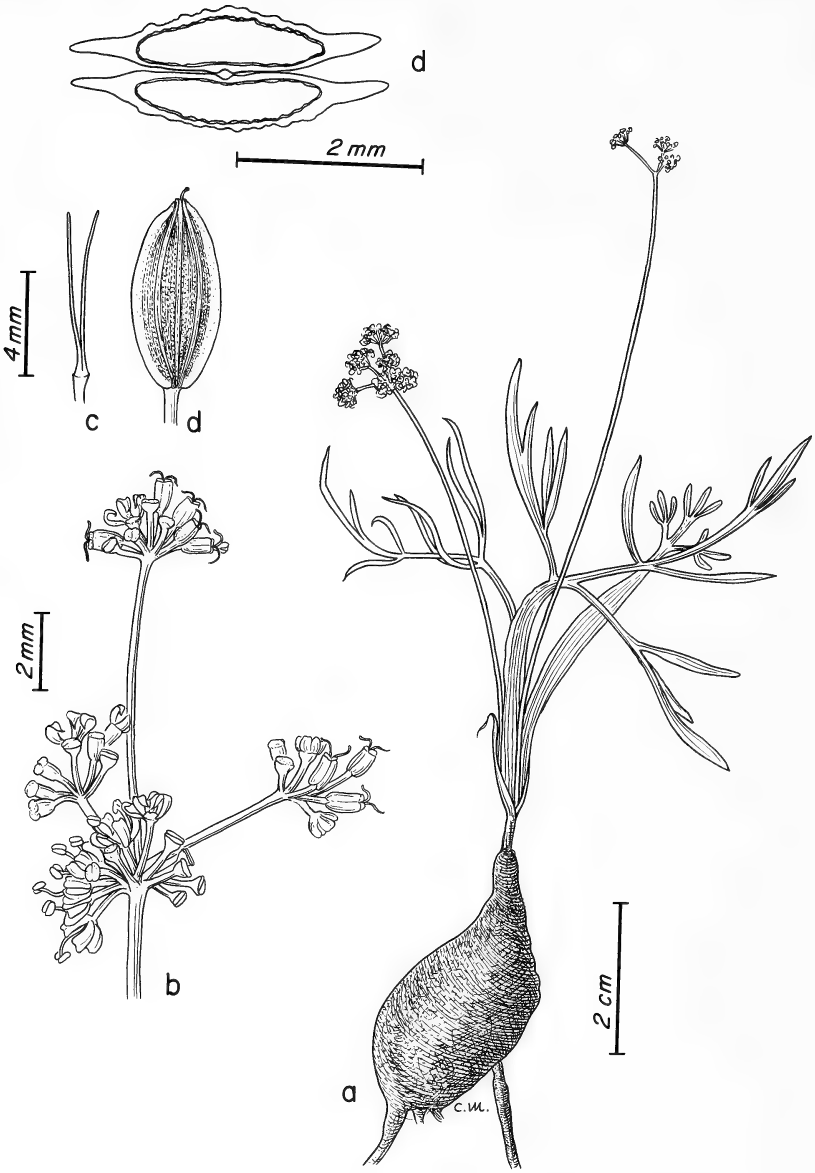

FIG. 2. *Lomatium stebbinsii*. a. Habit. b. Single umbel. c. Carpophore. d. Dorsal view of fruit. e. Transection of fruit. a. and b. from *Stebbins 9031,* c.–e. from *G. L. Stebbins s.n.,* 18 June 1971.

tanum Ridge, lithosol, Upper Sonoran, at edge of east side of Interstate 82, just north of the summit of the ridge, associated with *Viola trinervata, Lomatium canbyi, L. macrocarpum* and *Eriogonum,* ca. 2400 ft. (727 m), 8 April 1978, *E. Hunn 897* (WTU); 7.6 miles (12.2 km) north of L.T. Murray on Durr Road, 1.4 miles (2.2 km) north of Yakima Co. line, on south side of Umtanum Ridge, ca. 2800 ft. (848 m), 15 April 1978, *E. Hunn* 906 (WTU).

Derivation of the epithet: From the Latin, in reference to the quinately divided blades of the leaves.

Lomatium quintuplex was discovered by Mr. Thomas G. Nielsen, an inquisitive and persistent amateur botanist who has collected extensively in the Yakima region. We are especially grateful for his assistance in locating the Durr Road population.

The filiform ultimate segments of the leaves of *Lomatium quintuplex* closely resemble those of *L. bicolor* (Watson) Coulter & Rose from Idaho, northern Utah, and Wyoming. The new species differs from *L. bicolor* in having quinately rather than ternately divided leaves, more flowers per umbellet, shorter bractlets, longer fruiting pedicels and shorter, wider fruit.

Dr. Amy Jean Gilmartin (unpub. data) has used numerical analyses of a large number of morphological characters to determine the phenetic dissimilarities among population samples of *Lomatium quintuplex* and four other lomatiums. The taxa chosen for comparison were *L. leptocarpum* (Torrey & Gray) Coulter & Rose, *L. ambiguum* (Nuttall) Coulter & Rose, *L. howellii* (Watson) Jepson and *L. triternatum* (Pursh) Coulter & Rose. *Lomatium leptocarpum* and *L. ambiguum* are tuberous lomatiums, the former having been treated as conspecific with *L. bicolor* (Mathias, 1938; Mathias and Constance, 1945). The mean phenetic distances (MPD's) between *L. quintuplex* and each of the other taxa are approximately equal and within the range expected for comparisons of distinct species. The phenetic dissimilarities between the new species and the other tuberous lomatiums are the same as those between the new species and the presumably more distant taxa. *Lomatium quintuplex* is morphologically distinct and apparently not closely related to other tuberous lomatiums.

Lomatium stebbinsii Schlessman & Constance, sp. nov.

Herba perennis, acaulescens, aliquando caule subterraneo (pseudoscapo), glabra, 5–15 cm alta; radix tuberosa, globosa usque ovoidea, 0.7–2 cm diametro; folia 2–5, triangulares; lamina 2–5 cm longa, e ternatis ad ternatis-pinnatis variantes, divisionibus ultimis linearis, 2–12 mm longis, 1–2 mm latis; petioli 2–3 cm longi, ad medium vel aliquando omnino vaginati; pedunculi 1–3, 4–15 cm longi, patentes, folia excedentes; radii 2–7, patentes, inequales, 1–12 mm longi; involucellum nullum; petala, antherae et stylopodia citrini; pedicelli fructificantes 1–2 mm longi; fructus ellipticus, 6–9 mm longus, 3–4 mm latus, glabris, alis 0.5–1 mm latis; vittae pusillae, in valleculis 1–4, ad commissuras nullis; $n = 11$ (Fig. 2).

Acaulescent perennial, occasionally with an underground stem (pseudoscape) bearing leaves at ground level, glabrous, 5–15 cm tall; root tuberous, globose to ovoid, 0.7–2 cm in diameter; leaves 2–5, triangular in general outline; blades 2–5 cm long, ternate to ternate pinnate, the ultimate divisions linear, 2–12 mm long, 1–2 mm wide, often narrowed toward the base, the apices acute; petioles 2–3 cm long, sheathing to the middle or occasionally throughout; peduncles 1–3, 4–15 cm long, spreading, exceeding the leaves; rays 2–7, spreading, unequal, 1–12 mm long; involucel lacking; umbellets 2–15 flowered; petals, anthers and stylopodia lemon-yellow; pedicels 1–2 mm long in fruit; fruit dorsally compressed, elliptic in outline, 6–9 mm long, 3–4 mm wide, glabrous, the wings 0.5–1 mm wide; vittae small, 1–4 in the intervals, absent on the commissure; $n = 11$.

TYPE: United States: California: Tuolumne Co.: 4 miles (6.4 km) east of Long Barn on northeast side of Bald Mt., S2 T3N R17E, gravelly open volcanic slope and ridge crest with *Allium, Calyptridium, Arabis, Crepis, Penstemon,* and *Ceanothus; Pinus ponderosa* association; peduncles spreading, nearly prostrate, fruits shining, heavily grazed by rabbits, 4100 ft. (1242 m), 26 May 1978, *Constance 3895* (Holotype: WTU; Isotypes: NY, UC, WS).

Distribution: Thin, gravelly volcanic soils in open *Pinus ponderosa* forest, 1200–1700 m on the western slope of the Sierra Nevada in Tuolumne and Calaveras counties, California.

Phenology: Leaves appear in March; flowers from late March to early April; fruits mature from mid April through mid June.

Specimens examined: United States: California: Tuolumne Co.: scattered over the thin-soiled, almost bare ground on volcanics (mud flow breccia) northwest of Bald Mt., close to Sonora Pass road (Hwy. 108), 5600 ft. (1700 m), 18 June 1971, *G. L. Stebbins s.n.* (DAV, UC); clearing in forest of *Pinus ponderosa,* on thin soil of volcanic formation, 1 mile (1.6 km) southwest of Confidence, near county road to Tuolumne, S10 T2N R16E, 4100 ft. (1242 m), 25 March 1973, *Stebbins 9031* (DAV, UC); around rocks on gravelly flat with *Allium, Lupinus, Dudleya, Sitanion,* and *Microsteris* with scattered *Arctostaphylos* and *Ceanothus,* a natural opening in *Pinus ponderosa-Calocedrus* forest, 1 mile (1.6 km) southwest of Confidence, ca. 4100 ft. (1242 m), 24 March 1978, *Constance 3892* (UC, WTU); gravelly open volcanic slope and ridge crest with *Claytonia, Allium,* and *Microsteris* in *Pinus ponderosa-Calocedrus* association, 4 miles (6.4 km) east of Long Barn on northeast side of Bald Mt., S2 T3N R17E, 4100 ft. (1242 m), Sierra Nevada, 24 March 1978, *Constance 3893, n* = 11 (UC, WTU). Calaveras Co.: Folsom Guard Station, 14 miles (22.4 km) east of West Point, 29 May 1972, *G. L. Stebbins s.n.* (DAV).

Derivation of the epithet: Named in honor of the discoverer, G. Ledyard Stebbins.

Lomatium stebbinsii occurs at the southern limit of the range of tuberous lomatiums. The yellow flowers and spreading peduncles of the new species give it a superficial resemblance to *L. farinosum* var. *hambleniae* (Mathias & Constance) Schlessman, a taxon confined to the scablands and steppe of central Washington and Oregon. *Lomatium stebbinsii* differs from the latter in having an irregularly shaped root, a shorter and less slender pseudoscape, wider and shorter divisions of the leaves, no involucel, much shorter fruiting pedicels and somewhat wider fruit. The low stature, short fruiting pedicels and relatively short segments of the leaves of *L. stebbinsii* are more similar to *L. piperi* Coulter & Rose, or to *Tauschia hooveri* Mathias & Constance, than to *L. farinosum* var. *hambleniae*. *Lomatium stebbinsii* appears to have no close relatives among the tuberous lomatiums.

The relative obscurity of early-flowering umbels is underscored by the fact that these new species appear to have gone unnoticed until they were recently collected by Mr. Nielsen and Professor Stebbins.

ACKNOWLEDGMENTS

We thank Amy Jean Gilmartin for bringing the umtanum umbel, alias Brand X, to our attention, for the loan of specimens, and for permission to cite results of her research. We also thank Charlotte Mentges for preparing the illustrations, and Melinda F. Denton, David H. French, Lisa A. Standley and Daniel E. Stuntz for comments on the manuscript. Field studies by M. A. Schlessman were supported by a Graduate School Special Fellowship from the University of Washington and by NSF Dissertation Grant DEB 78-02482.

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A NEW SPECIES OF TAUSCHIA (UMBELLIFERAE) FROM CHIHUAHUA, MEXICO

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ABSTRACT

Continued taxonomic and ethnobotanical field work in Chihuahua, Mexico, has enabled the senior author to add three species to the list of Umbelliferae (Apiaceae) known to occur in that state, as compiled by the authors in 1976. One of these, *Tauschia allioides,* remarkable for its "rachis-leaves," is described. Differential use of the local *Tauschia* species by the Tarahumara Indians is described.

In a recent summation of our knowledge of Umbelliferae (Apiaceae) occurring in the Mexican State of Chihuahua (Constance and Bye, 1976) we noted that some 30 taxa had been recorded from the state up to that time. In the same publication, which was based largely on materials resulting from ethnobotanical and taxonomic studies of Bye, we proposed four new species and noted that Bye had collected 20 different Umbelliferae in the area. His subsequent field work has added three more species to the overall list, including a new state record for *Tauschia madrensis* C. & R. [Chihuahua: Municipio de Bocoyna, valley of Choguita, NW of Creel, elevation ca 2200 m, 25 Jul 1977, *Bye 7671* (COLO, UC), 2 Aug 1977, *Bye & Weber 7835* (COLO, UC)], and a remarkable new species of *Tauschia.*

Tauschia allioides Bye & Constance, sp. nov.

Plantae graciles caulescentes ramosae, caulibus gracilibus 1 vel 2, 25–45 cm altis e caudicibus elongatis carnosis flavidis, sed nodis inflorescentis exceptis hoc loco scaberulis glabrisque; folia basalia lineari-filiformia subteretia 10–40 cm longa diametro ca 1 mm striata subintegra, 1 vel 2 foliolis linearibus minutis ad apicem versus exceptis instructa; petioli haud distincti basi anguste scarioso-vaginantes; folia caulina reducta sessilia vaginis conspicue praedita; pedunculi 1–3, 5–15 cm longi terminales graciles infra umbellas scaberulentes; involucrum plerumque 0; radii 6–13, 5–15 mm longi inaequales scaberuli; involucellum bracteolis 4–6 linearibus 2–4 mm longis; pedicelli fertiles 1–8, 1.5–3 mm longi; flores rhodo-purpurei; styli graciles ca 1 mm longi caduci, stylopodio 0; carpophorum crassum bipartitum; fructus ovoideus 3–4 mm longus, 2–3 mm latus apici obtusus basi rotundatus, costis obtuse angulatis quam intervallis latioribus; vittae magnae unica in intervallis in commissuris 2; seminum superficies sulcata; chromosomatum numerus $n = 22$; cotyledones lineares (Fig. 1).

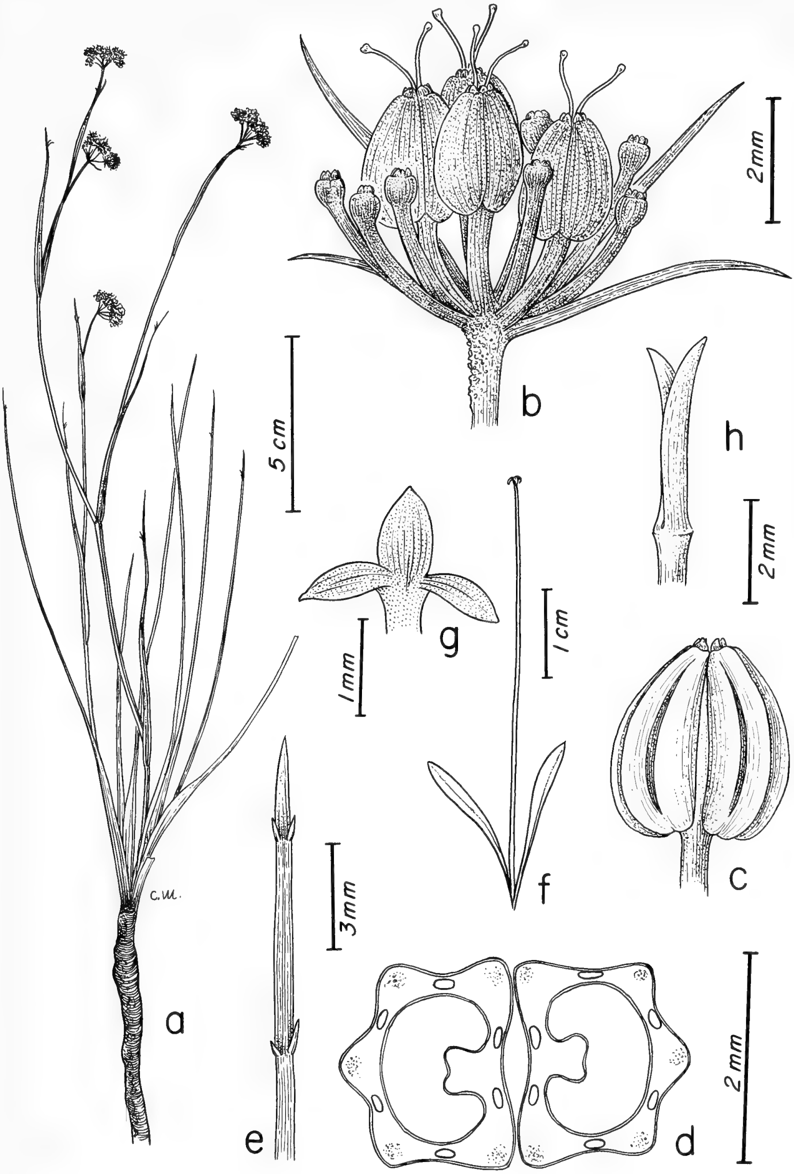

FIG. 1. *Tauschia allioides*. a. Habit. b. Fruiting umbellet. c. Mature fruit, lateral view. d. Mature fruit, transection. e. Apex of foliage leaf. f. Seedling, showing cotyledons and first foliage leaf. g. Apex of first foliage leaf. h. Carpophore. (All from *Bye 7666* and *Bye & Weber 8275*.)

Plants slender, caulescent, branching, the stems slender, 1 or 2, 24–25 cm tall, from a somewhat swollen yellowish vertical rhizome, scaberulous at nodes, beneath umbel, and on rays; basal leaves weakly clustered, linear-filiform, subterete, 10–40 cm long, ca 1 mm in diameter, striate, entire except for usually 2 pairs of minute linear lobes near apex, narrowly sheathing at base; cauline leaves few, ascending, like the basal, the sheaths conspicuously scarious-margined; peduncles slender, 1–3, terminal, 5–15 cm long; involucre of a linear bract, or usually 0; rays 6–13, 5–15 mm long, unequal, scaberulous; involucel of 4–6 linear bractlets 2–4 mm long; pedicels about 12, 1–8 fertile, 1.5–3 mm long; flowers deep red-purple; calyx teeth evident, low and rounded; petals oval, with a narrower inflexed apex nearly equaling limb; styles very slender, ca 1 mm long, purple, deciduous, the disk inconspicuous; carpophore stout, biparted, the halves broad, approximate; fruit ovoid, 3–4 mm long, 2–3 mm broad, truncate at apex, rounded at base, the ribs prominent, obtusely angled, broader than intervals; vittae large, solitary in intervals, 2 on commissure; seed face sulcate; chromosome number $n = 22$; cotyledons linear.

TYPE: Mexico: Chihuahua: Municipio de Bocoyna, E of Gonogochic (N27°45′ W107°30′), in llano in pine-oak forest, in *Quercus* cf. *duraznillo* Trel. scrub and under isolated *Pinus ponderosa* Dougl., elevation 2225 m, 12 Aug 1977, *Robert A. Bye, Jr. 7936* (COLO: holotype; MEXU, UC: isotypes).

Other collections: Chihuahua: Municipio de Bocoyna, E of Gonogochic (fruiting material from type locality), 17 Oct 1977, *Bye & Weber 8275* (COLO, MEXU, UC), ca 1 km N of San Juanito sawmills, elevation 2400 m, 23 Jul 1977, *Bye 7666* (COLO, UC—chromosome voucher), ca 5 miles N of San Juanito, elevation ca 2500 m, 3 Aug 1977, *Bye 7870* (COLO, UC), and E of Creel, on W side of Laguna Arareco, elevation ca 2225 m, 25 Jul 1977, *Bye 7681* (COLO). Municipio de Guachochic, E of Yahuírachic (E of Cusárare), elevation 2134 m, 25 Jul 1977, *Bye 7689* (COLO).

This rare and inconspicuous herb occurs in drier, open parts of llanos (moist, upland meadows), often with oak scrub, or along margins of llanos or wide arroyo valleys under isolated pines with such herbaceous associates as *Odontotrichum globosum* (Fern. & Rob.) Rydb., *Pionocarpus madrensis* (S. Wats.) S. F. Blake, *Tagetes lucida* Cav., *Geranium niveum* S. Wats., *Ornithocarpa torulosa* Rollins, and *Rorippa* sp. The deep rootstock (apparently arising as a perpendicular branch of a horizontal rhizome ca 20 cm below the surface) and the bright red-purple flowers resemble those of *Tauschia tarahumara* Const. & Bye, which occurs in wetter portions of some of the same llanos. [The known range of *T. tarahumara* has been extended from the San Ignacio Arareco region (Municipio de Bocoyna) to the Mesa de Aboriachic (Municipio de Guachochic, E of Cusárare and Yahuírachic), elevation 2250 m, 26 Jul 1977, *Bye 7694* (COLO, UC).] The closest relationship of *Tauschia allioides* is, however, doubtless with *T. linearifolia* C. & R., which has recently been rediscovered in Nayarit [*Norris & Taranto 14,563* (MICH, UC)]. The latter species has broadly linear, flat, entire leaves, and ovate-orbicular, laterally imbricate involucel bractlets.

The most distinctive feature of the new taxon is undoubtedly its foliage leaf, which, although it simulates an elongated petiole bearing pinnae primordia distally, doubtless represents considerable leaf rachis as well. The resemblance is striking to the leaves of *Oxypolis greenmanii* Math. & Const. figured by Kaplan (1970, figs. 6, 7), and interpreted by him as "rachis-leaves." The prevalence in the llano habitat of narrow-leaved species of many different families including Umbelliferae (e.g., in the northern Sierra Madre Occidental, *Tauschia allioides, Eryngium gentryi* Const. & Bye, *E. mexicanum* S. Wats.) invites speculation on their past and present environmental significance, and on whether they may not represent Pleistocene relicts with morphological adaptations for aquatic habitats.

Tauschia allioides and *T. tarahumara* are found in open valleys of the San Ignacio Arareco region. Some Tarahumara Indians apply the name "basiáwari" to both species because of the similarity of the inflorescences. Only *T. tarahumara,* however, was consumed as a cooked green or quelite in the past. The term "basiáwari" and its variants appear to be the common designation for edible umbelliferous greens collected before flowering and prepared for consumption. Other members of Umbelliferae which serve as quelites under the name of "basiáwari" include *Arracacia edulis* S. Wats., *Tauschia bicolor* Const. & Bye, and *T. madrensis*. Tarahumara who are unfamiliar with *T. allioides* because they do not live near the llanos and do not exploit the plant as food indicate that it is a form of "bariguchi." *Eriogonum atrorubens* Engelm., the common edible "bariguchi," is said to be similar to *T. allioides* because of its red flowers and lack of cauline laminar leaves.

ACKNOWLEDGMENTS

The writers express their appreciation to Dr. Tsan-Iang Chuang for obtaining a chromosome count of the new taxon and to Dr. William A. Weber for assistance in both the field and the herbarium. The senior author acknowledges support for field work from the National Geographic Society, the Graduate School of the University of Colorado, and the University of Colorado Museum.

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(Accepted 12 Mar 1978.)

NOTEWORTHY COLLECTIONS

POLANISIA JAMESII (T. & G.) Iltis (CAPPARACEAE).—USA, NM, Eddy Co., ca. 32 airline km E of Carlsbad (NE¼ S28 T22S R31E), 18 Sep 1976, *Willson 108* (NMC). Rare, on red sand dunes, only 3 plants observed in 12.8 km of vegetation analysis transects (Sandia Radioactive Waste Storage Project) in an area covering 10.25 km^2. Associated with *Prosopis glandulosa, Quercus havardii, Paspalum setaceum, Senecio, Artemisia filifolia, Yucca, Aristida, Pectis angustifolia, Schizachyrium scoparium, Croton, Eriogonum, Cenchrus incertus, Sporobolus cryptandrus, Leptoloma cognatum,* and *Bothriochloa saccharoides*. Plants were in very late flower, setting abundant seed.

Previous Knowledge—Previously known from W and NW TX to CO and KS, E to WI and IL, in sandy soils. (Herbaria consulted: NMC, SMU, UNM, TEX, OKL; published sources: Correll & Johnston, *Man. Vasc. Pl. Tex.* 1970; Harrington, *Man. Pl. Colo.* 1954; Iltis, SW Naturalist 3:133–144. 1958; Martin & Castetter, *Cklst. Gymnosp. & Angiosp. NM*. 1970).

Significance—First record in NM. Apparently a 120 km NW disjunction from nearest known populations in Ward and Winkler cos., TX.

BRACHIARIA CILIATISSIMA (Buckl.) Chase (POACEAE).—USA, NM, Eddy Co., ca. 32 airline km E of Carlsbad (NE¼ S28 T22S R31E), 18 Sep 1976, *Willson 109* (NMC). Frequent throughout 10.25 km^2 surveyed for vegetation analysis (Sandia Radioactive Waste Storage Project), on red sand dunes. Associated species and phenology as for *Polanisia jamesii*. Verified by S. Hatch.

Previous Knowledge—Previously known to be widespread though central TX, less frequent in W TX, extending to S OK and NE AR on sandy prairies. (Herbaria consulted: NMC, SMU, TEX, OKL; published sources: Correll & Johnston, op. cit.; Gould, *Gr. Tex.* 1975; Hitchcock, *Man. Gr. U. S.* 1951; Martin & Castetter, op. cit.).

Significance—First record in NM. Apparently a 120 km NW disjunction from nearest known populations in Ward and Winkler cos., TX.—J. WILLSON, R. SPELLENBERG, and H. WOLFE, Department of Biology, New Mexico State University, Las Cruces 88003. (Accepted 8 Oct 1978.)

CAREX WHITNEYI Olney (CYPERACEAE).—USA, CA, Fresno Co., Sierra National Forest (SE¼ SE¼ S8 T10S R26E), Dinkey Creek: dry sandy slope 100 m west of Arkansas Road (Forest Service Road 10S36) at the upper end of Camp Fresno, 1752 m, 1 Aug 1978, *P. Smith 78-610* (CAS, Kings River Conservation District); on both sides of main road running through Dinkey Creek Campground, close to camp's amphitheater, 1752 m, 9 Sep 1978, *P. Smith, s.n.* (Kings River Conservation District). Rare. Two populations of 80–90 individuals each, in sandy, somewhat disturbed soil, mixed community of widely scattered *Abies concolor, Pinus ponderosa, Ceanothus cordulatus, Ribes roezlii*. In fruit in Aug. Verified by J. T. Howell, Sep 1978.

Previous Knowledge—Known from Tuolumne and Mariposa cos., CA. (Herbaria consulted: CAS, DS, JEPS, UC; published sources: Munz, P. A., *A Calif. Fl.* 1959; Howell, J. T., *Leafl. West. Bot.* 8:220–224, 1958; Powell, W. R., *Inventory Rare End. Vasc. Pls. Calif.*, 1974). *Diagnostic characters*—leaf blades flat, 2–6 mm wide, pubescent on both sides; culms 6–9 dm tall; styles 3, withering; perigynia glabrous, ovate, scales spreading.

Significance—First location south of Mariposa Co., a disjunction of 87 km. Discovered during a survey for a proposed hydroelectric dam on Dinkey Creek. Unconfirmed reports suggest additional populations downstream, at least one within the proposed reservoir site. One population reported here lies in the path of a proposed road realignment. Further study of the distribution of this rare carex is needed before work on the dam proceeds.—PEGGY SMITH, 4322 E. Alamo, Fresno, CA 93726 (Accepted 26 Dec 1978.)

SEDUM SPATHULIFOLIUM Hook. ssp. YOSEMITENSE (Britt.) R. Clausen.—USA, CA, San Diego Co., Agua Tibia Mt., NE slope Eagle Crag (near 33°23′N, 116°57′W), 1380 m, 30 May 1976, *Sproul s.n.* (SD 94819). Scattered clumps totalling ca. 1000 rosettes, in decomposed granite shelves and scree, 70% slope, extending downslope into the abandoned Palomar Divide road. Associated with *Silene lemmonii* Greene, *Monardella macrantha* Gray ssp. *macrantha* in a community of *Pinus coulteri* D. Don, *Pseudotsuga macrocarpa* (Torr.) Mayr and *Ceanothus leucodermis* Greene. Verified by Reid Moran, May 1976.

Previous Knowledge—Known from CA: W slope Sierra Nevada and Transverse ranges (*Sedum of N. Am.,* Clausen, 1975); Santa Monica Mts., (Gordon & Grayum, Madroño 23:454, 1976). Clausen reported only 27 populations. Flowers late May–Jun.

Significance—First record in Peninsular Range, 108 km disjunction from San Gabriel Mts. and 195 km from Santa Monica Mts. Gordon & Grayum reported this plant as new to the Sta. Monica Mts., but it seems long established on Eagle Crag. Though highly localized, it does not appear threatened because it is in the Agua Tibia Wilderness Area.—FRED T. SPROUL, Natural History Museum, San Diego, CA 92112. (Accepted 23 Sep 1978.)

RIBES VIBURNIFOLIUM A. Gray (SAXIFRAGACEAE).—USA, CA, San Diego Co., San Diego, San Clemente Canyon W of Genesee Ave., N slope, 55 m (near 32°50.7′N, 117°12.1′W), 5 Feb 1977, *Moran 23917* (SD & to go). Thriving very locally, in ca. 15 patches scattered over 75 m in a significantly linear population, near foot of 45° slope, with scattered *Quercus agrifolia,* some *Platanus racemosa,* abundant *Artemisia palmeri, Mimulus puniceus,* and *Toxicodendron diversilobum.* Verified by Karl Schnizler, Feb 1977.

Previous Knowledge—Known from CA, Santa Catalina Island, mostly on east side, ca. 25–450 m; MEXICO, Baja Calif. Norte, Isla de Cedros, and within 15 (and mostly 5) km of coast from La Joya (32°29′N, 117°06′W, 6 km S of US border) to Cañada la Matanza (31°02′N, 116°12.5′W), 5–400 m. Locally common, mostly on N slopes, in sage scrub or under shrubs of chaparral. (Herbaria consulted: RSA, SD; published sources: Thorne, Aliso 6(3):65, 1967; Raven & Axelrod, Univ. Calif. Publ. Bot. 72:65, 1978.)

Significance—This apparent first record for mainland USA and 42 km N-ward range extension, reported by Raven & Axelrod, has less significance than it appeared—or at least a different significance. Through a yet-unexplained personal non-communication (likely my fault), they omitted important details, such as the linear population structure. Karl Schnizler, of the San Diego City Park Department, told me the shrubs were planted 8 years before.—REID MORAN, Natural History Museum, San Diego, CA 92112. (Accepted 10 Oct 1978.)

AGAVE NEOMEXICANA Woot. and Standl. (AGAVACEAE).—USA, NM, Luna Co., S end Florida Mountains, E side of Baldy Peak, 2042 m, 32°05′20″N, 107°37′15″W, abundant on the capping Paleozoic limestones, 27 May 1978, *R. Worthington 2865* (UTEP, Gentry herbarium, to be distributed). USA, NM, Luna Co., Cooks Range, S-facing slopes of unnamed peak 5 km N of Cooks Peak, 1830 m, 32°33′N, 107°43′W, on limestone with *Pinus edulis* and *Cupressus arizonica,* 8 Oct 1978, *W. Reid 1342,* (UTEP, Gentry herbarium, to be distributed). Verified by H. S. Gentry, Nov 1978.

Previous Knowledge—Known from San Andres and Oregon mountains of Doña Ana Co., NM, and in TX from mts. in El Paso, Hudspeth, and Culberson cos. Most frequently on calcareous substrates, 1525–2250 m. (Herbaria consulted: UTEP, NMSU; published sources: Wooten, E. O. and P. C. Standley, Contr. U. S. Natl. Herb. 19:5–794, 1915; Correll, D. S. and M. C. Johnston, *Man. Vasc. Pls. Texas,* 1970; Burgess, T. L., M.S. Thesis, Texas Tech. Univ., Lubbock, 1977).

Significance—100 km range extension. These populations also isolated by 100 km from *A. lecheguilla* Torr., implicated with *A. neomexicana* in the hybrid origin of *A. gracilipes* Trel. (Freeman, C. E. and W. H. Reid, Bull. N. M. Acad. Sci. 18:10, 1978). No *A. gracilipes* have been found at the isolated sites, supporting the previous observation that it occurs only in the few locations where *A. lecheguilla* and *A. neomexicana* are sympatric. *Agave* collecting (a matter of *sangre y corazon*) has been spotty, making resolution of frequent hybridization problems among the 200–250 species difficult without extensive field work (Gentry, H. S., U.S.D.A. Handbook 399, 1972).—WILLIAM H. REID and RICHARD D. WORTHINGTON, Biological Sciences, University of Texas at El Paso 79968. (Accepted 26 Jan 1979.)

NOTES AND NEWS

EIGHTEEN NEVADA RARE PLANTS LISTED

The Nevada Division of Forestry, effective 14 February 1979, has listed 18 rare native plants protected under Nevada state law. A permit, good for one taxon and one occasion within the calendar year, is now required to collect any of them on private or state lands. For additional taxa and/or occasions, additional permits are needed. Applications may be obtained from the Division of Forestry, 201 S. Fall Street, Carson City, Nevada 89701. The taxa involved are: *Arctomecon californica* Torr. & Frem., *Arenaria stenomeres* Eastw., *Astragalus beatleyae* Barneby, *A. geyeri* Gray var. *triquetrus* (Gray) Jones, *A. lentiginosus* Doug. var. *sesquimetralis* (Rydb.) Barneby, *A. nyensis* Barneby, *A. phoenix* Barneby, *Castilleja salsuginosa* N. Holmgren, *Cryptantha insolita* (Macbr.) Payson, *Eriogonum argophyllum* Reveal, *E. lemmonii* S. Wats., *E. viscidulum* J. T. Howell, *Frasera gypsicola* (Barneby) D. M. Post, *Lathyrus hitchcockianus* Barneby & Reveal, *Mentzelia leucophylla* Bdg., *Penstemon thurberi* Torr. var. *anestius* Reveal & Beatley, *Phacelia inconspicua* Greene, and *Primula capillaris* N. Holmgren & A. Holmgren.—MARGARET WILLIAMS, Northern Nevada Native Plant Society, P.O. Box 8965, Reno 89507

GEORGE H. M. LAWRENCE MEMORIAL FUND

The Hunt Institute for Botanical Documentation announces establishment of the George H. M. Lawrence Memorial Fund, based at the Institute as a permanent Fund to honor the memory of Dr. Lawrence (1910–1978), its founding Director. Income from the Fund will be used to provide an annual Award (beginning in 1979) in support of a doctoral candidate's travel for dissertation research in one or more of Dr. Lawrence's fields of special interest in the plant sciences: systematic botany; horticulture; or history of botany or horticulture, including literature and exploration. An Awards Committee, comprising representatives of the Lawrence family, The Hunt Foundation, the Hunt Institute, and the botanical community, will review nominations and select recipients. Awards will be made strictly on the basis of merit—that of the proposed research, and the recipients' general scholarly promise in their fields. Notice of invitation for nominations for the first award (1979) will appear in a few months.

The Fund has been constituted initially by contributions from the Lawrence family and The Hunt Foundation, and is recognized by them and the Institute as the vehicle for contributions from others honoring the memory of Dr. Lawrence. Donations to the Fund are should be made payable to the Hunt Institute (address: Carnegie-Mellon University, Pittsburgh, PA 15213) and designated for the "Lawrence Memorial Fund."

VASCULAR PLANTS OF NORTH AMERICA NORTH OF MEXICO

The Flora North America project (FNA) was recently revitalized by the Man and Biosphere Program (MAB) as a binational effort between the United States and Canada to produce a conventional flora of the vascular plants of North America north of Mexico using traditional methods. Initial funding for the proposed five-volume work is being provided by the National Park Service of the Department of the Interior. The MAB/FNA Program Council plans to coordinate the research that will be necessary to produce a floristic publication of high scientific quality pertinent to national needs.

The Program Council has appointed an Editoral Subcommittee consisting of Dr. Reed C. Rollins, Chairman, Gray Herbarium of Harvard University; Dr. Howard S. Irwin of the New York Botanical Garden; and Dr. Roy L. Taylor of the University of British Columbia Botanical Garden. Dr. James L. Reveal of the University of Maryland has been appointed Editor. Their function will be to stimulate and coordinate the efforts of the botanical community in the writing of the flora. Toward this goal, the Editoral Subcommittee is currently working on a proposed format for the flora. Initial efforts will be toward the production of a volume treating the monocotyledonous plants, with a volume on the sympetalous dicotyledonous plants to follow next. The remaining three volumes will be worked on in the future.

Long-term funding for the flora project is being explored by the Program Council, chaired by Dr. Peter H. Raven of the Missouri Botanical Garden. It is hoped that the flora project will be completed by 1990.

Individuals wishing additional information or interested in contributing to the project, and in particular treatments of the monocots and sympetalous dicots should write to Dr. James L. Reveal, Editor, MAB/FNA Project, Department of Botany, University of Maryland, College Park, MD 20742.

SECOND INTERNATIONAL CONGRESS OF SYSTEMATIC AND EVOLUTIONARY BIOLOGY

The Second International Congress of Systematic and Evolutionary Biology (ICSEB-II) will be held at The University of British Columbia, Vancouver, Canada, 17–24 July 1980.

The provisional list of symposium topics includes: Arctic refugia and the evolution of Arctic biota; origins and evolution of the north Pacific marine biota; evolution of reproductive strategies; evolutionary epigenetics; evolution of community structure; green algae and land plant origins; macromolecular mechanisms in evolution; allozymes and evolution; coevolution and foraging strategy; evolution of colonizing species; rare species and the maintenance of gene pools; paleobiology of the Pacific rim.

Sessions for contributed papers and for papers in specialized fields, taxonomic as well as methodological, will also be organized.

Those interested in receiving an information circular in the spring of 1979, should write to: Dr. G. G. E. Scudder, Department of Zoology, The University of British Columbia, Vancouver, B.C. V6T 1W5 Canada.

ROBERT JOSEPH RODIN

Bob Rodin, sustained by his strong Christian commitment, succumbed to cancer on June 27, 1978, after a courageous struggle of nearly four years. Born in Turlock on July 15, 1922, Rodin received an A.B. degree from the University of California, Berkeley, in 1943, and served with the U.S. Marines on Guam in 1944–45, where he made a large plant collection. In 1947–48 he filled the role of botanist for the University of California African Expedition under the direction of Charles L. Camp, and made important collections in South-West Africa (Namibia). It was this latter experience that led to his interest both in *Welwitschia,* on which he completed his Ph.D. thesis at Berkeley with Adriance S. Foster in 1950, and his work on the ethnobotany of Ovamboland, stimulated by Edwin Loeb.

After completing his doctoral work, he taught at Forman Christian College, Lahore, Pakistan, and then joined the faculty at Cal Poly in 1953. He was very active there and remained affiliated with the institution until the end of his life, having achieved a full professorship in 1967. The year 1960–61 was spent on sabbatical leave at Cornell with Harlan P. Banks, supported by a NSF grant. He went to the University of Delhi, India, in 1966–67 as a Fulbright Professor. He had intended to write a book on Gnetales with P. Maheshwari, but Maheshwari died before his arrival. The National Geographic Society awarded him a travel grant to enable him to return to Namibia in 1972 to complete work on his ethnobotanical studies.

Bob Rodin published more than a dozen scientific articles, most of them on Gnetales (*Welwitschia* and *Gnetum*), but also one with E. H. Walker on the flora of Guam, and an attractively illustrated booklet, "Ferns of the Sierra" (1960). He completed a substantial manuscript on the ethnobotany of Ovamboland, for which funding is still being sought. In later years he was a very active participant in the conservation movement. He remained professionally engaged throughout his career, attending the 10th and 11th International Botanical Congresses and the Indian Science Congress of 1966. He was Vice President of the California Botanical Society in 1975.

Bob and Elva celebrated their 25th wedding anniversary in 1973. His widow and three daughters survive him.—LINCOLN CONSTANCE, Department of Botany, University of California, Berkeley 94720.

BOOKS RECEIVED AND LITERATURE OF INTEREST

Native orchids of North America north of Mexico. By DONOVAN S. CORRELL. Stanford University Press, Stanford, CA 94305. 1978. $28.50. This lavish book, first published by Chronica Botanica in 1950, was reissued by Stanford Univ. Press in Nov 1978. Out of print for many years, its renewed availability will be of interest to many. Still an excellent reference as well as good bedside reading.

An illustrated guide to pollen analysis. By P. D. MOORE and J. A. WEBB. John Wiley & Sons, Somerset, NJ 08873. 1978. $19.95.

Radiostrontium movement in soils and uptake in plants. By C. W. FRANCIS. Technical Information Center, U. S. Department of Energy. 1978. $4.75. Available as TID-27564 from National Technical Information Service, U. S. Department of Commerce, Springfield, VA 22161.

The Agaves of Baja California. By HOWARD SCOTT GENTRY. Occasional paper No. 130 of the California Academy of Sciences, San Francisco 94118. $8.00.

Flora of Barro Colorado Island. By THOMAS B. CROAT. Stanford University Press, Stanford, CA 94305. 1978. $55.00.

Common Texas grasses: An illustrated guide. By FRANK W. GOULD. Texas A&M University Press, College Station 77843. 1978. $10.95.

BACK COVER EMBLEM

The silhouette of *Arbutus menziesii* Pursh gracing the back cover was designed by Jacqueline Broughton of the Santa Barbara Botanical Garden. The Council of the Society judged it the winning entry in the emblem contest announced in January, 1978 issue. The emblem will continue to appear on the cover and in promotional literature. The Council expresses its thanks to all those who submitted emblems and logos.

Membership in the California Botanical Society is open to individuals ($15 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Institutional subscriptions to MADROÑO are available ($22 per year). The membership or subscription year begins on January 1.

Back issues of MADROÑO are available at the following rates (some issues are out of print):

Vol. 1 (1916–1929) and Vol. 2 (1930–1934), each consisting of 17 numbers: $1.50 per issue and $25.50 per volume for members; $3.00 per issue and $51.00 per volume for institutions.

Vol. 3 (1935–1936) through Vol. 23 (1975–1976), each biennial, consisting of 8 numbers: $3.00 per issue and $24.00 per volume for members; $5.00 per issue and $40.00 per volume for institutions.

Vol. 24 (1977) et seq., one volume per year, each consisting of 4 numbers: $4.00 per issue and $15.00 per volume for members; $6.00 per issue and $24.00 per volume for institutions.

Applications for membership (including dues), orders for subscriptions, requests for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary. Renewal payments should be sent to the Treasurer.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the Editor. Membership in the California Botanical Society is prerequisite to review.

Manuscripts and review copies of illustrations must be submitted in triplicate for articles and in duplicate for 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. All measurements should be in S.I. (metric) units.

Line copy illustrations should be clean and legible, proportioned (including their captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in Figures, as should explanation of symbols. In addition, 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 board and mailed flat.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren and Keuken's list (*Index herbariorum, Part 1. The herbaria of the world*. Sixth edition. 1974. Regnum Veg. vol. 92). Abbreviations of names of journals should be those in *Botanico-Periodicum-Huntianum* (Lawrence, G. H. M. et al. 1968. Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full title of the journal should be used. Titles of books should be given in full, together with the place and date of publication, name of publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted eight pages in the journal over a two-year period. Beyond that number of pages, a required editorial fee of $40.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. 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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CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1979

ARTIFICIAL INTERSPECIFIC HYBRIDIZATIONS IN MELAMPODIUM SECTION ZARABELLIA (COMPOSITAE)

Tod F. Stuessy and Jere N. Brunken
Department of Botany, Ohio State University, Columbus 43210

Abstract

Interspecific hybridization experiments were completed for three of the five species in *Melampodium* section *Zarabellia*. Hybrids between the two diploid species, *M. gracile* ($n = 9$) and *M. microcephalum* ($n = 9$) showed normal bivalent pairing at metaphase I but were highly sterile. The observation of an occasional quadrivalent during diakinesis in these hybrids indicates that at least one reciprocal translocation exists between the genomes of these two diploid species. Artificial hybrids between *M. paniculatum,* a tetraploid species with $n = 18$, and the two diploid species were triploid and sterile. Analysis of pairing relationships in the triploid hybrids indicates that perhaps one, but not both, of the diploid species contributed a genome to tetraploid *M. paniculatum*.

Melampodium (Compositae, Heliantheae) of Latin America contains 37 species that are classified into six taxonomic sections (Stuessy, 1972). Of these, sect. *Melampodium* has received the most intensive study to determine evolutionary relationships. Particular emphasis has been placed on the white-rayed complex of series *Leucantha,* in which detailed cytological and chemical studies have been completed (Stuessy, 1971a; Stuessy et al., 1975; Fishback et al., 1976). This paper summarizes evolutionary studies on sect. *Zarabellia* (Cass.) DC., which is distributed primarily in Mexico and Central America and contains five species (Stuessy, 1972): *M. longifolium* Cerv. ex Cav.; *M. mimulifolium* Robins.; *M. gracile* Less.; *M. microcephalum* Less., and *M. paniculatum* Gardn. The last three species are unique within the section in possessing an outer involucre of three phyllaries, and stipitate-glandular hairs. For this reason the three taxa are believed to be related very closely.

Melampodium microcephalum, M. gracile, and *M. paniculatum* are differentiated morphologically by a number of features (Figs. 1–6; Stuessy, 1972). In general, *M. paniculatum* is the most easily distinguished of the three species. The other two species are separated most easily by the subauriculate leaf bases in *M. gracile* versus the attenuate to obtuse leaf bases in *M. microcephalum*. With regard to distributions, *M. paniculatum* is confined primarily to Central America, whereas the other two species are principally Mexican (Fig. 7). Within Mexico, *M. gracile* and *M. microcephalum* have partially overlapping ranges especially in the states of Michoacán and Morelos. Chromosomal numbers of *M. gracile* and *M. microcephalum* are $n = 9$, and *M. paniculatum* is known usually as $n = 18$ (Stuessy, 1971b, 1971c; Figs. 8–15). A hexaploid ($n = 27$) has been reported in this species

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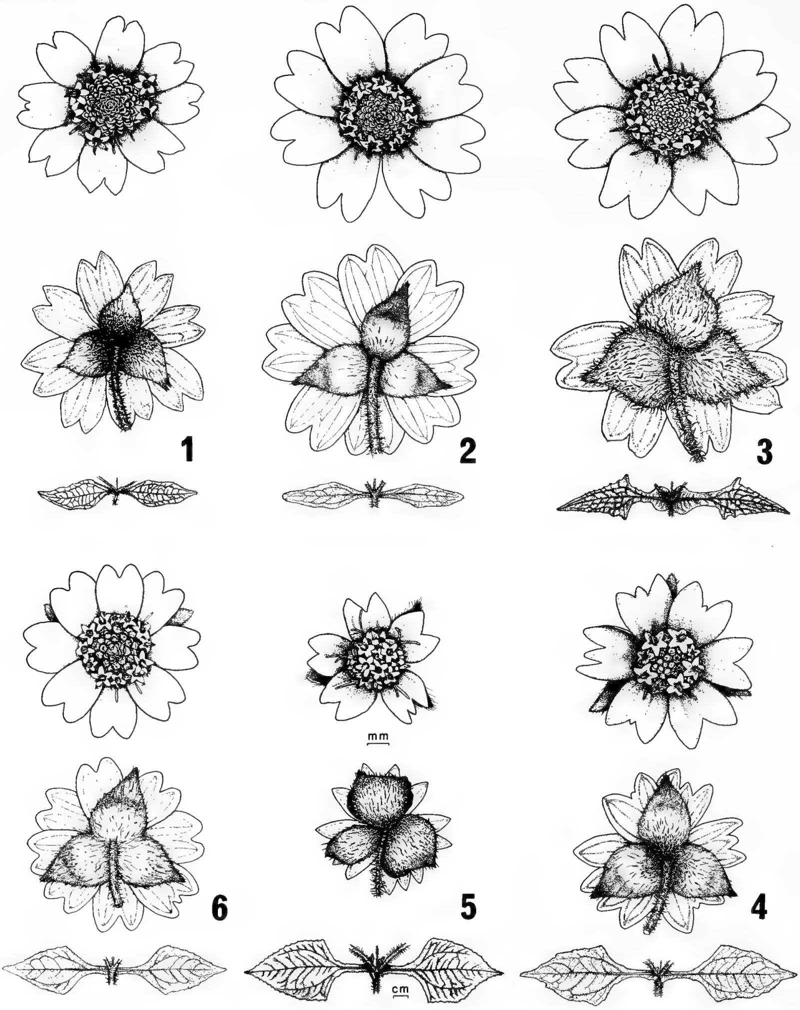
Madroño, Vol. 26, No. 2, pp. 53–104, August 9, 1979



FIGS. 1–6. Representative heads (both top and bottom view) and mature leaves of species and F_1 hybrids of *Melampodium*. All same scale. 1. *M. microcephalum, Stuessy 681*. 2. *M. gracile* × *M. microcephalum*. 3. *M. gracile, Stuessy 537*. 4. *M. gracile* × *M. paniculatum*. 5. *M. paniculatum, Stuessy 579*. 6. *M. paniculatum* × *M. microcephalum*.

from a population in Brazil (Coleman, 1970). These diploid and polyploid chromosomal levels plus morphological similarity suggest a possible polyploid origin for *M. paniculatum* involving one or both of the two diploid species. A program of interspecific hybridizations among all three taxa was initiated to determine patterns of evolution in the section. This paper reports results of these hybridizations.

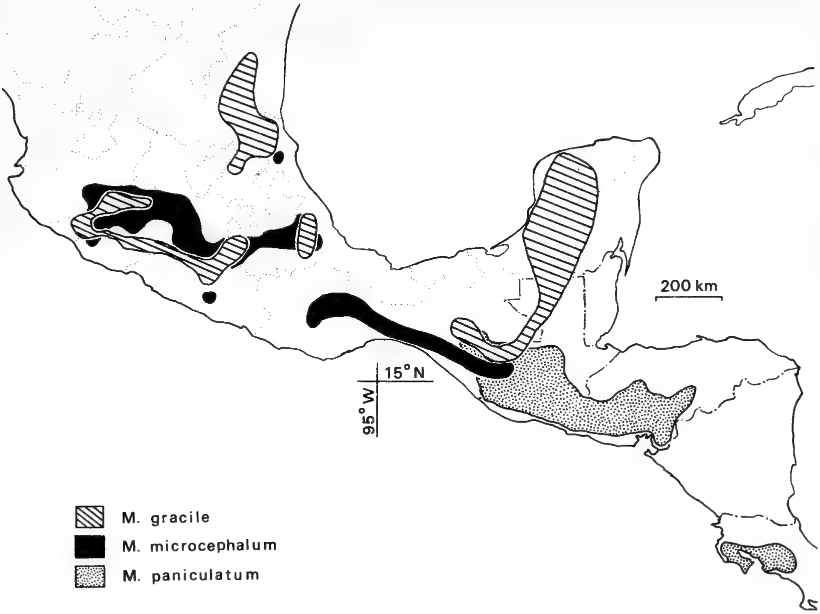
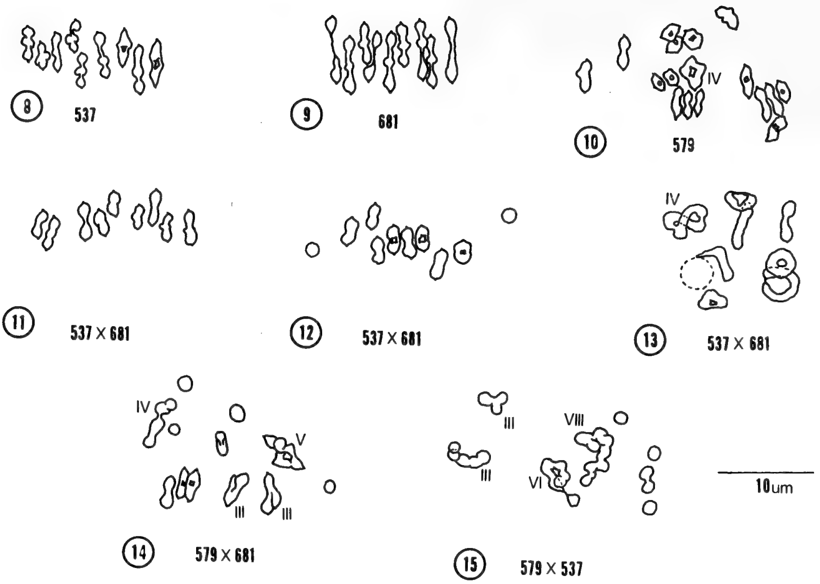


FIG. 7. Generalized distributions in Mexico and Central America of *Melampodium gracile, M. microcephalum,* and *M. paniculatum*. Isolated Colombian and Brazilian localities of *M. paniculatum* not shown.

METHODS

Melampodium is well suited for controlled crossing experiments because the ray florets are carpellate and fertile, and the disc florets produce copious amounts of viable pollen but have abortive ovaries. Removal of disc florets when young, therefore, results at maturity in a functionally female head of ray florets only. Preliminary interplant crosses within species of sect. *Zarabellia* and within *M. divaricatum* (Rich. in Pers.) DC. of sect. *Serratura* (Stuessy, 1968) indicated that the emasculation technique does not hinder or retard normal development of ray florets.

Seeds produced by open-pollination were gathered in the field and grown in the greenhouse to serve as the parental plants. One population of each was used from the following localities: *M. gracile,* México, Yucatán, 13 km N of Mérida, *Stuessy 537*; *M. microcephalum,* México, Michoacán, 5 km SE of Ciudad Hidalgo, *Stuessy 681*; *M. paniculatum,* Guatemala, Huehuetenango, 3 km S of Huehuetenango, *Stuessy 579*. In the crosses, six plants of *M. gracile* and three plants each of *M. microcephalum* and *M. paniculatum* were used. Voucher specimens of these parental stocks and all hybrids described below are in OS.



FIGS. 8–15. Camera lucida drawings of meiotic chromosomes of species and hybrids of *Melampodium* sect. *Zarabellia*. All same scale. 8. *M. gracile* (*n* = 9, *Stuessy 537*). 9. *M. microcephalum* (*n* = 9, *Stuessy 681*). 10. *M. paniculatum* (*n* = 18 [2*n* = 16II + 1IV], *Stuessy 579*). 11–13. *Melampodium gracile* × *M. microcephalum*. 11. Metaphase I. Nine bivalents. 12. Metaphase I. Eight bivalents and two univalents. 13. Diakinesis. Seven bivalents and one quadrivalent. 14. *M. paniculatum* × *M. microcephalum*. Metaphase I. One pentavalent, one quadrivalent, two trivalents, four bivalents, and four univalents. 15. *M. paniculatum* × *M. gracile*. Metaphase I. One octavalent, one hexavalent, two trivalents, one bivalent, and five univalents.

Lens paper bags were used to cover all heads employed in the crossing program. Preliminary checks were carried out for autonomous apomixis in both parental and hybrid generations by removing the disc florets and bagging the heads. To determine the breeding systems of the three species, selfings of individual heads were completed. Crosses between plants of the same species were accomplished to serve as a background against which to evaluate the interspecific crosses. All crosses were accomplished in greenhouses at The University of Texas and The Ohio State University with conditions of high humidity and a temperature of ca. 27°C. For determining pollen viability, acetocarmine and lactophenol-cotton blue stains were used. A positive pollen grain coloration by the two was assumed to indicate pollen viability (Hauser and Morrison, 1964). A minimum of 500 pollen grains was examined per plant. Because changes in the environment can affect pollen viabilities (Jones, 1976), pollen samples were taken only from greenhouse plants grown under uniform conditions. In both

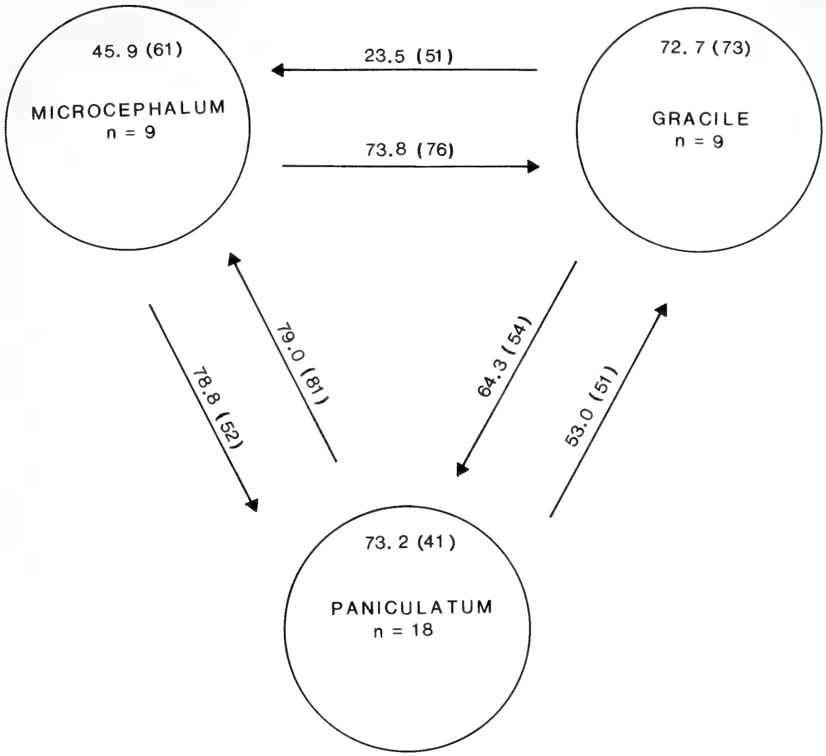


FIG. 16. Summary of crossing relationships within and among *Melampodium gracile, M. microcephalum,* and *M. paniculatum.* Numbers in circles indicate percent seeds obtained in intraspecific crosses. Arrows and numbers indicate percent seeds obtained in interspecific reciprocal crosses (arrows point toward female parent). Numbers in parentheses indicate total number of florets in each type of cross carried out.

cross- and self-pollinations, pollen was dusted on receptive stigmas on three consecutive days to insure effective pollination.

Modified Carnoy's solution (4 chloroform:3 absolute ethanol:1 acetic acid) was used to kill and fix flower buds of both parents and hybrids. Buds prepared in this fashion were refrigerated until processed by the method described by Snow (1963).

RESULTS

Crossing data. Seed set was absent in emasculated heads of *Melampodium gracile* (40 florets/3 plants), *M. microcephalum* (38/3), and *M. paniculatum* (23/3). The absence of any fertile seed indicates that autonomous apomixis is not present in the three populations. The results of self-pollinations indicate that all species are self-fertile to some extent with the tetraploid, *M. paniculatum,* being the most fer-

TABLE 1. SURVIVAL AND FERTILITY IN THE F_1 GENERATION.

Hybrid (♀ × ♂)	Survival Data: # seeds produced	Survival Data: % survival to maturity	Pollen Stainability: # plants examined	Pollen Stainability: % stained (range)	Seed Set (# hybrids/ % seed set): selfed	Seed Set (# hybrids/ % seed set): crossed
microcephalum × *paniculatum*	64	36	36	12 (6–25)	7/0	14/0
paniculatum × *microcephalum*	41	23	13	10 (5–20)	5/0	10/0
paniculatum × *gracile*	36	19	5	6 (2–10)	7/0	7/0
gracile × *paniculatum*	27	10	9	6 (4–10)	4/0	4/0
gracile × *microcephalum*	56	17	13	11 (6–25)	7/0	5/3.6
microcephalum × *gracile*	12	0	—	—	—	—

tile (80.1 percent; 121 out of 151 florets) and the diploids being less so with 15.0 percent (30/200) and 28.8 percent (80/278) in *M. microcephalum* and *M. gracile,* respectively. Relatively high intraspecific crossabilities of approximately 73 percent were found in *M. gracile* and *M. paniculatum. Melampodium microcephalum* had a lowered crossability of 46 percent (Fig. 16).

The interspecific crosses among the three taxa were very successful (Fig. 16). Three principal results were observed. First, the percentages of crossability in three hybrid combinations [*M. gracile* (♀) × *M. microcephalum* (♂); and reciprocals of *M. microcephalum* × *M. paniculatum*] were as high or higher than those of intraspecific crosses. Second, the reciprocal crosses between each pair of species produced equivalent seed set except a lowered seed production between *M. microcephalum* (♀) and *M. gracile* (♂). Third, the highest crossability (79 percent) occurred between the diploid *M. microcephalum* and the tetraploid *M. paniculatum.*

Characteristics of hybrid generation. Seeds produced from all reciprocal interspecific crosses germinated and survived to maturity (Figs. 2, 4, 6) except for *M. microcephalum* (♀) × *M. gracile* (♂) (Table 1). These data closely parallel those of the percentages of hybrid seeds set (Fig. 16). In both instances the highest percentages of hybrid seed produced and the highest percentage of surviving hybrids occur in the reciprocal crosses between *M. microcephalum* (diploid) and *M. paniculatum* (tetraploid). The very small number of fertile seeds produced in the hybrid progeny indicates again the absence of autonomous apomixis (Table 1).

For the meiotic behavior of the artificially produced hybrids to be analyzed effectively, a few comments need to be made first about the diploid parents. In most cases, meiosis appears normal in the three parental species (Stuessy, 1971b). From diakinesis through metaphase I, nine bivalents are invariably observed in both *M. microcephalum* (Fig. 9) and *M. gracile* (Fig. 8). Some variation in pairing was noted in the tetraploid parent, *M. paniculatum.* Eighteen bivalents were observed in most meiocytes through metaphase I. Occasionally, however, one quadrivalent was formed (Fig. 10). Disjunction and microspore formation in the tetraploid appeared normal. In the hybrid between the two diploid species, *M. gracile* × *M. microcephalum,* meiosis appeared normal with most meiocytes exhibiting nine bivalents from diakinesis through metaphase I (Fig. 11). Two univalents (Fig. 12) were found in 12 of 50 meiocytes observed in metaphase I. These unpaired chromosomes may have been the result of the early disjunction of a bivalent because such univalents were not observed at earlier meiotic stages. At anaphase I, one or two chromosomes occasionally remained on the metaphase plate, and micronuclei were noted in 12 of 236 cells sampled. Both of these irregularities may have been the result of early disjunction. A single quadrivalent (Fig. 13) was seen in two of 50 meiocytes observed at diakinesis, indicating the presence of at least one reciprocal translocation between the two diploid genomes. Such quadrivalents were not detected in approximately 50 cells sampled at metaphase I. Disjunction and tetrad formation appeared normal in most meiocytes of the diploid hybrid.

Chromosomal pairing in the triploid hybrids was highly variable. In the reciprocal hybrids of both *M. paniculatum* × *M. gracile* and *M. paniculatum* × *M. microcephalum,* from a sample of approximately 50 cells of each cross, meiocytes exhibited various combinations of univalents, bivalents, trivalents, and higher order multivalents. Unlike those observed in the diploid hybrid, multivalents in both triploids usually persisted through metaphase I. In *M. paniculatum* × *M. gracile,* one hexavalent and one octavalent were observed in one meiocyte (Fig. 15), indicating the presence of at least three reciprocal translocations among the three diploid genomes. The maximum association observed in *M. paniculatum* × *M. microcephalum* (Fig. 14) was one quadrivalent and one pentavalent, indicating the presence of at least two reciprocal translocations. Disjunction and tetrad formation in both triploid hybrids were highly irregular. Multiple lagging chromosomes were common at anaphase I, and multiple micronuclei were present at the tetrad stage.

The F_1 hybrids of all combinations are highly pollen sterile (2–25 percent stainable grains; Table 1). Pollen stainability in parental plants was 80–95 percent. Among the hybrid progenies, the lowest values (about 6 percent) prevail in crosses between the diploid *M. gracile* and the tetraploid *M. paniculatum*. The stainability was approximately the same (10–12 percent) in the two other hybrid combinations.

The data from both selfing of individual heads and interplant crosses within the same hybrid type indicate that an F_2 generation is developed only with difficulty. In all of the attempted crosses to produce an F_2 generation, only two seeds were obtained out of 263 florets examined; these were from the diploid hybrid, *M. gracile* × *M. microcephalum*. Frequent observations of flowering heads of all hybrid plants disclosed abortive ovaries. The hybrids as a group, therefore, are male and female sterile. As a result, the development in nature of large numbers of individuals of advanced hybrid generations would be unlikely.

DISCUSSION

Evolutionary relationships

In assessing evolutionary relationships among *Melampodium gracile, M. microcephalum,* and *M. paniculatum* an important caution is that only single populations of each species were used in the crossing program. The interspecific relationships of these species, therefore, have not been determined from crosses among several to many populations from throughout their ranges, as would be desirable. Because of the fragmented nature of the distributions of the diploids (Fig. 7), it is possible that genetic and/or chromosomal divergence has taken place among the isolated populational segregates; such divergence would not have been detected in the present study. Although additional crosses are needed to provide a more complete view, some suggestions can be made concerning evolutionary and taxonomic affinities among these three species based upon available data.

Between the diploids. Although *Melampodium microcephalum* and *M. gracile* have identical chromosome numbers ($n = 9$), they differ in chromosomal rearrangements, including at least one reciprocal translocation. Bivalent formation is normal in most meiocytes of the diploid hybrids, but early disjunction results in two univalents in some cells at metaphase I. However, even when taken together, these results do not account for the observed level of pollen sterility (ca. 89 percent) and low seed set (ca. 4 percent) in interplant crosses of F_1's. Thus additional, cryptic, structural differences or some other genetic imbalance must exist between the two species. If these additional differences are structural (e.g., translocations, inversions) they may not be of sufficient magnitude to influence pairing. However, they could reduce fertility.

The successful yield of interspecific hybrids (Fig. 16) provides evidence that the two diploid species are closely related and of the same evolutionary line within the genus. The geographic distributions of the diploids plus the available crossing data suggest three alternative hypotheses for their evolution. All three hypotheses assume that the present sympatry in central Mexico occurred after the speciation event(s). (1) One of the species once possessed a wide distribution (*M. gracile* and *M. microcephalum* seem equally plausible), and the other evolved in one region as a peripheral isolate that was then dispersed to other favorable habitats. (2) The same situation prevailed as above, but different derivative isolates originated in different parts of the range of the parent (i.e., there was a polyphyletic origin for one of the diploids). (3) The two taxa evolved from a common ancestor and the present pattern of partial sympatry is the result of range extensions. Of these alternatives, the second possibility seems the least likely because the morphologies of isolated populations within the two diploid species are not very different. The first and third alternatives seem more plausible, but no data are at hand to favor one over the other.

Between the diploids and tetraploid. The level of multivalent formation in the triploid, *M. paniculatum* × *M. microcephalum,* was lower than that found in the triploid, *M. paniculatum* × *M. gracile.* Multivalents in both of these diploids may have two separate origins. First, they may be the product of reciprocal translocations between the single genome from the diploid parent and the two genomes of the tetraploid parent. Second, they may also result from reciprocal translocations between the two genomes of the tetraploid parent. It is true that pairing in the tetraploids is primarily as bivalents. However, such bivalent pairing may be under genetic control (deWet and Harlan, 1972). If genetic control for bivalent pairing is present, it may break down in the triploid hybrids under the influence of the additional genome from the diploid parent. Only in the absence of such genetic control can it be said that the three haploid genomes of the *M. paniculatum* × *M. microcephalum* hybrid are structurally more similar than those in the *M. paniculatum* × *M. gracile* hybrid.

Based upon these data, it cannot be said definitely that either of the diploids contributed to the formation of the tetraploid species. However, they probably were not both involved, and *M. microcephalum* does seem more probable as one of the parents than does *M. gracile.* The former species has fewer observed translocations between it and *M. paniculatum,* and the F_1 hybrids have a higher survival rate, are more robust, and have a higher percentage of viable pollen than in the cross with *M. gracile.*

A program of artificial hybridization among the three species studied here and the other species of sect. *Zarabellia* (*M. longifolium* Cerv. ex Cav. and *M. mimulifolium* Robins.; Stuessy, 1972) would be of value. The former is known cytologically as $n = 9$ (Stuessy, 1971b), but the latter is known only from the type collection (Robinson, 1901) and has not yet been studied chromosomally. Although *M. longifolium* lacks the stipitate-glandular peduncles and three outer phyllaries of the taxa treated in this paper, the leaves resemble those of *M. paniculatum* and the heads are of similar, small size. *Melampodium longifolium* also is Mexican in distribution and is especially common in San Luis Potosí near where *M. gracile* occurs (Fig. 7).

Taxonomic implications

The two diploid species, *M. gracile* and *M. microcephalum,* are very similar morphologically. They are sufficiently similar, in fact, that difficulty was experienced in sorting some of the herbarium material of the two taxa during the previous revisionary study (Stuessy, 1972). The results of the present investigation reaffirm the closeness of the taxonomic relationship of the two species. At the same time, the documentation of at least one reciprocal translocation between the two taxa, plus sterile F_1 hybrids, supports their recognition as good species. Furthermore, the ease of artificial hybridization of the two diploids and the robust nature of the hybrids suggests that natural hybridization may not be uncommon. This could account for at least some of the difficulty experienced in distinguishing them morphologically.

The cytogenetic data between the diploids and the tetraploid reconfirm the latter's taxonomic distinctness based on morphological, distributional, and cytological grounds. Populations of *M. paniculatum* from Central and South America are morphologically very similar. However, one population of this species from Brazil has been determined to be hexaploid with $n = 27$ (Coleman, 1970). These $6x$ cytotypes probably arose from the tetraploid level through nonreduction during meiosis in one of the gametophytic lines followed by normal fertilization, a common mechanism for the production of higher ploidy levels (Harlan and deWet, 1976). In view of the small sample size examined to date, the presence of tetraploid *M. paniculatum* in South America certainly cannot be ruled out.

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A POTENTIAL ROLE OF COASTAL SAGE SCRUB UNDERSTORIES IN THE RECOVERY OF CHAPARRAL AFTER FIRE

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ABSTRACT

Fifty-eight percent of the herb species recorded on recently burned sites of chaparral in southern California are to be found in the understories of southern coastal sage scrub stands that have not burned for seven years or more. Because coastal sage scrub is found near chaparral at lower elevations throughout southern California, it may serve as an important seed source for the herbland phase of chaparral succession after fire. The dispersal of seeds from sage scrub to chaparral lands each year provides an alternative to the hypothesis that post-fire herbs arise from seeds that have remained viable *in situ* for the 40–90 years or more that may intervene between fires. At the same time, it would appear that mechanisms such as increased shading, or possibly allelopathy, act to inhibit the germination of herb seeds under mature chaparral canopy. The large degree of similarity between the understory flora of mature coastal sage scrub and the post-fire flora of chaparral challenges the notion that the latter are mostly "pyrophyte endemics". The possibility of a partial dependence of chaparral succession on dispersal from coastal sage scrub suggests a new argument for the conservation of coastal sage scrub areas, remaining examples of which are currently endangered by development pressures.

The first three to six years of growth after fire in chaparral areas of California are characterized by a marked increase in growth of annual and perennial herbs. In a recent review of chaparral ecology, Hanes (1977, p. 433) has stated that "most of these herbaceous species on chaparral burns . . . are 'pyrophyte endemics,' that is, they are found on burn sites but not elsewhere." On the basis of a recently completed survey of 67 sites of coastal sage scrub in southern California, I report that a majority of post-fire chaparral herbs are to be found in the understories of coastal sage scrub sites that have not burned in at least seven years, and in most cases not for one or two decades and more.

Southern coastal sage scrub is a vegetation type dominated by drought-deciduous, mesophytic shrubs, 0.5–2.0 m tall, typically of the genera *Salvia, Encelia,* and *Eriogonum,* and by *Artemisia californica.* The community is found below 900 m elevation on the coastal and interior sides of the evergreen, sclerophyllous chaparral shrubland (2–3 m tall) of coastal mountains. Typical chaparral dominants include *Adenostoma* and *Ceanothus* spp. Recent synecological accounts of coastal sage scrub are those of Mooney (1977) and Kirkpatrick and Hutchinson (1977). If coastal sage scrub is acting as a repository and seed source for post-fire chaparral herbs, there is less need to explain post-fire herb blooms by postulating seed dormancy periods of several decades (Hanes, 1977). Secondly, it implies a partial dependence of chaparral on adjacent coastal sage scrub for post-fire successional processes that hitherto has not been considered.

METHODS

Sites of southern coastal sage scrub, both coastal and inland, were sampled in a region extending from the base of the San Pedro Martir near San Telmo (Baja California) in the south, to Mt. Diablo, east of San Francisco, in the north. Sixty percent of the sites were in the region from Ventura County to the California-Mexico border, reflecting the concentration of sage scrub habitat in this region. The identity of all species within a 25 m × 25 m plot at each of 67 sites was recorded. The mean time since last fire ± std. dev. was 17 ± 9 years (range: 7–40+ years), as determined by local fire records and ages of shrub stems. Shrub stem ages provide a minimum time since past fire, so the mean figure is a conservative estimate. The influence of past grazing by sheep and cattle could not be ruled out for any site, but current grazing activity was sporadic or nonexistent in all cases. A more detailed account of the floristics and habitat features of the sites, including disturbance influences, is in preparation.

Sampling was conducted in June and July, 1977 and March–May, 1978. Seventeen of the 44 sites sampled in 1977 were revisited in the spring of 1978 to identify additional understory ephemerals. The fact that only 3.4 ± 0.7 additional species were recorded per site (31 species, total) suggests that the unusually heavy rains of the 1977–78 winter season did not increase the size of the coastal sage scrub understory flora inordinately.

RESULTS AND DISCUSSION

The understory flora of coastal sage scrub sites that had not burned in seven years or more was compared with herbs and subshrubs found on chaparral sites that had burned or been cleared 1–4 years previously. Two of the chaparral sites were in coastal southern California (McPherson and Muller, 1969; Christensen and Muller, 1975), and two were inland (Horton and Kraebel, 1955; Vogl and Schorr, 1972). Of 111 post-fire chaparral herbs thus considered, 58 percent were found also in southern coastal sage scrub sites. Both annuals and perennials are held in common between chaparral and sage scrub by this proportion. When the fourteen introduced species (all annuals) are removed from consideration, 56 percent of species are held in common. When 44 additional post-fire chaparral herbs encountered from chaparral sites 150–300 km north (Sampson, 1944; Sweeney, 1956) of the northernmost coastal sage scrub site sampled (Mt. Diablo) are included in the comparison, the proportion of species held in common drops by only 9 percent.

These figures suggest that a substantial proportion of herbs and subshrubs appearing on post-fire chaparral sites could have arisen from seed dispersed from nearby coastal sage scrub sites. This is not to imply that the seeds have arrived only after a fire. Sweeney (1956) has shown that many post-fire chaparral herb seeds are present in the soil before a burn. Presumably, seeds arrive from adjacent coastal sage scrub sites each year, but are stimulated to germinate on chaparral sites by conditions that pertain during and following fire (Sampson, 1944; Sweeney, 1956; Hanes, 1977). While no studies have been done on seed longevity for the herbs discussed here, a study of seed viability for a selection of southern California chaparral and desert species stored in dry cabinets indicates that very few retain viability for even twenty years (Went, 1969).

The suppression of germination of many post-fire herb seeds under the canopy of mature chaparral relative to coastal sage scrub may be a function of the denser and more continuous shade under chaparral shrubs or possibly of the action of allelopathic substances associated with chaparral dominants. A number of workers have examined this question since the early studies of Went et al. (1952). McPherson and Muller (1967) have demonstrated the ability of *Ceanothus* (a chaparral shrub) to suppress *Salvia leucophylla* seedlings by shading. McPherson and Muller (1969), Chou and Muller (1972), and Christensen and Muller (1975a) have argued that light is not a factor in herb suppression in chaparral, because bare areas within chaparral occur in canopy openings. Herb suppression in bare areas has been explained in terms of grazing and seed removal by animals, patchiness in soil moisture, and allelopathy in chaparral (Muller et al., 1968; McPherson and Muller, 1969; Christensen and Muller, 1975a). Because factors contributing to herb suppression in both communities are multiple, variations in herb density in both cases are to be expected. Nevertheless, a more intense and continuous shade does distinguish the environment beneath a chaparral canopy from that beneath the canopy of coastal sage shrubs, and herbs under the canopies of the two communities may be expected to respond to this difference (see also Christensen and Muller, 1975b).

Allelopathic effects have been demonstrated in bioassays for both coastal sage scrub and chaparral species (Muller et al., 1964; McPherson and Muller, 1969). To the extent that this phenomenon applies in the field, more effective inhibition of herbs under chaparral relative to coastal sage scrub will depend upon the species density and composition of the particular stands being compared.

While areas of coastal sage scrub interdigitate with those of chaparral at lower elevations of coastal mountains and in areas of mosaic fire pattern, the contribution of the coastal sage scrub understory to seed stores in areas of chaparral remote from sage scrub sites could be expected to be less. A quantitative study of the seed reservoir of post-fire herbs in chaparral litter and surface soil at increasing distances from mature coastal sage scrub sites could help test this hypothesis.

If in fact seeds of many post-fire chaparral herbs are not of decades-long viability, but are rather renewed in quantity each year by influx from mature coastal sage scrub sites, a dependence of chaparral on sage scrub for post-fire recovery is implied. This implication has practical significance to plans for preserving examples of chaparral in the Santa Monica Mountains and elsewhere in southern California, now being considered by the U. S. Congress and other government entities. The Santa Monica Mountains Planning Commission is currently preparing a plan for the development and preservation of this area, which contains examples of both coastal sage scrub and chaparral. Legislation recently has been enacted that will permit Federal purchase of land in the Santa Monica Mountains for park purposes. It may also have significance for efforts to minimize erosion damage following recurrent chaparral fires throughout southern California. Although coastal sage scrub is a distinct community type, it is frequently not distinguished from chaparral by planners considering proposals to preserve or develop southern California shrublands. It is widely agreed by ecologists, however, that southern coastal sage scrub is one of the most endangered habitats in California (see, e.g., Hanes, 1976).

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THE VASCULAR FLORA OF PUNTA BANDA, BAJA CALIFORNIA NORTE, MEXICO

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ABSTRACT

Punta Banda, a peninsula 24 km south of Ensenada, northwestern Baja California Norte, Mexico, has a flora of 258 species, 208 of which are native. This report includes an annotated checklist of the species with a description of the vegetation, physical environment, and a brief discussion of floristic and biogeographic considerations.

Species richness on Punta Banda is roughly comparable with that on the California Channel Islands. The treeless, shrubby vegetation, characteristic of coastal areas in northwestern Baja California, is marked by the conspicuous presence of succulent species (*Agave shawii, Dudleya brittonii,* six genera of cacti) in appropriate situations, particularly in steep or rocky areas and on slopes with a southerly exposure.

Typical chaparral-coastal sage scrub taxa make up about half of the native flora with another 15 percent of the species endemic to the coastal sage scrub-chaparral transition zone centered in northwestern Baja California. About 11 percent of the native flora are desert taxa and about 17 percent are widespread Pacific Coast taxa. Two species (*Dudleya campanulata* and *Astragalus sanctorum*) are endemic to the peninsula and four species (*Eriogonum grande, Dudleya anomala, Hemizonia greeneana* ssp. *peninsularis,* and *Ribes viburnifolium*) represent limited mainland occurrences of otherwise insular taxa.

Punta Banda, 15 km south of Ensenada (Baja California Norte, Mexico), has attracted botanists for many years with its spectacular topography and rich flora. To date, however, no biogeographical or ecological studies have described the flora and vegetation of this peninsula. This paper, the first in a series, gives a brief introduction to the geographic characteristics and vegetation of the peninsula and provides an annotated checklist of the vascular plants.

PHYSICAL GEOGRAPHY

Geographically, Punta Banda represents a seaward extension of Punta Banda Ridge, a range of hills continuing eastward toward Santo Tomas (Fig. 1). The peninsula itself is approximately 13 km in length and varies from 2 to 3 km in width. The steep backbone of the peninsula reaches a maximum height of 400 m at Banda Peak (Pico Banda) near its tip. East of the peninsula, Punta Banda Ridge reaches 1100 m. Recent uplift has produced steep cliffs around most of the coast of the peninsula, with vertical escarpments of 20–60 m in most areas. A long sand spit, Playa de Punta Banda, extends northeast from near the

FIG. 1. Punta Banda, Baja California Norte. Topography and place names. The heavy dashed lines indicate the approximate boundaries of the area covered.

base of the peninsula toward Ensenada, providing the only really sandy beaches. A larger estuary, Estero de Punta Banda, separates this sand spit from the mainland.

Geologically, the majority of the peninsula is composed of Lower Cretaceous (Albian) metamorphic rocks as is Punta Banda Ridge to the east. Massive formations of andesite porphyry form prominent sea bluffs and hills on the south side from La Bufadora northwestward

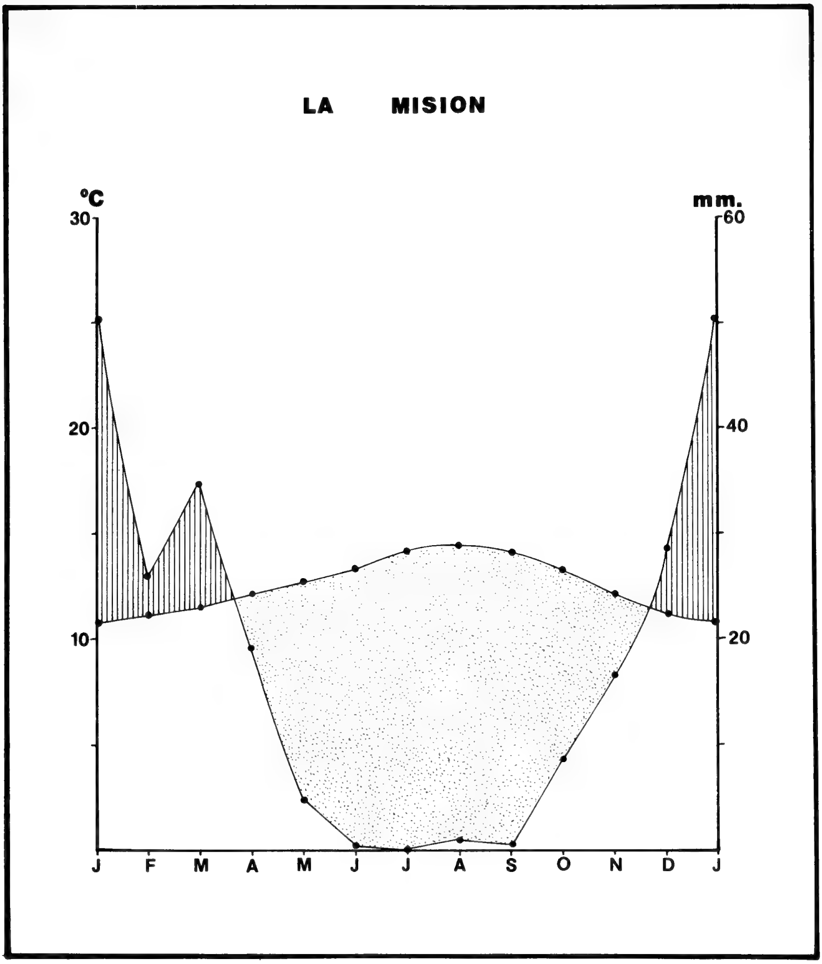

FIG. 2. Monthly climatic pattern of mean temperature (°C) and precipitation (mm) at La Misión, Baja California. Data for 18-year record ending in 1965 from Hastings and Humphrey (1969).

toward the tip. However, the north-central part contains a 5 km^2 exposure of Upper Cretaceous (Maestrichtian) sedimentary rock (Allen et al., 1961). Much of the contact between these two formations is part of the Agua Blanca fault system (Allen et al., 1961). Right-lateral strike-slip fault movement of this system along the northern flanks of Punta Banda has produced the peninsula's gross outline.

Quaternary marine deposits cover many local slopes on the peninsula to depths up to 30 m (Orme, 1972). Irregular tectonic uplift of these deposits through the Quaternary has resulted today in at least 13 levels of marine terraces, the highest at 345 m. Terraces are present on all parts of Punta Banda but are best developed on the steeply dipping Upper Cretaceous sediments (Orme, 1972). Steep sea cliffs below these terraces are richly fossiliferous (Allen et al., 1961). The extensive development of terraces on Punta Banda is unique on the northwest coast of Baja California but they are comparable with the complex series of marine terraces occurring on San Clemente Island. The San Clemente terraces, formed on a submarine escarpment, are presumed to reflect the northwestward continuation of the Agua Blanca fault system (Orme, 1972).

Climatic data are not available for Punta Banda. Although extensive climatic records are available for Ensenada, the mesoclimatic regimes of the two areas are totally different. Cold water upwelling on the southern side of the peninsula contacts warmer coastal waters near the tip, producing frequent marine fogs. Often these fogs are extremely local, confined to Banda Peak and Isla Todos Santos or to the southern side of the peninsula. The ecological significance of moisture input as fog has not been investigated, but may have considerable local importance.

Mean annual precipitation at Isla Todos Santos (22 m elevation), a site comparable with Punta Banda, was 256 mm from 1933 to 1939. Over the same period Ensenada (24 m elevation) had a mean of 296 mm (Hastings, 1964), close to the 57-year mean of 280 mm (Hastings and Humphrey, 1969). Despite its proximity, summer temperatures at Ensenada are significantly higher than at Punta Banda owing to the lack of fog influence and the protection from strong winds. The most comparable station to Punta Banda is La Misión, 50 km north (Fig. 2). The mean annual temperature there is 15.2°C, 1.5° lower than at Ensenada. Mean monthly temperatures are 1–2°C lower during every month of the year.

VEGETATION

Vegetation structure on Punta Banda is dominated by coastal sage scrub with low malacophyllous shrubs and a frequent admixture of succulent plants. This vegetation is part of a transitional zone between coastal sage scrub and chaparral communities of cismontane California to the north and Sonoran desert communities to the south. Shreve (1936) and Lewis and Epling (1942) discuss this transition zone. In the vegetation of Punta Banda, community structure is extremely diverse. Community patterns will be discussed in detail in a later paper. Rocky, south-facing slopes are characterized by a mixed *Eriogonum fasciculatum*–succulent scrub community of low, open growth-form. Less arid south-facing slopes are dominated by *Rhus integrifolia, Artemisia californica,* and *Agave shawii*. The more mesic north-facing slopes support a community dominated by large woody deciduous shrubs—*Aesculus parryi* and *Rhus integrifolia* (or *Salvia munzii*) with *Fraxinus trifoliata* or *Malosma laurina*. Less mesic sites have a coastal sage scrub community dominated by *Artemisia californica* and *Salvia munzii*.

Virtually pure stands of both *Adenostoma fasciculatum* and *Ambrosia chenopodiifolia,* present in many areas of the peninsula, are related to substrate. *Adenostoma* is associated with very rocky, shallow soil profiles, often on ridge tops. *Ambrosia* dominates many beach terraces and gentle hillsides, apparently associated with Indian middens. Several species are restricted to sandstone substrates on the peninsula, including *Quercus dumosa, Helianthemum scoparium,* and *Dudleya lanceolata*.

FLORA

The vascular flora of Punta Banda, exclusive of the Playa de Punta Banda and associated sandspit and salt marsh habitats, includes 258 species in 181 genera and 58 families. Of this total, 81 percent are native. This flora is surprisingly large considering the small diversity of habitat types present on the peninsula. These types are rocky hillsides and outcrops, dry arroyos, old beach terraces, and sea bluffs. No permanent water exists on the peninsula, and salt marsh, sandy beach, and dune habitats are absent from the area covered here. Elevational ranges are too small to produce vegetational zonation except that attributable to salt spray and slope exposure. Except for disturbed areas, all communities are dominated by shrubs, with woodlands, grasslands, and riparian communities absent.

Despite the low habitat diversity of Punta Banda, floristic diversity is somewhat greater than the general pattern of diversity demonstrated for the California Channel Islands (Johnson et al., 1973). Punta Banda, with an area of 32 km^2, has 208 native taxa.

The ten families best represented on Punta Banda are: Asteraceae (45 total species/34 native species); Poaceae (25/14); Fabaceae (21/18); Chenopodiaceae (13/7); Brassicaceae (13/7); Scrophulariaceae (9/9); Caryophyllaceae (8/5); Hydrophyllaceae (8/8); Solanaceae (8/7); and Cactaceae (7/7). These families make up 56 percent of the native flora, 82 percent of the introduced flora, and 61 percent of the total flora. Eight genera are represented by four or more species: *Atriplex* (8); *Lupinus* (7); *Phacelia* (5); *Haplopappus* (4); and *Ribes* (4). These genera are predominantly perennials.

The biogeographic relationships of the Punta Banda flora show a broad origin of taxa, following the pattern described by Shreve (1936). Of the native flora, 50 percent are typical coastal sage and/or chaparral taxa. The second largest group, 17 percent, are wide-ranging Pacific Coast taxa, characteristic of diverse community types. Desert taxa make up 11 percent of the flora, while coastal sage-desert transition zone endemics are 15 percent of these taxa. Finally, 5 percent are widespread species typical of weedy habitats, and 1 percent are coastal bluff species extending north into California. Introduced taxa are indicated by an asterisk (*) in the following list. Biogeographic relationships will be discussed in detail in a later paper.

Many taxa of the Punta Banda flora are typical of the floras of one or more of the Channel Islands. Such species as *Eriogonum grande* s.l. and *Ribes viburnifolium* have a restricted distribution on the Baja California peninsula. Other taxa occur with a limited distribution on the mainland and adjacent small offshore islands but not on the larger Channel Islands (e.g., *Dudleya anomala, Eriogonum grande* ssp. *testudinum,* and *Hemizonia greeneana* ssp. *peninsularis*—see Moran, 1969). Two species, *Dudleya campanulata* and *Astragalus sanctorum,* are endemic to Punta Banda. Several species reported by Moran (1950) from the adjacent Isla Todos Santos have not been observed on Punta Banda. These patterns of distribution and other data suggest that the majority of insular and coastal endemics in the southern California and Baja California transition zone floras are relictual rather than more recently evolved floristic elements (see Axelrod, 1967).

Voucher specimens are deposited in IRVC. Field collections were carried out over the period 1971–1977, with multiple trips covering each month of the year. The checklist follows.

LEPIDOPHYTA

Selaginellaceae

Selaginella bigelovii Underw. Common on rocky slopes.

S. cinerascens A. A. Eat. Common, forming a carpet between shrubs on flats and gentle slopes. Transition-zone endemic.

PTEROPHYTA

Aspidiaceae

Dryopteris arguta (Kaulf.) Watt. Occasional in arroyos on seasonally moist slopes.

Polypodiaceae

Polypodium californicum Kaulf. Common on seasonally damp banks and slopes.

Pteridaceae

Adiantum jordanii K. Müll. Frequent on shaded, seasonally moist slopes.

Pellaea andromedifolia (Kaulf.) Fée var. *pubescens* D. C. Eat. Occasional on dry, rocky slopes.

Pityrogramma triangularis (Kaulf.) Maxon var. *viscosa* (Nutt. ex D. C. Eat.) Weath. Frequent in rocky places such as steep N-facing slopes and arroyo banks, occasional on drier slopes.

CONIFEROPHYTA

Ephedraceae

Ephedra californica S. Wats. Stem-photosynthetic shrub. Occasional to frequent on slopes as in rocky areas.

ANTHOPHYTA—DICOTYLEDONEAE

Aizoaceae

**Mesembryanthemum crystallinum* L. [=*Gasoul crystallinum* (L.) Rotm.]. Succulent annual. Sea bluffs and disturbed areas.

* *M. nodiflorum* L. [=*Gasoul nodiflorum* (L.) Rotm.]. Succulent annual. Uncommon on peninsula on sandy or disturbed soil.

Carpobrotus aequilaterus (Haw.) N. E. Brown (=*Mesembryanthemum chilense* Mol.). Succulent perennial. Beaches.

Anacardiaceae

Malosma laurina Nutt. ex Abrams (=*Rhus laurina* Nutt. in T. & G.). Evergreen sclerophyll shrub. Infrequent in chaparral.

Rhus integrifolia (Nutt.) Benth. & Hook. var. *integrifolia*. Evergreen sclerophyll shrub. Common in chaparral and on windswept bluffs and hillsides among shrubs of lesser stature.

Apiaceae

Apiastrum angustifolium Nutt. Annual. Grassy places.

Daucus pusillus Michx. Annual. Grassy places.

**Foeniculum vulgare* Mill. Herbaceous perennial. Along road at top of Banda Peak.

Sanicula crassicaulis Poepp. ex DC. Herbaceous perennial. Frequent in arroyos and on shaded banks.

Asteraceae

Adenothamnus validus (Bdg.) Keck. Malacophyllous subshrub. Primarily restricted to Ensenada area but occurring to 32 km south of the U.S. border. Uncommon on north-facing chaparral slopes on sandstone.

Amblyopappus pusillus H. & A. Fragrant annual. Abundant on flats and bluff tops on the coast.

Ambrosia chenopodiifolia (Benth.) Payne. Malacophyllous shrub. Common in patches in sandy or silty soils either as nearly pure stands or with *Artemisia californica*. Often on old middens or burns (cf. Meigs, 1938).

Artemisia californica Less. Malacophyllous shrub. Common dominant on gentle slopes and old beach terraces.

Baccharis sarothroides A. Gray. Stem-photosynthetic shrub. Occasional, sandy disturbed places.

**Centaurea melitensis* L. Annual. Roadside weed.

Chaenactis artemisiifolia (Harv. & A. Gray) A. Gray. Annual. Occasional in gravelly soil.

**Chrysanthemum coronarium* L. Annual. Garden escape at dump and roadsides near La Joya, also present near settlement at La Bufadora.

**Conyza bonariensis* (L.) Cronq. Annual. Roadside weed.

C. canadensis (L.) Cronq. Annual. Roadside weed.

Coreopsis maritima (Nutt.) Hook. f. Herbaceous to suffrutescent perennial. Common on sea bluffs and north-facing slopes. Transition-zone and island endemic.

**Cotula australis* (Sieber) Hook. f. Annual. Weedy.

Encelia californica Nutt. Malacophyllous shrub. Common on slopes with coastal sage scrub and in disturbed places.

Eriophyllum confertiflorum (DC.) A. Gray. Herbaceous to suffrutescent perennial. Moderately common, mostly in disturbed areas.

Filago arizonica A. Gray. Annual. Herbaceous vegetation; often in heavy soil.

F. californica Nutt. Annual. Herbaceous vegetation, often in heavy soil.

Gnaphalium bicolor Bioletti. Herbaceous to suffrutescent perennial. Occasional in disturbed habitats.

G. californicum DC. Herbaceous to suffrutescent perennial. Disturbed habitats.

Haplopappus berberidis A. Gray. Malacophyllous subshrub. Common in old fields with a succulent-leaved form on beach bluffs. Transition-zone endemic.

H. orcuttii A. Gray. Malacophyllous subshrub. Common on flats; forming hybrids with *H. berberidis*. Transition-zone endemic.

H. palmeri A. Gray. Malacophyllous shrub. Locally common in sandy soils, especially in wash bottoms and on the north side of the peninsula. Transition-zone endemic.

H. venetus (H.B.K.) Blake ssp. *oxyphyllus* (Greene) Hall. Malacophyllous subshrub common in disturbed habitats. This subspecies is a transition-zone endemic, reaching up into the montane zone of the Sierra San Pedro Martir.

**Hedypnois cretica* (L.) Willd. Annual. Collected once on south slope between La Bufadora and Puerto Arbolitos.

Hemizonia fasciculata (DC.) T. & G. Annual. Common in late spring and summer on flats and gentle slopes.

H. greeneana Rose ssp. *peninsularis* Moran. Malacophyllous subshrub. Occasional as isolated individuals or in small populations; present on Banda Peak; south side of peninsula west of La Bufadora, and on adjacent offshore sea stacks on the south shore near tip of the peninsula. Endemic to Todos Santos islands, Punta Banda, and west of La Misión. Banda Peak is the type locality for this subspecies.

**Heterotheca grandiflora* Nutt. Annual. Disturbed habitats, probably introduced.

**Hypochoeris glabra* L. Annual. Roadside weed.

Lasthenia californica DC. ex Lindley. Annual. In herbaceous cover and among shrubs.

L. coronaria (Nutt.) Ordnuff. Annual. Primarily on north-facing slopes.

Microseris linearifolia (DC.) Sch.-Bip. Uncommon annual occurring with grasses and other herbaceous vegetation.

Perezia microcephala (DC.) A. Gray. Herbaceous perennial. Seen only on steep north-facing slope of Banda Peak at about 150 m in openings in dense chaparral.

Perityle emoryi Torr. Annual. Rocky open places, sometimes in salt spray zone with virtually no associates.

Porophyllum gracile Benth. Herbaceous to suffrutescent perennial. Uncommon in rocky places with southern exposure.

Rafinesquia californica Nutt. Weak-stemmed annual. Frequent among shrubs, mostly on the north side of the peninsula.

Senecio californicus DC. Annual.

S. douglasii DC. Suffrutescent perennial. Uncommon on peninsula in disturbed areas.

**S. vulgaris* L. Annual. Weed.

**Sonchus asper* (L.) Garsault. Annual. Weed about old habitations and disturbed areas.

**S. oleraceus* L. Annual. Weed about old habitations such as at Los Arbolitos.

Stephanomeria diegoensis Benth. Annual. Disturbed habitats.

Stylocline gnaphalioides Nutt. Annual. Among other herbs, usually in heavy soils.

Trixis californica Kell. Malacophyllous subshrub. Frequent on south-facing slopes and rocky places.

Verbesina dissita A. Gray. Weak-stemmed malacophyllous perennial. Mostly north-facing slopes and arroyos in chaparral. Transition-zone endemic.

Viguiera laciniata A. Gray. Malacophyllous shrub. Common on slopes.

**Xanthium strumarium* L. Cosmopolitan annual weed. Disturbed sites near La Joya.

Boraginaceae

Amsinckia intermedia F. & M. Annual. On burn northeast of Los Arbolitos.

Cryptantha intermedia (A. Gray) Greene. Annual. Common on open slopes.

C. micromeres (A. Gray) Greene. Annual. Collected on north slope of peninsula below Banda Peak and on burned area northeast of Los Arbolitos.

Pectocarya linearis DC. var. *ferocila* I. M. Johnst. Annual. Common on grassy flats and slopes.

Plagiobothrys californicus (A. Gray) Greene. Annual. Frequent in open herbaceous vegetation.

Brassicaceae

**Brassica geniculata* (Desf.) J. Ball. Herbaceous perennial weed.

**B. tournefortii* Gouan. Annual weed.

**Cakile maritima* Scop. Annual. Individual growing in a runnel on dirt road above 200 m. Typically found on beach dunes, as at Playa de Punta Banda.

Capsella rubella Reut. Annual weed.

Cardamine californica (Nutt.) Greene var. *californica* (=*Dentaria californica* Nutt.). Herbaceous perennial. Relatively frequent on shaded banks, often under shrubs.

Descurainia pinnata (Walt.) Britton ssp. *menziesii* (DC.) Detl. Annual. Common, especially in disturbed places.

Draba cunefolia Nutt. ex T. & G. var. *integrifolia* S. Wats. Annual.

Lepidium nitidum Nutt. Annual. Common.

**Raphanus sativa* L. Annual. In fields near Los Arbolitos.

**Sisymbrium irio* L. Annual weed, common.

**S. orientale* L. Annual weed, common.

Streptanthus heterophyllus Nutt. Annual. Occasional in chaparral; mostly north-facing slopes.

Thelypodium lasiophyllum (H. & A.) Greene. Annual.

Buxaceae

Simmondsia chinensis (Link.) C. K. Schneid. Evergreen sclerophyll shrub. Frequent on south-facing slopes and in rocky places.

Cactaceae

Bergerocactus emoryi (Engelm.) Britt. & Rose. Succulent. Common and conspicuous on south-facing slopes and rocky habitats. Transition-zone endemic.

Echinocereus maritimus (M. E. Jones) K. Schum. Succulent. Frequent on south-facing slopes. Transition-zone endemic.

Ferocactus viridescens (Nutt.) Britt. & Rose var. *littoralis* Lindsay. Succulent. Transition-zone endemic. Common in rocky soils and also as a dwarf form 2–5 cm or less high (but with normal width of 12–20 cm) in heavy soils on windswept flats with *Selaginella* *cinerascens* and *Agave*. This dwarf form is most extreme on soils derived from volcanic parent materials, as at La Misión to the north.

Machaerocereus gummosus (Engelm.) Britt. & Rose. Succulent. Infrequent but conspicuous on steep south-facing slopes, especially near ridge tops. This is near the northern limit of this taxon which is a characteristic element of the Baja California desert flora.

Mammillaria dioica K. Bdg. Succulent. Common in open vegetation; especially in rocky places on south-facing slopes.

Opuntia oricola Philbrick. Succulent. Occasional on south-facing slopes.

O. prolifera Engelm. Succulent. Occasional in open vegetation primarily on south-facing slopes. Frequently associated with Indian middens or otherwise disturbed areas.

Capparidaceae

Cleome isomeris Greene (=*Isomeris arborea* Nutt.). Malacophyllous shrub, normally evergreen. Occasional among shrubs on flats and on most slope exposures.

Caprifoliaceae

Sambucus mexicana Presl. Winter deciduous shrub to low tree. Infrequent on north side of peninsula near La Joya.

Caryophyllaceae

Cardionema ramosissimum (Weinm.) Nels. & Macbr. Herbaceous perennial. Infrequent tuft-forming plant in sandy or compacted bare soil.

Polycarpon depressum Nutt. Prostrate annual.

P. tetraphyllum (L.) L. Prostrate annual. Roadsides and paths.

Silene antirrhina L. Annual. Common in disturbed grassy areas.

S. gallica L. Annual. Weed in old fields, etc.

S. laciniata Cav. ssp. *major* Hitchc. & Maguire. Herbaceous perennial. Occasional on north-facing slopes in chaparral.

Spergularia macrotheca (Hornem.) Heynh. Herbaceous perennial. Flat area near the tip of the peninsula.

S. villosa (Pers.) Camb. Herbaceous perennial. Hard-packed soil along roadside near Tres Hermanas (Three Sisters) and near La Bufadora.

Chenopodiaceae

Aphanisma blitoides Nutt. Succulent annual. Terraces and bluffs near the ocean.

Atriplex californica Moq. in DC. Suffrutescent perennial. Apparently uncommon. Our collections are from an offshore islet and a sea bluff on the south side of peninsula.

Atriplex canescens (Pursh) Nutt. ssp. *canescens*. Shrub. Uncommon; a few plants near Los Arbolitos. Occurs sporadically along the coast in this area, usually associated with old Indian encampments.

A. coulteri (Moq.) D. Dietr. Suffrutescent perennial. Collected twice in disturbed places on soils from sedimentary rocks. Sandstone wash area near La Joya and roadside.

A. julacea S. Wats. Semi-succulent shrub. Common, dry flats and gentle slopes. Transition zone and Vizcaino Region.

**A. lentiformis* (Torr.) S. Wats. ssp. *breweri* (S. Wats.) Hall & Clem. Shrub. Roadside north side of peninsula west of La Joya. Probably introduced at this site.

**A. lindleyi* Moq. Perennial herb. Uncommon weed in roadside depression near La Bufadora.

A. pacifica Nels. Annual. Sea bluffs and offshore stacks.

**A. semibaccata* R. Br. Suffrutescent perennial. Common in disturbed areas and with native vegetation, especially in grazed areas.

**Chenopodium album* L. Annual. Common weed.

**C. ambrosioides* L. Annual or herbaceous perennial. Roadside weed.

C. californicum (S. Wats.) S. Wats. Herbaceous perennial. Common on banks and slopes in chaparral and in disturbed habitats.

**Salsola iberica* Sennen & Pau. Annual. Weed in old fields and disturbed places; among native species in overgrazed areas.

Cistaceae

Helianthemum scoparium Nutt. var. *vulgare* Jeps. Stem-photosynthetic subshrub on sandstone; a small colony with *Quercus dumosa* Nutt. in canyon west of La Joya, on north side of peninsula.

Convolvulaceae

Calystegia macrostegia (Greene) Brummitt ssp. *longiloba* (Abrams) Brummitt. Perennial vine. Common, twining among shrubs.

Dichondra occidentalis House. Perennial herb. Uncommon on sandstone.

Cuscutaceae

Cuscuta californica H. & A. Annual parasite. Common on *Eriogonum fasciculatum, Haplopappus venetus, Salvia munzii,* etc.

Crassulaceae

Crassula erecta (H. & A.) Berger (=*Tillaea erecta* H. & A.). Diminutive succulent annual. Common in dry shallow soils.

Dudleya anomala (Davids.) Moran. Rosette succulent. Steep north-facing beach cliffs bordering Todos Santos Bay. Known otherwise only from Todos Santos and Los Coronados Islands.

Dudleya attenuata (S. Wats.) Moran ssp. *orcuttii* (Rose) Moran. Rosette succulent. Common on dry slopes. Transition-zone endemic.

D. brittonii D. A. Johansen. Rosette succulent. Common and conspicuous in open vegetation and rocky areas on south-facing slopes. A more or less glaucous form occurs locally with the more common non-glaucous form in three areas: two populations on steep north-facing rocky slopes and a third in sand on Playa del Punta Banda. Transition-zone endemic.

D. campanulata Moran. Rosette succulent. Local endemic occurring only on the south side of the peninsula on large sea stacks and on igneous ridges west of La Bufadora.

D. lanceolata (Nutt.) Britt. & Rose. Rosette succulent. Locally common on arroyo banks. On Punta Banda, near the southern limit of the species, it appears to be restricted to sedimentary formations; elsewhere it occurs on a variety of substrata.

D. × *semiteres* (Rose) Moran. Rosette succulent. Apparently a recurrent natural intersubgeneric hybrid between *D. attenuata* ssp. *orcuttii* and *D. brittonii*. Infrequent; observed in several places with the putative parent species. Transition-zone and insular endemic.

Cucurbitaceae

Marah macrocarpus (Greene) Greene. Herbaceous vine with large perennial root stock. Occasional on bare ground and climbing by tendrils among shrubs.

Euphorbiaceae

Acalypha californica Benth. Malacophyllous shrub or subshrub. Infrequent on south-facing slopes.

Eremocarpus setigerus (Hook.) Benth. Annual. Common roadside and old field weed.

Euphorbia misera Benth. Malacophyllous semi-succulent shrub. Frequent on south-facing slopes, rocky places, and beach cliffs.

E. polycarpa Benth. var. *polycarpa*. Herbaceous perennial. Fire successional species on granite. Frequent on open slopes. Apparently flowers the first year.

E. spathulata Lam. Annual. Infrequent in disturbed habitats.

Fabaceae

Astragalus didymocarpus H. & A. Annual. Grassy places.

A. sanctorum Barneby. Herbaceous perennial, known only from Banda Peak where it was discovered by Reid Moran.

Astragalus trichopodus (Nutt.) A. Gray var. *lonchus* (Jones) Barneby [=*Astragalus trichopodus* ssp. *leucopsis* (T. & G.) Thorne]. Herbaceous perennial. Common, especially in disturbed areas.

Lathyrus laetiflorus Greene ssp. *glaber* C. L. Hitch. Herbaceous perennial vine. Common among shrubs in arroyos. Variable, especially in leaf characters; leaflets range from linear to oblong or elliptic. The subspecies is a transition-zone endemic.

Lotus hamatus Greene. Annual. Common.

L. salsuginosus Greene. Annual. Dry slopes.

L. cf. *strigosus* (Nutt. in T. & G.) Greene. Annual. (May be *L. subpinnatus* Lag.)

L. watsonii (Vasey & Rose) Greene. Common weak stemmed perennial. Transition-zone endemic. Usually growing in other shrubs. Similar to *L. scoparius* but with pedunculate umbels.

Lupinus agardhianus Heller. Annual.

L. bicolor Lindl. ssp. *microphyllus* (S. Wats.) D. Dunn. Annual.

L. concinnus J. G. Agardh. Annual.

L. hirsutissimus Benth. Annual.

L. longifolius (S. Wats.) Abrams. Herbaceous perennial, subshrub. Bluffs on north slope of the peninsula.

L. sparsiflorus Benth. Annual.

L. truncatus Nutt. ex H. & A. Annual.

**Medicago polymorpha* L. Annual.

**Melilotus indicus* (L.) All. Annual.

**M. officinalis* (L.) Lam. Annual.

Trifolium gracilentum T. & G. Annual. Approaching *T. palmeri* Wats. of Santa Catalina, San Clemente, and Guadalupe Islands.

T. tridentatum Lindl. var. *aciculare* (Nutt.) McDer. Annual.

Vicia exigua Nutt. in T. & G. Annual.

Fagaceae

Quercus dumosa Nutt. Evergreen sclerophyll shrub. One local population growing on sandstone in a canyon on the north side of the peninsula west of La Joya with *Helianthemum scoparium*.

Gentianaceae

Centaurium venustum (A. Gray) Rob. Annual. Los Arbolitos.

Geraniaceae

**Erodium cicutarium* (L.) L'Her. Annual weed. Common in disturbed habitats.

**E. moschatum* (L.) L'Her. Annual weed. Common in disturbed habitats.

Hippocastanaceae

Aesculus parryi A. Gray. Summer-deciduous shrub. Common on gentle to steep slopes mostly with a northern exposure. This plant is leafless most of the year. Leaves emerge in late fall or early winter and wither in March or April when the flowers are produced (Mooney and Bartholomew, 1974).

Hydrophyllaceae

Emmenanthe penduliflora Benth. Annual.

Eucrypta chrysanthemifolia (Benth.) Greene. Annual.

Phacelia cicutaria Greene var. *hispida* (A. Gray) J. T. Howell. Robust annual. Relatively common, slopes and canyons.

P. distans Benth. Annual. Common on burns and gravelly slopes. Often growing in shrubs.

P. hirtuosa A. Gray. Annual. Transition-zone endemic. Closely related to *P. cedrosensis* Rose.

P. ixodes Kell. Viscid herbaceous to suffrutescent perennial. Probably flowering the first year. Occasional, rocky places. Transition zone and Baja California Islands including Todos Santos, Cedros, and San Martín. This species is close to *P. lyonii* Gray, endemic to San Clemente and Santa Catalina islands.

P. parryi Torr. Common on dry slopes and in burned areas.

Pholistoma racemosum (Nutt.) Const. Annual. Infrequent on moist slopes.

Lamiaceae

Hyptis emoryi Torr. A typical Sonoran Desert wash shrub that may occur or did occur at La Joya (*fide* Reid Moran). This species was reported from Punta Banda by Hastings et al. (1972) based on a specimen collected by C. F. Harbison (SD).

**Marrubium vulgare* L. Malacophyllous subshrub. Short-lived weedy perennial; common.

Salvia apiana Jeps. Malacophyllous shrub. Occasional on granitic soil on ridge of peninsula east of Los Arbolitos.

S. munzii Epl. Malacophyllous shrub. Common on benches and slopes, sometimes forming nearly pure stands. Transition-zone endemic.

Malvaceae

Malacothamnus fasciculatus (Nutt.) Greene. Malacophyllous shrub. Occasional in chaparral. Fruits extensively damaged by insect larvae.

**Malva parviflora* L. Annual weed.

Sphaeralcea fulva Greene. Locally common in sandy, disturbed soil as near Los Arbolitos. Transition-zone endemic.

Myrtaceae

**Eucalyptus camaldulensis* Denhardt. Evergreen tree. Occurs in an old grove at Los Arbolitos (whence the place name). Probably able to persist through interception of moisture from frequent fogs.

Nyctaginaceae

Mirabilis californica A. Gray. Malacophyllous subshrub. Variable, with some individuals ± woody well above the base, others strictly herbaceous above perennial root. Common in open vegetation, mostly on south-facing slopes.

Oleaceae

Fraxinus trifoliata (Torr.) Lewis & Epl. (=F. *dipetala* H. & A. var. *trifoliata* Torr.). Winter-deciduous shrub to low tree. Common on north-facing slopes and canyon sides.

Onagraceae

Camissonia californica (Nutt. ex T. & G.) Raven (=*Eulobus californica* Nutt. ex T. & G.; *Oenothera leptocarpa* Greene). Annual. Los Arbolitos trail to beach and on north slope near tip.

C. robusta Raven. Annual. Common in disturbed habitats.

Clarkia epilobioides (Nutt.) Nels. & Macbr. Annual. Knoll north of Los Arbolitos, and on north slope near tip.

Oxalidaceae

Oxalis californica (Abrams) Kunth. Herbaceous perennial. Occasional in rocky openings in chaparral.

Papaveraceae

Eschscholzia californica Cham. Annual or herbaceous perennial.

Platystemon californicus Benth. Annual. Locally common on mesic slopes.

Stylomecon heterophylla (Benth.) G. Tayl. Annual. Locally common on mesic slopes.

Plantaginaceae

Plantago erecta Morris ssp. *erecta*. Annual. Dry open places.

Polemoniaceae

Gilia angelensis V. Grant. Annual. Common in grassy places.

Linanthus dianthiflorus (Benth.) Greene. Annual. Locally common on flats and gentle slopes.

Navarretia hamata Greene ssp. *leptantha* (Greene) Mason. Annual. Dry rocky slopes.

Polygonaceae

Chorizanthe procumbens Nutt. Annual. Dry open places.

Eriogonum fasciculatum Benth. ssp. *fasciculatum.* Needle-leaved semi-sclerophyllous shrub. Common on both sides of the peninsula. On steep, windswept, south-facing slopes it has a ground hugging form with tiny leaves; on the steep north-facing slopes of Banda Peak it is a robust, woody shrub.

E. grande Greene var. *testudinum* Reveal. Suffrutescent perennial. Transition-zone and insular endemic. Rocky cliffs near the ocean on both sides of the peninsula. Otherwise known from S. Todos Santos Island.

Pterostegia drymarioides F. & M. Weak, prostrate annual. Mostly in shady places associated with rocks.

Portulacaceae

Calandrinia ciliata (R. & P.) DC. var. *menziesii* (Hook.) Macbr. Annual. With herbaceous vegetation.

C. maritima Nutt. Succulent annual. In openings between shrubs on sandy or gravelly soils.

Claytonia perfoliata Donn [=*Montia perfoliata* (Donn) T. J. Howell]. Annual. In canyons and on vernally moist banks adjacent to Los Arbolitos. Both the varieties *parviflora* (Dougl.) J. T. Howell and *perfoliata* are present.

Primulaceae

Dodecatheon clevelandii Greene ssp. *clevelandii.* Herbaceous perennial. Relatively common on mesic slopes in chaparral.

Ranunculaceae

Clematis pauciflora Nutt. in T. & G. Herbaceous perennial vine. Occasional growing over chaparral shrubs.

Delphinium parryi A. Gray. Herbaceous perennial. Infrequent. Collected once on the north slope of Punta Banda Peak at ca. 100 m.

Resedaceae

Oligomeris linifolia (Vahl.) Macbr. Annual. Common.

Rhamnaceae

Ceanothus spinosus Nutt. Malacophyllous shrub. Rare on peninsula. Isolated plants in dense chaparral in arroyos on north side of peninsula.

C. verrucosus Nutt. Evergreen sclerophyllous shrub. Local in chaparral, occurring in dense stands often associated with *Adenostoma fasciculatum* on the north side of the peninsula. Transition-zone endemic.

Rhamnus insula Kell. Evergreen sclerophyllous shrub. Frequent on hillsides and in arroyos in chaparral. Transition-zone and insular endemic.

Rosaceae

Adenostoma fasciculatum H. & A. Evergreen sclerophyllous shrub. Locally dominant, occurring in nearly pure stands on the crests of certain hills along the peninsula, on gentle north-facing slopes on sandstone west of La Joya and on the north slope of Banda Peak. Associated with *Eriogonum fasciculatum, Cneoridium dumosum,* and *Ceanothus verrucosus*. Many stunted stands are exposed to fog or moisture-laden air and grow in shallow, rocky, apparently poor soils derived from sedimentary rock.

Heteromeles arbutifolia M. Roem. Evergreen sclerophyllous shrub. Occasional in chaparral on north-facing slopes and in arroyos.

Rubiaceae

Galium angustifolium Nutt. Subshrub; quite woody. Common among shrubs.

G. nuttallii A. Gray ssp. *nuttallii*. Suffruticose clamberer among shrubs.

Rutaceae

Cneoridium dumosum (Nutt.) Hook. f. Evergreen malacophyllous shrub. Frequent in open chaparral. Transition-zone endemic.

Ptelea aptera Parry. Winter-deciduous woody shrub. North-facing slopes in chaparral. Transition-zone endemic.

Salicaceae

Salix lasiandra Benth. Winter-deciduous tree. Several on sandstone in arroyo near La Joya.

Saxifragaceae

Jepsonia parryi (Torr.) Small. Herbaceous perennial. Shaded slopes and banks. Only a few individuals were observed until the spring of 1973, when hundreds were found. The corm-like rootstocks can clearly persist for several years without sending up leaves.

Lithophragma affine A. Gray ssp. *mixtum* R. L. Taylor. Herbaceous perennial. Uncommon; steep north-facing slopes or shaded banks.

Ribes malvaceum Sm. var. *viridifolium* Abrams. Evergreen malacophyllous shrub. Infrequent on north-facing slopes in chaparral.

R. tortuosum Benth. Malacophyllous shrub. Occasional in open chaparral or coastal sage scrub. Deciduous; with flowers appearing before leaves. Transition-zone and insular endemic.

R. viburnifolium A. Gray. Evergreen procumbent shrub. Common, mostly on north-facing slopes, among shrubs and in arroyos. Transition-zone and insular endemic.

Scrophulariaceae

Antirrhinum nuttallianum Benth. in DC. Annual. Among herbs and shrubs.

Castilleja foliolosa H. & A. Suffrutescent perennial root-hemiparasite. Infrequent in chaparral.

C. jepsonii Bacig. & Heckard. Herbaceous perennial root-hemiparasite. Frequent among shrubs.

Collinsia heterophylla Buist ex Grah. Annual. Vernally moist shaded banks.

Cordylanthus orcuttianus A. Gray. Annual root-hemiparasite. Flowers in late spring and summer. Usually occurs with herbaceous vegetation. Transition-zone endemic.

Galvesia juncea (Benth.) Ball. Stem-photosynthetic shrub. Infrequent in dry places, heavily browsed. Occurs in both viscid puberulent and glabrous, sometimes glaucous, forms. Transition-zone and insular endemic.

Linaria canadensis (L.) Dum-Cours. var. *texana* (Schelle) Penn. Grassy places with other herbs.

Mimulus aurantiacus Curt. ssp. *australis* (McMinn.) Munz. Malacophyllous shrub. Frequent on north-facing slopes and in arroyos.

Orthocarpus purpurascens Benth. Annual root-hemiparasite. Grassy places with other herbs.

Solanaceae

Lycium brevipes Benth. Woody shrub. Common, on alluvial soils and sandstone.

L. californicum Nutt. Leaf succulent shrub. Sea bluffs.

Nicotiana clevelandii A. Gray. Annual. In scattered populations mostly on flats or gentle slopes.

**N. glauca* Grah. Malacophyllous shrub. Infrequent weed. Sometimes in dense stands.

Physalis crassifolia Benth. Perennial herb. On Punta Banda (*fide* Reid Moran).

Physalis greenei Vasey & Rose. Annual. Collected once in sandy bottom of deep arroyo on southwest side near tip.
Solanum douglasii Dunal. Weak malacophyllous subshrub. Disturbed habitats.
S. xanti A. Gray var. *intermedium* Parish. Malacophyllous subshrub. Principally in disturbed habitats.

Urticaceae

Hesperocnide tenella Torr. Annual. Occurs in patches on shaded, seasonally damp banks.

ANTHOPHYTA—MONOCOTYLEDONEAE

Agavaceae

Agave shawii Engelm. Rosette succulent. Common and conspicuous in rocky places, dry flats, and south-facing slopes.

Amaryllidaceae

Allium praecox Bdg. Herbaceous perennial. Infrequent on north-facing grassy slopes.
Dichelostemma pulchella (Salisb.) Heller. [=*Brodiaea pulchella* (Salisb.) Greene]. Herbaceous perennial. Common on grassy slopes and among shrubs.

Liliaceae

Calochortus splendens Dougl. ex Benth. Herbaceous perennial. Uncommon on flats and gentle slopes in heavy soils.
Zygadenus fremontii Torr. Herbaceous perennial. Rare on peninsula, north slope of Banda Peak at ca. 120 m.

Poaceae

Agrostis sp. Perennial. Represented by a single sterile specimen.
**Avena barbata* Brot. Annual.
Bothriochloa barbinodis (Laq.) Herter. Perennial.
**Bromus arenarius* Labill. Annual.
**B. mollis* L. (=*B. hordeaceus* L.) Annual.
**B. rubens* L. Annual.
B. trinii Desv. Annual.
**Cynodon dactylon* (L.) Pers. Perennial. Weed at La Joya.
Elymus condensatus Presl. Semi-woody perennial. Frequent on arroyo banks and steep north-facing slopes in chaparral.
**Hordeum leporinum* Link. Annual.
**Lamarckia aurea* (L.) Moench. Annual. Waste places as at Los Arbolitos.

Melica frutescens Scribn. Herbaceous perennial. Common on open slopes.

M. imperfecta Trin. Herbaceous perennial.

Monanthochloë littoralis Engelm. Perennial. Old fields near Los Arbolitos.

Muhlenbergia microsperma (DC.) Kunth. Annual.

Poa scabrella (Thurb.) Benth. ex Vasey. Herbaceous perennial. Uncommon, hillsides among shrubs.

**Schismus barbatus* (L.) Thell. Annual.

**Setaria verticillata* (L.) Beauv. Annual.

Stipa cernua Steb. & Love. Herbaceous perennial.

S. coronata Thurb. in Wats. var. *depauperata* (Jones) Hitchc. Herbaceous perennial.

S. pulchra Hitchc. Herbaceous perennial.

S. diegoensis Swall. Herbaceous perennial. Upper slopes of Banda Peak and near La Bufadora.

**Vulpia megalura* (Nutt.) Rydb. Annual.

**V. myuros* (L.) K. C. Gmelin. Annual.

V. octoflora (Walt.) Rydb. Annual.

Zosteraceae

Phyllospadix scouleri Hook. Herbaceous perennial. Surf-beaten rocky shores.

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THE TAXONOMIC STATUS OF GILIA CAESPITOSA (POLEMONIACEAE)

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ABSTRACT

The status of the rare Utah endemic, *Gilia caespitosa* A. Gray (Polemoniaceae) was evaluated with respect to morphological and chromosomal data. The possession of a concolorous corolla with included to barely exserted anthers, zonocolporate, reticulate pollen and a chromosome number of $2n = 16$ are a combination of characters which suggest a relationship to *G. subnuda* A. Gray and allies within sect. *Giliandra* A. Gray. However, the possession of a perennial habit, multicipital caudex and graduated entire leaves characterize *G. caespitosa* as a distinct taxon.

The binomial *Gilia caespitosa* A. Gray has had an interesting taxonomic history leading to temporary obscurity. Nelson (1898) elevated *Gilia pungens* Benth. var. *caespitosa* A. Gray (basionym = *Leptodactylon caespitosum* Nutt.) to specific status under *Gilia* and proposed *G. grayi* as a substitute for Gray's earlier name. Nelson's binomial represents a nomenclatural synonym. Brand (1907) apparently misinterpreted the adherence of fine sand grains to the glandular hairs as "calcareo-glandulosis", concluded that this was "abhorret" within Polemoniaceae and without further comment suggested an affinity to the Saxifragaceae. This treatment was later followed by Grant (1959). *Gilia caespitosa* was rediscovered through recent botanical studies in southcentral Utah and its status as a rare taxon was recently reviewed (Welsh et al., 1975). The apparent restriction of *Gilia caespitosa* to the vicinity of the type locality and a combination of morphological characters unique within *Gilia* provide the justification for this paper.

METHODS

Flowers, seeds, and a voucher specimen were collected 1.6 km south of Teasdale, Wayne Co., UT, currently the only known locality for the species. Seeds were germinated for determination of chromosome number using the Feulgen technique. Pollen was removed from anthers, vapor-coated with gold and examined on a Hitachi HHS-2R SEM. Additional specimens of *Gilia caespitosa* and putatively related taxa were examined through the courtesy of COLO, CS, GH, NY, RM, RSA, UC, and UTC.

RESULTS AND DISCUSSION

Gilia caespitosa was first collected by L. F. Ward in "Rabbit Valley, Utah" in 1875. Rabbit Valley includes the upper Fremont River drainage and the locality near Teasdale (Anonymous, 1952). Two specimens of the Ward collection are at GH and are annotated in Gray's handwriting. However, both specimens lack corollas and well-developed fruits. One of these specimens clearly matches the protologue and includes the designation "*Gilia* (*Ipomopsis*?) *caespitosa* n. sp." Associated with the latter specimen is a note signed by Ward. The note includes the pertinent statements "corolla . . . is clearly monopetalous", "the ovary is 3-valved and 3-celled", and "I . . . believe the plant to belong to the Polemoniaceae." If Gray had any unpublished doubts regarding the taxonomic identity of the Ward collection, they were apparently dispelled by Ward's recorded observations, these being associated with the type collection.

The following treatment is presented as a more complete description of the taxon.

GILIA CAESPITOSA A. Gray, Proc. Amer. Acad. Arts 12:80. 1876.—*Gilia grayi* A. Nelson, Bull. Torrey Bot. Club 25:547. 1898. nom. superfl., illegit. (Substitute for *Gilia caespitosa* A. Gray).—TYPE: "Rabbit Valley, Utah, on barren cliffs of sandstone, at 7000 feet, L. F. Ward, in Powell's Expedition, 1875." (GH!).

Caespitose perennial, the underground woody caudex with few to numerous stems 4–30 cm tall. Basal and lower leaves densely crowded, spatulate to obovate, entire, 4–15 mm long, 2–4 mm wide, densely glandular-pubescent, in most specimens appearing grayish because of adherence by light-colored, fine sand. Upper leaves reduced, entire, lanceolate to narrowly spatulate, glandular, 3–6 mm long, to 2 mm wide. Flowers 1–5 in loose, cymose clusters. Pedicels 2–5 mm long. Calyx glandular-pubescent, 4–5 mm long at anthesis, lobes 1.5–2 mm long at anthesis, up to 3 mm in fruit, the tips minutely mucronate, the narrow sinuses hyaline. Corolla funnelform, red to pink throughout, the tube 9–17 mm long, lobes 4–6 mm long, 3–4 mm wide, the exterior surface of the lobes with glandular trichomes. Anthers included to barely exserted, these 8–12 mm above the base of the tube, filaments slightly unequally inserted. Style 9–11 mm long. Ovary with 1–2 ovules per locule, the mature fruit about 4 mm long. Seeds to 1 mm long, narrowly elliptical, angular and slightly mucilaginous when wet.

Distribution. Crevices and small outcrops of decomposing, white sandstone at the margin of a pinyon-juniper-sagebrush community at 2100–2600 m, 1.6 km south of Teasdale, Wayne Co., Utah. June–July.

Representative specimens: 10 June 1947, *Ripley & Barneby 8607* (NY,UTC); 23 June 1964, *Clark 4* (CS, UTC); 4 July 1965, *Holmgren 2138* (CS, NY, UTC); 7 July 1976, *Wilken 12,685* (CS).

The perennial habit, glandular vestiture, reduced upper leaves, and

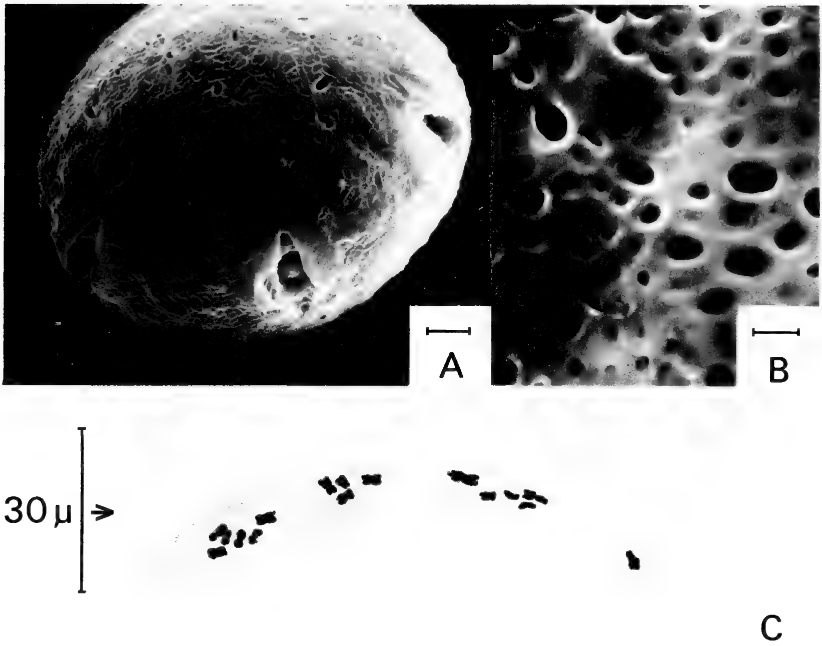

FIG. 1. Pollen grain morphology and chromosome number of *Gilia caespitosa*. A. Pollen grain. Bar = 4 μm. B. Pollen grain. Bar = 2 μm. C. Mitotic root-tip cell showing 16 chromosomes.

funnelform, concolorous corolla are a combination of characters found within sect. *Giliandra* Gray (Grant, 1959). Entire basal leaves are known in a number of annual taxa elsewhere in *Gilia* but are rare in perennial species of *Gilia*. I have seen entire leaves among some specimens of *G. pentstemonoides* Jones and the biennial *G. subnuda* Gray. Entire leaves were described in the otherwise poorly known *G. sedifolia* Brandegee. The corollas of *G. pentstemonoides,* however, are blue with conspicuously exserted stamens. The reddish, concolorous corollas and included to barely exserted anthers of *G. caespitosa* also are found in *G. subnuda* and most if not all conspecific allies (i.e., *G. crandallii* Rydberg, *G. haydenii* Gray, *G. montezumae* Tidestrom & Dayton, *G. superba* Eastwood). Morphological differences between *G. caespitosa* and *G. subnuda* are summarized in Table 1.

Surveys of polemoniaceous pollen (Stuchlik, 1967; Taylor and Levin, 1975) offer the opportunity to examine relationships among *G. caespitosa* and putative relatives. The pollen grains of *G. caespitosa*

TABLE 1. MORPHOLOGICAL DIFFERENCES BETWEEN *Gilia caespitosa* AND *Gilia subnuda*. Character states given for *G. subnuda* generally apply to close if not conspecific allies, including *G. crandallii, G. haydenii, G. montezumae,* and *G. superba.* Similarities among these taxa are discussed in the text.

Character	*G. caespitosa*	*G. subnuda*
Habit	perennial	annual to biennial, monocarpic
Caudex	multicipital from a woody base	1 to few from the basal rosette
Leaves	gradually reduced above the basal rosette	abruptly reduced above the conspicuous basal rosette
Leaf Margin	lower and upper leaves entire	lower leaves pinnatifid to rarely entire; upper leaves entire

(Fig. 1A, 1B) are zonocolporate with (4)5(6) slightly sunken colps and an oblate spheroidal shape (polar diam. 42–49 μm; equatorial diam. 46–54 μm). The exine is 2–3 μm thick and the sexine is reticulate with muri to 2 μm wide. Most *Gilia* pollen grains are zonocolporate with either striato-reticulate or pertectate sexines. A zonocolporate, reticulate pollen was described only for *G. subnuda* (Stuchlik, 1967).

Root tip preparations of *G. caespitosa* revealed a chromosome number of $2n = 16$ (Fig. 1C). Within *Gilia* this chromosome number has been reported for only four taxa, all of these being in sect. *Giliandra*: *G. micromeria* A. Gray, *G. pentstemonoides* Jones, *G. pinnatifida* Nuttall, and *G. subnuda* A. Gray (Grant, 1959).

A consideration of chromosome number and floral, vegetative, and pollen morphology strongly indicates a relationship among *G. caespitosa* and taxa within sect. *Giliandra,* particularly *G. subnuda* and its allies. This relationship was first suggested without explanation by Gray (1886) whereas Rydberg (1917), emphasizing the perennial habit, implied a relationship among *G. caespitosa, G. pentstemonoides,* and *G. sedifolia.* However, with a perennial habit, multicipital caudex, and graduated, entire leaves, *G. caespitosa* clearly represents a well-defined taxon and may represent one of the more primitive elements within sect. *Giliandra.* The significance of this species to future studies of systematic relationships within sect. *Giliandra* and the intricate phylogenetic patterns within *Gilia* provide a strong argument for protection of *G. caespitosa.*

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CHROMOSOME NUMBERS IN ANNUAL LINANTHUS SPECIES

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Abstract

Chromosome numbers are reported for nineteen species of *Linanthus,* of which 15 are new counts. These establish further the base chromosome number for the genus as $x = 9$. Based on these counts, polyploidy appears to be extremely rare in annual species of *Linanthus*.

Chromosome numbers of all 19 genera of the Polemoniaceae have been determined since the initial work of Flory (1937). Certain genera have been studied chromosomally in some detail, including *Gilia* (Grant, 1950, and papers following), *Phlox* (Smith and Levin, 1967), *Ipomopsis* (Grant, 1956), and *Allophyllum* (Grant and Grant, 1955). Other genera in the family consist of so few species that chromosome numbers are known for all, e.g. *Gymnosteris* (McMillan, 1949; Grant, 1959) and *Microsteris* (Mason, 1941; Kinch, 1956). There are, however, genera that are relatively unknown chromosomally, with counts being restricted to a small percentage of their species. The predominantly Californian genus *Linanthus* is one example. Among 42 species, only thirteen have had chromosome numbers determined (Flory, 1937; Heuther and DeJong, 1970; Hartman and Crawford, 1971; Patterson, 1977). In this paper I present chromosome numbers for 19 species of *Linanthus* (15 of them first reports), and discuss the results in terms of their bearing on the systematics of the family.

Methods

Members of 19 species of *Linanthus* were surveyed chromosomally from collections made during the spring and summer of 1977 and 1978. Floral buds were collected in the field and fixed in Newcomer's fixative. Preparations were made according to the method of Beeks (1955) and stained with aceto-carmine. All counts were made from microsporocytes during diakinesis or metaphase I. Voucher specimens have been deposited at UCSB.

Results

All of the populations examined possessed a chromosome number of $2n = 18$ (Table 1). There appeared to be some difference in size of chromosomes among different species, but the course of meiosis appeared normal in all samples. Populations examined chromosomally are listed in Table 1.

TABLE 1. TAXA OF ANNUAL *Linanthus* EXAMINED CHROMOSOMALLY. All taxa were $2n = 18$, and all collections are from California. Patterson collections are abbreviated to P. Asterisk denotes taxa for which chromosome numbers are previously unreported. Voucher specimens are in UCSB.

Sect. *Dactylophyllum*

**L. ambiguus* (Rattan) Greene. San Benito Co., Clear Creek, *P & P 1279*; Hernandez Road, *P & P 1281*.

L. aureus (Nutt.) Greene subsp. *aureus*. San Bernardino Co., Camp Rock Road, *P 1159*; Old Woman Springs Road, *P & P 1247*. Kern Co., Kelso Creek Road, *P 1174*. Inyo Co., Lone Pine Creek Campground, *P 1260*.

**L. aureus* (Nutt.) Greene subsp. *decorus* (Gray) Jeps. San Bernardino Co., Morongo Valley, *P & P 1155*.

**L. filipes* (Benth.) Greene. Madera Co., Bass Lake, *P & P 1034*. Tulare Co., Coffee Campground, *P 1290*.

**L. lemmonii* (Gray) Greene. Riverside Co., 13 km S of Corona, *P & Howald 1234*.

**L. liniflorus* (Benth.) Greene. Monterey Co., Memorial Campground, *P 1167*; Camp Hunter-Liggett, *P & P 1285*.

**L. pygmaeus* (Brand) J. T. Howell subsp. *continentalis* Raven. San Benito Co., Clear Creek, *P & P 1280*.

Sect. *Dianthoides*

**L. demissus* (Gray) Greene. Inyo Co., Saline Valley Road, *P 1259*.

L. dianthiflorus (Benth.) Greene. Santa Barbara Co., Los Prietos Campground, *P & Tanowitz 1231*.

**L. parryae* (Gray) Greene. San Bernardino Co., Mojave-Randsburg Road, *P 1254*. Inyo Co., Lone Pine Creek Campground, *P 1261*.

Sect. *Leptosiphon*

**L. androsaceus* (Benth.) Greene subsp. *luteolus* (Greene) Mason. San Diego Co., Sunrise Highway, *P, Mason, Trager, & Nemzer 1304*; S of Laguna, *P, Mason, Trager, & Nemzer 1309*; Palomar Mountains, *P, Mason, Trager, & Nemzer 1311*.

L. androsaceus (Benth.) Greene subsp. *micranthus* (Steud.) Mason. San Luis Obispo Co., Friis Campground, *P 1164*. Monterey Co., Memorial Campground, *P 1166*; Parkfield, *P & P 1276*.

**L. bicolor* (Nutt.) Greene. Madera Co., Bass Lake, *P & P 1036*. Kern Co., Bodfish-Caliente Road, *P 1292*.

**L. breviculus* (Gray) Greene. Los Angeles Co., Table Mountain Campground, *P, Mason, Trager, & Nemzer 1315*; West of Bigpines, *P, Mason, Trager, & Nemzer 1316*.

L. ciliatus (Benth.) Greene var. *ciliatus*. Santa Barbara Co., Los Prietos Campground, *P & Tanowitz 1233*. Kern Co., Rancheria Road, *P 1171*. Madera Co., Bass Lake, *P & P 1061*. Tuolumne Co., W of Dodge Ridge, *P, Mason, Allen, & Santarosa 1320*. San Benito Co., Hernandez Road, *P & P 1282*.

* *L. ciliatus* (Benth.) Greene var. *neglectus* (Greene) Jeps. Mono Co., E of Sonora Pass, *P, Mason, Allen, & Santarosa 1322*.

L. montanus (Greene) Greene. Madera Co., Bass Lake, *P & P 1035*. Tulare Co., Balch Park Road, *P 1286*.

**L. nudatus* Greene. Tulare Co., Troy Meadows, *P, Wall, & Ikeda 1190*; Fish Creek, *P, Smith, & Steele 1215*; Sherman Pass Road, *P 1291*.

Sect. *Pacificus*

L. grandiflorus (Benth.) Greene. Marin Co., Point Reyes, *P & Meyers 1294*.

TABLE 1. Continued.

Sect. *Linanthus*

**L. bigelovii* (Gray) Greene. San Bernardino Co., Black Rock Campground, *P & P 1246*. Tulare Co., Chimney Peak Campground, *P 1268*. Inyo Co., Lone Pine Creek Campground, *P 1262*.

L. dichotomus Benth. Kern Co., Willow Springs Road, *P 1237*. San Luis Obispo Co., E of Santa Margarita, *P 1240*; Friis Campground, *P 1241*.

**L. jonesii* (Gray) Greene. Riverside Co., Aqueduct Road, *P & P 1243*.

DISCUSSION

In his monographic study of the Polemoniaceae, Grant (1959) considered the base chromosome number of *Linanthus* to be $x = 9$. This determination was based on the earlier counts by Flory (1937) of 5 species: *L. androsaceus* subsp. *micranthus, L. aureus, L. dianthiflorus, L. dichotomus,* and *L. grandiflorus*. Although these five species represent five of the six sections of *Linanthus,* they make up only 12 percent of the species. The chromosome counts in this report, along with those of Heuther and DeJong (1970), Hartman and Crawford (1971), and Patterson (1977), constitute 57 percent of the species in the genus, thereby reinforcing the base chromosome number of *Linanthus* as $x = 9$.

Heuther and DeJong (1970), studying members of *Linanthus* sect. *Leptosiphon,* found *L. montanus* and certain populations of *L. ciliatus* to possess chromosome numbers of $2n = 16$; however, all populations of these species examined in the present study had chromosome numbers of $2n = 18$ (Fig. 1). Populations studied by Heuther and DeJong were not among those examined here. It would be worthwhile to investigate further the chromosome numbers of these two species, because the populations with $2n = 16$ might represent the beginnings of new evolutionary trends. Two other genera in the Polemoniaceae, *Allophyllum* and *Gilia,* have been shown to possess two base chromosome numbers, $x = 8$ and $x = 9$ in both cases. Hence the possibility exists that similar patterns of chromosome evolution have taken place in these three genera.

It is also noteworthy that the occurrence of polyploidy in *Linanthus* is relatively rare and restricted to two perennial species, *L. melingii* and *L. pachyphyllus* (Patterson, 1977), and one annual species, *L. ciliatus* (Heuther and DeJong, 1970). This is in marked contrast to the related genus *Gilia,* where 32 percent of the species are polyploid (Grant, 1959), and where polyploidy has played an important role in the evolution of this genus (Day, 1965; Grant, 1954a, 1954b, 1964, 1965, 1966; Grant and Grant, 1956; Grant et al., 1956). This suggests that the role of polyploidy is probably minor in the evolution of the annual species of *Linanthus*.

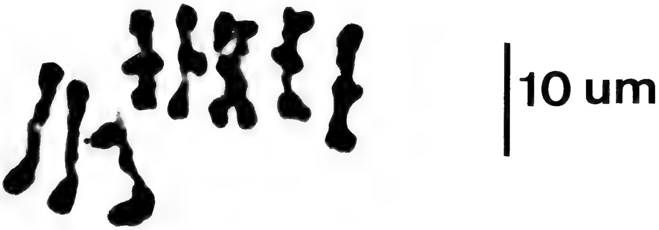

FIG. 1. Metaphase I configuration of *Linanthus ciliatus* (*Patterson & Tanowitz 1233*) showing *2n* = 9 II. Voucher deposited at UCSB.

ACKNOWLEDGMENTS

Appreciation is extended to the students in my plant taxonomy classes at Occidental College and Santa Barbara City College for their aid during collecting trips.

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(Accepted 19 Jan 1979.)

NOTEWORTHY COLLECTIONS

DISTICHLIS SPICATA var. STRICTA (Torr.) Beetle (POACEAE).—Ecuador, Galapagos Islands, Gardner Bay, Española, 12 Jan 1975, *Norman and James s.n.* (US); Feb 1977, *Falco s.n.* (Darwin Research Station Herbarium). A single population 10 m by 20 m in bare sandy area subject to occasional wave action and salt spray (Porter, pers. comm., 1978). Both specimens with ♀ inflorescences. Verified by A. A. Beetle, Jan 1978 (*Falco s.n.*).

Previous knowledge. Known from W N.A., S to Chile and in Australia (Beetle, pers. comm., 1978). Specifically excluded by Reeder and Reeder in Wiggins and Porter (*Flora of the Galapagos Islands*. 1971) because earlier report was based on misindentification.

Significance. 800 km disjunction. Probably recent introduction to the archipelago. Perhaps only ♀ plants present.—ELIANE M. NORMAN, Department of Biology, Stetson University, DeLand, FL 32720. (Accepted 31 Mar 79.)

CROSSOSOMA CALIFORNICUM Nutt. (CROSSOSOMATACEAE).—USA, CA, Los Angeles Co., Palos Verdes Peninsula, Rancho Palos Verdes, 33°44′22″N, 118°20′45″W, 5 Dec 1977, *Henrickson 16341* (RSA, CSLA) in fruit; 10 Jan 1979, *Henrickson 17810* (CAS, CSLA, RSA, SB) in flower. Two plants observed at ca. 175 m, ca. 165 m NE of Forrestal Dr., NE of Ladera Linda Elementary School at base of granitic NW-facing slope at mouth of steep abandoned granite quarry. Lower plant ca. 2.4 m high, 2.2 m wide, upper plant ca. 2.5 m high, 3.5 m wide with basal stem to 54 mm. In coastal sage scrub vegetation with *Artemisia californica, Rhus integrifolia, Salvia mellifera, Eriogonum cinereum, Dudleya lanceolata,* and *Galium angustifolium* var. *angustifolium*.

Previous knowledge. Known only from 3 Channel ids.: San Clemente Id. where rare in 1 population on W slope at 460 m (Raven, Aliso 5:289–347. 1963); Santa Catalina Id. where common from 5–490 m (Thorne, Aliso 6(3):1–77. 1967); and Guadalupe Id. where rare and now restricted to rocky, inaccessible exposures from 50 to 950 m. It also occurs on Outer Islet, a small rocky island at the S end of Guadalupe Id. not inhabited by goats. (Moran, pers. com.)

Significance. First record from mainland USA, however, it must be noted that "the Palos Verdes Hills area was an island itself until joined to the mainland during the Quaternary (Pleistocene or Recent)" (Valentine and Lipps, *In* Philbrick, Proc. Symp.

Biol. Calif. Islands. 1967). Thorne (pers. com.) notes *C. californicum* often establishes on exposed slippage slopes in open soil. These two specimens may date from disturbances associated with quarrying in the 1940's. Whether population is relictual or derived from those on Santa Catalina Id. (ca. 34 km away—perhaps by seeds dispersed to mainland by birds or possibly man) is not known. No other intentionally cultivated plants occur near the site. Specimens from Palos Verdes exhibit no noticeable morphological divergence from other known populations. The general area is slated for development though this specific area will not be disturbed. Size of family has dramatically increased from only 1 genus with 2–3 species to 3 genera with 11–13 species with description of *Apacheria chiricahuensis* Mason (Madroño 23:105–108. 1975) and the transfer of *Forsellesia* Greene with ca. 8–9 species from the Celastraceae to Crossosomataceae (Thorne, Aliso 9:171–178. 1978).—JAMES HENRICKSON, Department of Biology, California State University, Los Angeles 90032. (Accepted 2 Apr 79.)

PHYSALIS LOBATA Torr. (SOLANACEAE).—USA, CA, San Bernardino Co., Clark's Pass (T15 R14E S17 SE¼), 25 Nov 1975, *Jones, Ericson, Colin, and Overman 23* (MACF, UC). Common in sink area just E of Clark's Pass, off hwy 62, ca. 47 km E of Twenty-Nine Palms, 580 m; soil primarily decomposed granite. Flowers sporadically all year with rains, peak flowering Sep–Jan, fruits Oct–Mar. Root perennial, numerous seeds. Verified by Robert Thorne, 1976. Other specimens: San Bernardino Co., 8 km N of Clark's Pass, N side Sheep Hole Mtns in alkaline dry lake, 11 Apr 1976, *Shade s.n.* (UCR); San Bernardino Co., Homer Wash, 28 km SE of Essex and 35 km SW of Needles (Stepladder Mtns 15′ Quad.), 6 Apr 1978, *Twitchell and Sanders s.n.* (BLM desert plan collections).

Previous knowledge. Range: KS to TX, S NV, AZ, and N Mex. Nearest records in Maricopa, Pinal, and Pima cos., AZ (Kearney and Peebles, *Arizona Flora*. 1960). (Herbaria consulted: MACF, UCR, RSA). *Diagnostic characters*—fls violet to purple, rarely white, central eye of corolla white, anthers yellow; lvs long-petioled, cuneate at base, sinuately denticulate to dentate.

Significance. New to California; 160 km disjunction. Apparently bird disseminated and establishing westward. Referred by some botanists to *Quincula lobata* Raf., because it differs from other species of *Physalis* by having a violet to purple corolla and a lobed stigma.—C. EUGENE JONES, LARRY J. COLIN, TRUDY R. ERICSON, and R. JOHN LITTLE, Department of Biological Science, California State University, Fullerton 92634; and ANDREW SANDERS, Biology Department, University of California, Riverside 92521. (Accepted 4 Feb 1978.)

NOTES AND NEWS

SEED ABORTION IN *Anagallis arvensis* ON SOUTHEAST FARALLON ISLAND, CALIFORNIA.—Seed mortality in the period between pollination and maturation is difficult to measure and its significance in plant life histories has often been ignored. Because pollination efficiency is usually unknown, seed set is an unsatisfactory measure of pre-maturation seed mortality. For self-pollinating species the problem of pollination efficiency is reduced. If one can count the number of apparently viable seeds shortly after flowering then, by comparing this with the number of seeds matured, one can obtain an estimate of seed mortality.

During the springs and summers of 1974 and 1975, I investigated the pre-maturation seed mortality in *Anagallis arvensis* L. (Primulaceae), a self-pollinating (Fryxell, Bot.

Rev. 23:135–233. 1957), annual species, on Southeast Farallon Island, San Francisco County, California. I counted the number of filled seeds in green capsules about ten days after flowering and compared this with the number of matured seeds in brown capsules about three or more weeks later.

The coast of California has a Mediterranean climate with a winter wet season and a summer dry season. *Anagallis arvensis* flowers from mid-winter (wet season) to early summer (dry season). Because I thought seasonal variation would affect seed mortality, I performed counts in winter and in summer.

Pre-maturation seed mortality (Table 1) rose from -1.2 percent ($t = 0.24$, $n = 24$, $p > 0.1$) in March, 1975, to 18 percent ($t = 2.07$, $n = 24$, $0.1 > p > 0.05$) by June, 1975. There was a simultaneous decrease in the average number of seeds per green capsule from 40 to 30, a decline of 25 percent ($t = 4.55$, $n = 29$, $p < 0.001$). Total seed production over this period fell by 39 percent, of which somewhat less than half was due to seed mortality and the remainder either to a decline in ovules initiated or to mortality before my counts. Counts from July, 1974, are consistent with these trends of increase in seed mortality and decrease in seed set through the season. They suggest a conservative estimate for July seed mortality of 38 percent ($t = 5.93$, $n = 25$, $p < 0.001$). When data for the two years are combined, there is a suggested decline in seed production of up to 58 percent ($t = 13.27$, $n = 26$, $p < 0.001$), about half of which was due to pre-maturation seed mortality.

TABLE 1. SEED COUNTS FOR *Anagallis arvensis* ON SOUTHEAST FARALLON ISLAND, CALIFORNIA.

Date	Capsule Color	n	Average Number of Seeds per Capsule	s_e
23 Mar 1975	Green	10	39.9	1.95
	Brown	14	40.4	1.15
4 Jun 1975	Green	19	29.9	1.21
	Brown	5	24.6	1.96
18 Jul 1974	Green	13	26.8	1.02
19 Jul 1974	Brown	12	16.8	2.28

Two observations suggest that the decline in water availability was important in effecting these trends. First, the decline in rainfall was the most obvious seasonal change. Second, *Anagallis arvensis* acts as an annual on the islands, yet a late summer drizzle in 1974 resulted in revival and prolonged life of dying plants, a situation not observed during summers without precipitation.

Pre-maturation seed mortality is variable and high, and I suggest that seasonal variation in resource supply (in this case water) may be important in causing this mortality.

For assistance I thank R. Tasley, the U. S. Coast Guard, the Point Reyes Bird Observatory, and personnel of the Farallon Island National Wildlife Refuge. J. Church, R. Hart, D. Janzen, P. Raven, D. Reznick, A. Smith, and R. Yeaton provided helpful comments. This is contribution number 168 of the Point Reyes Bird Observatory.—
MALCOLM C. COULTER, Department of Ornithology, The American Museum of Natural History, New York, NY 10024. (Accepted 21 Dec 1978.)

Acacia glandulifera (LEGUMINOSAE): DISTRIBUTION AND CHROMOSOME NUMBER.—*Acacia glandulifera* S. Watson is an endemic to limestone hills at upper elevations (1000–2150 m) in the Chihuahuan Desert of northern Mexico. Originally described from material collected by Pringle at Carneros Pass, Coahuila (Watson, Proc. Amer. Acad. Arts 25:124–163. 1890), this species has long been thought to be restricted to that state (Britton and Rose, N. Amer. Fl. 23:77–136. 1928). Recent interest in the Chihuahuan Desert flora and renewed interest in the genus *Acacia* have led to the accumulation of specimens from E Chihuahua, NE Durango, N Zacatecas, and W Coahuila. As one Zacatecas population (El Salitre, *Shreve 9362,* GH) is only 4 km from San Luis Potosi, we may expect *Acacia glandulifera* in that state also. A list of the specimens examined is available upon request.

Seeds were collected from two populations in July, 1977 (Coahuila: 0.6 km N of Zacatecas on hwy 54, *Parfitt et al. 2320*; Zacatecas: 17 km W of Bonanza on road to Los Cedros, *Parfitt et al. 2325,* both ASU) and were later germinated to acquire root-tips for chromosome determinations. Mitosis was stopped at metaphase in saturated aqueous para-dichlorobenzene for 2–4 hours. Root-tips were fixed in 3 ethanol:1 glacial acetic acid and, after 24 hours, refrigerated. They were hydrolyzed in 1 N HCl at 60°C for 10 minutes and stained in iron-acetocarmine for 3–12 hours. Seedlings from both populations had the chromosome number $2n = 26$.

This first count for the species represents the base number for American *Acacia* (Atchison, Amer. J. Bot. 35:651–655. 1948). The apparently closely related *A. neovernicosa* Isely and *A. constricta* Bentham in A. Gray are diploid ($2n = 26$) and tetraploid ($2n = 52$), respectively (Turner and Fearing, Amer. J. Bot. 47:603–608. 1960).

I thank the curators of GH, NY, OSH, and LL for lending specimens used in part for this study. Travel to collect material for chromosome studies was funded by NSF grant DEB 77-00182 to Donald J. Pinkava and Timothy Reeves.—BRUCE D. PARFITT, Department of Botany and Microbiology, Arizona State University, Tempe 85281. (Accepted 30 Jan 1979.)

WHO WAS REDDING OF *Oxytheca reddingianum* M. E. JONES?—When Marcus E. Jones described *Oxytheca reddingianum* (Bull. Torrey Bot. Club 9:32.1882), a plant better known as *Eriogonum spergulinum* A. Gray var. *reddingianum* (M. E. Jones) J. T. Howell, he said: "dedicated to Mr. B. B. Redding, to whom we are indebted for much of our knowledge of California botany. Though his interest has been greater and his aid more substantial than that of almost any other man, his services have never yet been recognized. I therefore take this opportunity to dedicate to him this pretty little annual."

The name B. B. Redding is not a familiar one to California botany in spite of Jones' comments, and thus we present a few brief remarks on this gentleman.

Jones is not noted for his warmth or praise of his fellows (see, for example, his obituary of Edward L. Greene, Contr. W. Bot. 15:25–27. 1929), and we have been unable to discover any direct reason why Jones should have been so lavish in his praise of Redding, especially so to a person who left no (and knowing Jones perhaps that in itself may be the reason) obvious record of contributions to California botany in terms of scientific writings or collections.

Recently we have located a book dealing with him in the California State Library (a very tattered copy is in the Library of Congress). A brief review and portrait of Benjamin Barnard Redding were published by Ella Sterling Cummins (better known as Ella Sterling Mighels) in a book entitled *The story of the files, a review of Californian writers and literature* (San Francisco: Co-operative Printing Co. 460 pp.), issued under the auspices of the World's Fair Commission of California in 1893. The book was published as a result of critical acclaim the author had received from a series of newspaper articles that had appeared over a period of years discussing the newspapers, magazines, and writers that had been active during the early years of the state's history. With this lead we have discovered that Redding was indeed an imaginative and creative person, known to the members of the California Academy of Sciences as a friend of nature, to the people of Sierra and Yuba counties as their assemblyman (1853), the citizens of Sacramento as their mayor (1856), to Californians as their Secretary of State (1863–1867), and as an active contributor to *Californian Magazine* (1880–1882, later *Overland Monthly*), a noted literary publication edited by Frederick M. Somers.

Redding was born of American parents in Yarmouth, Nova Scotia, in 1824, and died in San Francisco on 21 August, 1882, some five months after Jones proposed the species. Cummins states that Redding "was a man of original mind, an investigator of economics, State resources, climatology and all practical questions of man's relation to the world he finds himself in." An example of Redding's imaginative writing style, and perhaps his passion for the natural world can be appreciated by reading the following passage from as essay published in *Californian Magazine* entitled "Fishing on the Cloud River":

> When the first of the run arrives and the fish are scarce, the ardent sportsman will climb rocks, crowd through bushes and whip pool after pool. When rewarded with a bite, he will play the fish as tenderly as if it were a maiden that he loved, and, when safely landed, bear it proudly into camp and tell the story of its capture with enthusiasm. But when the river-bed is black with the backs of the fish and every cast is rewarded with a bite, it then becomes labor and not sport. He looks back to see if he can clear the branches of the azaleas, whose gorgeous pink and white blossoms perfume the air, makes a few short casts to take out the kinks and wet the line, and then enters into that heaven where the houris are more beautiful than any pictured in the Koran. *Salmo quinnat* is the Bride of the Lammermoor, told in prose by Sir Walter Scott, very beautiful, very interesting and very matter-of-fact. But *Salmo iridea,* with its rainbow-and-silver sides, his handsome form and his delightfully aristocratic reserve, is the same story told in rich poetry and finely rendered with the aid of all Donizetti's deep harmony and charming melodies. Salmon is the practical joint of the dinner, very good and absolutely necessary to the feast, but a trout of the Cloud is the anecdote, the repartee and wit over the walnuts and the wine.

Redding wrote for several newspapers in California, among them the *Record-Union, Sacramento Bee, San Francisco Evening Bulletin, Rural Free Press,* and even Reno, Nevada's *Gazette*. While there is no direct information that Redding was responsible "for much of our knowledge of California botany", as Jones stated, it seems clear that Redding gave to his readers and friends an appreciation of nature through the use of language that would have moved the soul of even such a person as Marcus E. Jones.

In a memorial tribute to Redding offered by Robert E. C. Stearns held by the California Academy of Sciences, it was said of Redding: "He loved the breezy freedom of the hills and mountain peaks, and often climbed their slopes, for nature here he found in ample breadth." And of the man: "Here was one whose character in fine proportions stands well—form being excellent, with noble heart and great sincerity, in love with generous service for all mankind, who used his high intelligence to make things better than before and lift his fellows to a loftier plane" (quotes taken from Cummins).

Cummins reported that his son, Joseph Deighn Redding, an author and noted musician, was about to publish a book entitled *The life and writings of B. B. Redding,* but we can find no evidence that such a book was published.

We wish to thank Dr. Joseph Ewan for his comments. Publication support for this paper has been provided by the University of Maryland Agricultural Experiment Station (Scientific Article No. A2542, Contribution No. 5575).—James L. Reveal, Department of Botany, University of Maryland, College Park 20742, and Arlene H. Reveal, Mono County Library, Bridgeport, CA 93517. (Accepted 5 Jan 1979.)

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CALIFORNIA BOTANICAL SOCIETY, INC.

Officers for 1979

THE TAXONOMY OF HAZARDIA (COMPOSITAE: ASTEREAE)

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Abstract

Hazardia is treated as a distinct genus, elevated from its most recent position as a North American section of the large genus *Haplopappus*. As such, *Hazardia* includes 13 species in three sections. The closest relatives of *Hazardia* species are probably in *Haplopappus* section *Polyphylla* of South America. Members of the North American genera *Xylorhiza* and *Machaeranthera* appear to be more distantly related to *Hazardia*.

Hazardia is a genus of 13 species of mostly woody, perennial shrubs and subshrubs distributed in California and adjacent southern Oregon, southern Nevada, and northern Baja California (Fig. 1A–C). It was first designated a genus by Greene (1887), based on *Corethrogyne cana* Gray, in honor of Barclay Hazard, a California insular botanist. The most recent monograph of *Hazardia* was by Hall (1928), who relegated it to sectional rank within the large genus *Haplopappus* and suggested its closest relationships to be with *Haplopappus* sections *Isocoma* and *Ericameria* in North America and section *Polyphylla* in South America. This treatment has been followed in several major floras (McMinn, 1951; Munz, 1959; Abrams and Ferris, 1960) and by some current taxonomists (Jackson, 1966, 1968, 1978; Moran, 1969, 1976; Cronquist, pers. comm.). However, studies subsequent to Hall's (1928) monograph of *Haplopappus* have questioned the congeneric treatment of North American sections, suggesting that they be treated as separate genera (Shinners, 1950, 1951; Keck, 1956; Anderson, 1966; Turner, 1972; Anderson et al., 1974; Urbatsch, 1975, 1978; Hartman, 1976; Mayes, 1976). In this paper I evaluate the relationships of Hall's *Haplopappus* section *Hazardia* and discuss the merits of treating it as a separate genus. I also designate three natural groups within *Hazardia* as sections.

Generic Relationships

Hall (1928) suggested close relationships among *Haplopappus* sections *Hazardia, Isocoma, Ericameria, Asiris, Isopappus,* and *Hesperodoria* in North America. However, chromosome data do not support the inclusion of *Hazardia* in this group. Most of the 13 species of *Hazardia* have a chromosome number of $n = 5$, the exceptions being *H. brickellioides* with $n = 6$ and *H. whitneyi* with $n = 4$. *Erica-*

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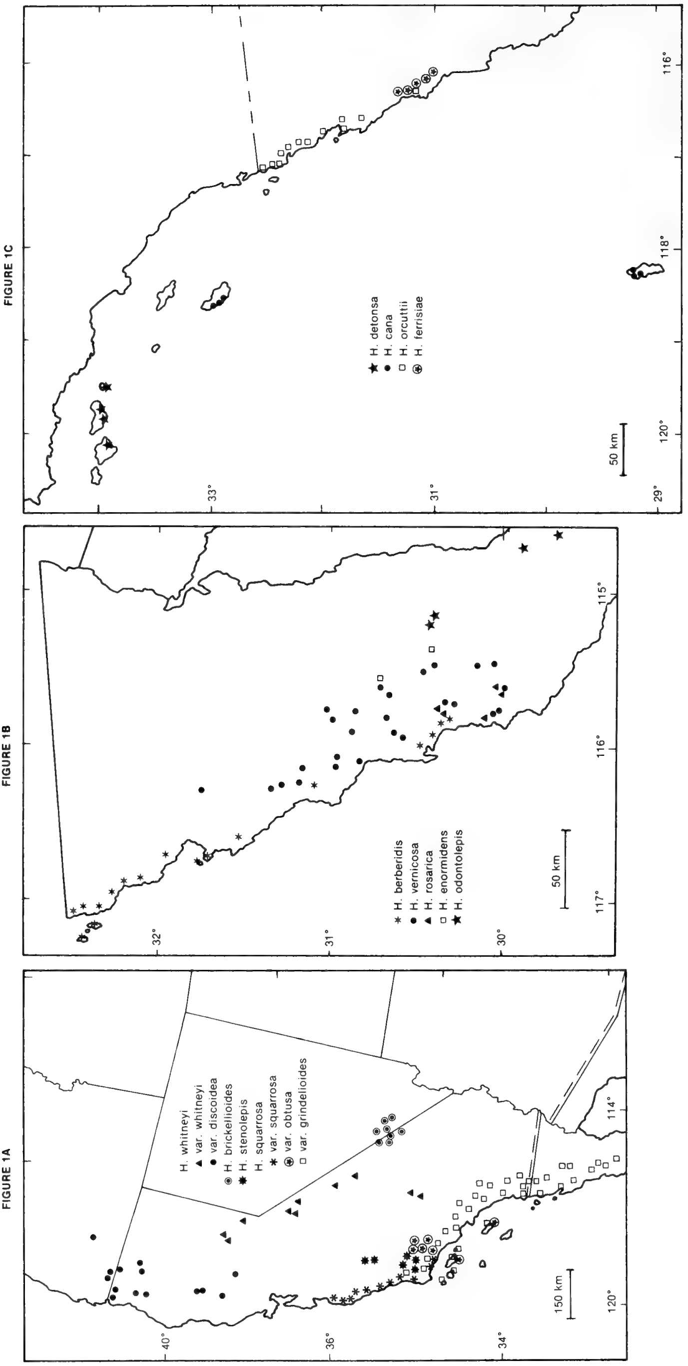

FIG. 1. Distribution of *Hazardia*.

meria and *Asiris* have numbers based on $x = 9$ and are more closely related to *Chrysothamnus* than to *Haplopappus* (Anderson, 1966; Anderson et al., 1974; Urbatsch, 1975, 1978). The affinities of *Hesperodoria* have not been determined, but a chromosome number of $n = 9$ has been reported for its two species (Anderson et al., 1974). *Isopappus,* with $n = 4$, 5, 6, and 7 has been split into two groups and treated as *Benitoa* (Keck, 1956) and *Croptilon* (Shinners, 1951), though Smith (1965) retained *Croptilon* in *Haplopappus*. *Benitoa* ($n = 5$) and *Croptilon* ($x = 7$) are slender annuals, a habit unknown in *Hazardia*. The former are probably more closely allied to *Chrysopsis*.

Hall (1928) suggested that *Hazardia* is more closely related to *Isocoma* than to any other section of *Haplopappus* in North America. This suggestion seems to be supported by a report of natural hybridization between *Hazardia brickellioides* and *Isocoma acradenia* Greene (Beatley, 1976), but I have examined the specimen of this putative hybrid and it appears to be pure *Isocoma*. Furthermore, an attempted artificial cross between *H. brickellioides* and *I. veneta* Greene was unsuccessful (Jackson, 1968). *Isocoma* seems best treated as a genus (Shinners, 1950; Turner, 1972) and can be distinguished from *Hazardia* by its generally ovate style appendages, abruptly dilated disk corollas, and glomerate capitulescences. It has chromosome numbers based on $x = 6$ and is probably more closely related to other $x = 6$ genera in North America, such as *Grindelia* (Turner, pers. comm.), than to *Hazardia*. However, *H. brickellioides* ($n = 6$) probably represents a distant link to *Isocoma*.

There is some indication of a relationship between *Hazardia* and *Xylorhiza* (*sensu* Watson, 1977). *Hazardia brickellioides* and *Xylorhiza frutescens* (S. Watson) Greene share chromosome number ($n = 6$), habit (small, much-branched, woody shrub), leaf characteristics (spinulose-dentate margins, glandular-scabrid), stem characteristics (glandular-scabrid white bark), and habitat preference (rocky outcrops or hillsides). However, *X. frutescens* has long, heterochromous ligules, monocephalous stems, large heads, and campanulate to hemispherical involucres that are typical of *Xylorhiza,* suggesting a more distant relationship with *Hazardia* through the South American elements of *Haplopappus*. This view is in agreement with Watson's (1977) opinion that *Xylorhiza* is not closely related to any of the North American sections of *Haplopappus* (*sensu* Hall), but may be related to the South American forms.

Hall (1928) considered *Haplopappus* section *Hazardia* and section *Blepharodon* to be distantly related in his phylogenetic scheme. Hartman (1976) has since included most of *Haplopappus* section *Blepharodon* in the genus *Machaeranthera*. Species of this section that have been transferred to *Machaeranthera* have chromosome numbers based on $x = 4$ (Hartman, 1976), while *Hazardia* is predominantly $n = 5$. An exception, *Hazardia whitneyi* ($n = 4$), has a habit, vegetative morphology, flavonoid chemistry, and geographical distribution that suggest a position near *Machaeranthera grindelioides* (Nutt.) Shinners var. *grindelioides* (formerly *Haplopappus nuttallii* Torr. & Gray). However, these similarities more likely indicate an ancient common origin for *Hazardia* and *Machaeranthera,* because the differences in the floral and fruit morphology between *H. whitneyi* and *M. grindelioides* do not support a close relationship. The remaining *Hazardia* species are woody shrubs or subshrubs, and can thus be distinguished from the mostly herbaceous, taprooted annuals, biennials, and perennials that characterize *Machaeranthera.* Disagreement exists, however, as to the degree of relationship between *Hazardia* and *Machaeranthera* (*sensu* Hartman). Based on chromosome pairing in the F_1 generation of artificial hybrids between *Haplopappus squarrosus* subsp. *squarrosus* (=*Hazardia squarrosa* var. *squarrosa*) and *Haplopappus arenarius* Benth. [=*Machaeranthera arenaria* (Benth.) Shinners], Jackson (1978) suggested a closer relationship and, following Hall (1928), continued to treat them in *Haplopappus* section *Hazardia* and section *Blepharodon,* respectively. However, there must be reservations in judging genomic and phylogenetic relationships strictly on chromosome pairing even in diploid hybrids (Riley and Law, 1965; DeWet and Harlan, 1972), except in networks of interrelated hybrids when the genetic systems of the parent taxa are well understood (Dewey, 1974). As yet, there are not enough cytogenetic data available for a meaningful evaluation within *Haplopappus* (*sensu* Hall). Studies by Jackson (1962, 1966, 1968, 1978) provide excellent examples of the kind of information that is necessary from a wide variety of interspecific and intergeneric hybrids before patterns of cytogenetic relationships can be interpreted taxonomically. At least for now I believe that it is more expedient to maintain *Hazardia* as a distinct genus and to judge its generic relationships on data that are more uniformly available for most or all taxa of concern: morphology, chromosome number, and chemistry (discussed below).

The generic segregation of *Hazardia* is supported for the most part by chemical studies. Except for *H. whitneyi,* which accumulates only flavonol derivatives, *Hazardia* species consistently produce a complex array of glycoflavones and O-glycosides of flavones and flavonols, and usually a number of highly methoxylated flavonol aglycones (Clark and Mabry, 1978). Such a high degree of chemical complexity is known only in *Ericameria* and *Asiris* of Hall's *Haplopappus* (Urbatsch, pers. comm.). Except for *Isocoma,* which appears chromatographically complex but is as yet chemically unknown (Clark, unpub. data), all other former sections of *Haplopappus* that have been examined for flavonoids produce a small number of compounds of usually one and sometimes two classes, i.e., flavones, flavonols, or glycoflavones (Hartman, 1976; Mayes, 1976; Urbatsch, pers. comm.; Clark, unpub. data).

It appears that, as suggested by Hall (1928), the closest relatives of *Hazardia* may be found in *Haplopappus* of South America. Morphologically, *Hazardia berberidis* is very similar to some members of *Haplopappus* section *Polyphylla,* particularly to *Haplopappus deserticolus* Phil. and *H. mucronatus* Hook. & Arn. Additionally, a chromosome number of $n = 5$ has been found for several South American species (Grau, 1976; Jackson, pers. comm.), and $n = 6$ has been counted for one species (Turner et al., 1979). Based on similarity of karyotypes and morphology, Grau (1976) maintains *Hazardia* and South American *Haplopappus* as congeners. In support of this congeneric status, Jackson (pers. comm.) has obtained hybrids between *Hazardia* and *Haplopappus* sections *Haplopappus* and *Polyphylla.* However, as discussed above in relation to chromosome pairing, I do not presently believe that karyotype similarities and mere crossability are useful taxonomic criteria. Future studies may prove otherwise, but the currently available morphological information indicates that South American *Haplopappus* species, except for the almost complete absence of a truly herbaceous habit, are as diverse as their North American counterparts that are treated as separate genera. *Haplopappus* section *Diplostephioides* has been reinstated as the genus *Llerasia* (Cuatrecasas, 1970). Character combinations in section *Haplopappus* suggest affinities with *Xylorhiza* (Watson, 1977) and distinguish it from *Hazardia*: monocephalous stems, long (5–45 cm), mostly leafless peduncles bearing medium-sized to large heads with long-ligulate (>10 mm) ray flowers and appressed phyllaries that form a hemispheric to broad-campanulate involucre. Section *Polyphylla* appears to be equally deserving of generic status separate from section *Haplopappus* and is perhaps congeneric with *Hazardia.* However, it remains for future studies to determine the relationship of *Polyphylla* to *Hazardia.*

Preliminary chemical studies of South American *Haplopappus* reveal a divergence from *Hazardia* (Clark, unpub. data). Species examined from *Haplopappus* sections *Haplopappus, Polyphylla,* and *Xylolepis* produce 6-oxygenated flavone glycosides. Compounds of this type are unknown in *Hazardia*; this lends further support to the generic distinctions between North and South American species.

TAXONOMY

HAZARDIA Greene, Pittonia 1:28. 1887.—*Haplopappus* Cass. sect. *Hazardia* (Greene) H.M. Hall, Publ. Carnegie Inst. Wash. 389:36. 1928.—TYPE: *Hazardia cana* (Gray) Greene [≡*Diplostephium canum* Gray].

Diplostephium H. B. K. subg. *Aplostephium* Gray, Proc. Amer. Acad. Arts 11:75. 1876.—TYPE: *Hazardia cana* (Gray) Greene [≡*Diplostephium canum* Gray].

Plants woody, at least at the base, up to 2.5 m tall. Stems erect, leafy throughout, much branched, glabrous to densely tomentose, usually resinous. Leaves entire to serrate or dentate, glabrous to densely tomentose, usually resinous, sessile or short-petiolate, usually clasping or subclasping, linear to broadly ovate, obovate, or spatulate, acute to obtuse, to 14 cm long and 5 cm wide. Heads radiate or eradiate, sessile or short-pedunculate. Involucres narrowly or broadly turbinate to campanulate, the bracts imbricate in several series, acute to mucronate or obtuse, frequently glandular-resinous, glabrous to pubescent, entire or few-toothed, frequently squarrose, rigid or herbaceous at apex, linear to oblong or oblanceolate. Ray florets none or 3–25, pistillate, sometimes fertile, yellow or sometimes changing to red-purple, the ligules to 9 mm long and 2 mm wide. Disk florets 4–60, hermaphroditic, fertile or sterile, yellow or sometimes changing to red-purple, usually glabrous, the tube gradually ampliate from the middle, 4–10 mm long, the style branches slightly exserted, puberulent throughout or the puberulent appendage shorter than the stigmatic portion. Ray achenes twice as long as or equal to disk achenes; achenes compressed or obcompressed, fusiform to cuneate, 1–10 mm long, 0.5–1.5 mm wide, 4–5-angled, glabrous to densely silky. Pappus of ray and disk similar, composed of about 20–60 scabrous, tawny to reddish-brown capillary bristles, 2.5–12.0 mm long.

Key to *Hazardia*

Stems mostly herbaceous, arising from a woody root-crown (sect. *Machaerantheroides*). . . . . 1. *H. whitneyi*.
Stems woody, arising from a woody trunk.
  Outer involucral bracts with toothed margins, graduating to leaves; disk florets sterile (sect. *Bracteofolia*).
    Involucres 9–13 mm high; ovaries of (sterile) disk florets equalling those of ray florets.
      Ray florets 6–8, the ligules 5–6.5 mm long; disk florets 11–15, involucres of 25–30 several-nerved bracts. . . . . 2. *H. odontolepis*.
      Ray florets 3–6, the ligules 3–4 mm long; disk florets 5–11; involucres of 16–21 one-nerved bracts. . . . . 3. *H. enormidens*.
    Involucres 6–7 mm high; ovaries of (sterile) disk florets half as long as those of ray florets. . . . . 4. *H. vernicosa*.
  Outer involucral bracts with entire margins; disk florets fertile (sect. *Hazardia*).
    Heads radiate, the ray florets conspicuous and much longer than the disk.
      Leaf margins serrate. 5. *H. berberidis*.
      Leaf margins entire. . . . . 6. *H. orcuttii*.
    Heads eradiate or with ray florets inconspicuous and shorter than the disk.

Heads eradiate.
  Leaf margins entire. .... 7. *H. ferrisiae.*
  Leaf margins sharply serrate to dentate.
    Pappus bristles 4–6 mm long; florets 5.5–6 mm long..... .... 8. *H. rosarica.*
    Pappus bristles 7–12 mm long; florets 9–11 mm long.
      Florets 4–8; involucres very narrowly turbinate; leaves 15–25 mm long, 7–12 mm wide. .... 9. *H. stenolepis.*
      Florets 9–30; involucres turbinate; leaves 15–50 mm long, 10–20 mm wide. .... 10. *H. squarrosa.*
Heads radiate, the ray florets inconspicuous and shorter than the disk.
  Leaves densely tomentose, at least abaxially; shrubs 6–25 dm tall.
    Leaves membranous, glabrate adaxially at maturity; bracts with a tuft of loose woolly pubescence at the apex; disk corollas 5–8 mm long. .... 11. *H. cana.*
    Leaves thick, densely tomentose adaxially at maturity; bracts mostly with dense woolly pubescence throughout; disk corollas 8–10 mm long. .. 12. *H. detonsa.*
  Leaves pilose to scabrid; shrubs 2–8 dm tall. .... 13. *H. brickellioides.*

Hazardia Section **Machaerantheroides** Clark, sect. nov.

A sectionibus *Hazardia* et *Bracteofolia* caulibus herbaceis pro maxima parte, caudicibus lignosis exorientibus, differt.

Stems mostly herbaceous, arising from a woody root-crown.

TYPE SPECIES: *Hazardia whitneyi* (Gray) Greene.

1. HAZARDIA WHITNEYI (Gray) Greene, Pittonia 3:43. 1896. For synonymy and typification see the varietal headings.

Mostly herbaceous perennials 2–5 dm tall. Stems arising from a woody root-crown, few-branched, ascending, tan or purplish to dark brown in age, 0.2–1.5 cm in diameter, 2–5 dm long, herbaceous to woody below, scabrid to sparsely tomentulose above with glandular-stipitate hairs, the internodes averaging 1.5–3.5 cm, striate, leafy throughout. Leaves sessile, clasping, broadly oblong to oblanceolate, acute, 25–50 mm long, 7–16 mm wide, glabrous or sparsely puberulent to glandular-scabrid, the midrib prominent abaxially, the lateral veins inconspicuous and pinnate, the margins serrate, mucronate. Heads radiate or eradiate, solitary, or in spicate, racemose, or cymose capitulescences. Involucre campanulate, shorter than the disk, 11–13 mm high, 8–12 mm wide; bracts 30–40, loosely imbricate in several series, graduating to leaves, the apex herbaceous and moderately stipitate-glandular, resinous, chartaceous at the base, linear-lanceolate, acute, often becoming purplish, the margins membranous, 5–12 mm long, 1–1.5 mm wide, occasionally squarrose. Disk florets 15–30, yellow, the anthers 3.5–4 mm long, the style branches 2–3 mm long, lanceolate, acute, the puberulent appendage equal to or slightly longer than the stigmatic portion. Achenes 5–10 mm long, 1–1.5 mm wide, narrowly ovate, glabrous, 5-angled and striate between the angles. Pappus of 40–60 scabrous, brownish bristles, 7–10 mm long. Chromosome number, $n = 4$ (Anderson et al., 1974).

Heads radiate; disk achenes mostly 5–7 mm long; Sierra Nevada, CA. . . . . 1a. var. *whitneyi*.
Heads eradiate; achenes to 10 mm long; mts of NW CA and adjacent OR. . . . . 1b. var. *discoidea*.

1a. HAZARDIA WHITNEYI (Gray) Greene var. WHITNEYI.—*Haplopappus whitneyi* Gray, Proc. Amer. Acad. Arts 7:353. 1868.—*Aster whitneyi* (Gray) Kuntze, Rev. Gen. Pl. 1:318. 1891.—TYPE: USA: CA: Mono Co.: Mono Trail and Sonora Pass, 2800 m, 1866, *Bolander 6008* (Holotype: GH!; Isotypes: F!, MO!, NY!, UC!, US!)

Ray florets 5–18, yellow, the ligules 5–8 mm long, 1–2 mm wide, oblanceolate, the corolla tubes 4–5 mm long, styles inconspicuous, achenes undeveloped. Disk achenes to 8 mm long.

Distribution. Uncommon in occasional localities throughout the Sierra Nevada from Plumas Co. to Kern Co., CA (Fig. 1A); usually associated with species of *Abies, Pinus, Tsuga, Ceanothus,* and *Arctostaphylos* at 1200–3500 m; flowering Jul–Sep.

1b. **Hazardia whitneyi** (Gray) Greene var. **discoidea** (J. T. Howell) Clark, comb. nov.—*Haplopappus whitneyi* var. *discoideus* J. T. Howell, Leafl. W. Bot. 6:84. 1950.—*Haplopappus whitneyi* ssp. *discoideus* (J. T. Howell) Keck, Aliso 4:103. 1958.—TYPE: USA: CA: Siskiyou Co.: Shackleford Creek Trail S of Sky High Valley, Marble Mountains, 9 Aug 1939, *J. T. Howell 15236* (Holotype: CAS!; Isotypes: DS!, GH!, US!)

Distribution. Uncommon in occasional localities of the inner North Coast Ranges from Lake Co. to Siskiyou and Del Norte cos., CA and adjacent OR (Fig. 1A); usually associated with species of *Abies, Pinus, Tsuga, Ceanothus,* and *Arctostaphylos* at 1000–2500 m; flowering Jul–Sep.

Placement of *Hazardia whitneyi* within the genus is problematical. B. L. Turner (pers. comm.) noted its superficial similarity to *Ma-*

chaeranthera grindelioides (Nutt.) Shinners. *Hazardia whitneyi* has a chromosome number ($n = 4$), habit (perennial herb, the new shoots arising from a tough woody rootstock), geographical distribution, and flavonoid chemistry (flavonol derivatives only) that suggest a position with or near *M. grindelioides*. However, comparison of floral and fruit characters of these two taxa does not suggest a close relationship. *Hazardia whitneyi* is therefore treated as a monotypic section of *Hazardia,* named for its superficial resemblance to *M. grindelioides*. Future workers might consider yet other positions among the various generic segregates of *Haplopappus,* but it seems best to me to consider the taxon as an ancient aneuploid derivative from an element, in the phyletic sense, of both *Machaeranthera* and *Hazardia*.

Hazardia Section **Bracteofolia** Clark, sect. nov.

A sectionibus *Hazardia* et *Machaerantheroides* floribus discibus sterilibus et bracteis cum marginibus dentatis differt.

Woody shrubs; involucral bracts with toothed margins, graduating to leaves; disk florets sterile.

TYPE SPECIES: *Hazardia vernicosa* (Brandegee) Clark.

The distinctness of the species here included in section *Bracteofolia* was pointed out by Moran (1976), who also noted the relationships within this group and between it and the present section *Hazardia*. Section *Bracteofolia* is so named to emphasize its toothed, leaflike outer bracts, which are unique within the genus.

2. **Hazardia odontolepis** (Moran) Clark, comb. nov.—*Haplopappus odontolepis* Moran, Trans. San Diego Soc. Nat. Hist. 15:157. 1969.—TYPE: Mexico: Baja California: Rare on the N slope at 1400 m, near the summit of Cerro Potrero (near 29°49′N, 114°37′W), 30 May 1965, *Moran 12162* (Holotype: SD!; Isotypes: CAS!, GH!, ICF, K!, KANU!, NY!, UC!, US!)

Glutinous shrublet 1–3 dm tall, with branches ascending from a woody stock 5–10 cm tall and to 2.5 cm in diameter. Young branches simple or few branched above, light tan, 1 mm in diameter, 1–2 dm long, sparsely hispidulous, leafy throughout, with internodes averaging 2–6 mm, angled from leaf margins and midrib downward, smaller leaves often fascicled in axils of larger ones; older stems dark gray, shredding, to 6 mm in diameter. Leaves sessile and subclasping, elliptic to cuneate-oblanceolate, acute, 5–20 mm long, 4 mm wide, coriaceous, glandular-pitted and slightly to heavily resinous, moderately hispidulous either mostly near margins and veins or throughout, the midrib prominent abaxially, the lateral veins less prominent to obscure, the apex deflexed, tipped with a white spine to 0.5 mm long, the margins with 4–6 spinose teeth, 0.5–1 mm long, irregularly spaced. Heads radiate, solitary at ends of branchlets or in cymose capitulescences with 2–4 heads on peduncles 1–12 mm long, from upper axils except when solitary. Involucre cylindric or subfusiform, shorter than disk, 9–13 mm high, 3–5 mm wide exclusive of squarrose tips; bracts 25–30, outer ones spiny-margined, graduating into leaves, inner ones subequal, oblong to linear, several-nerved, acute, yellowish, 8–10 mm long, 1–2 mm wide, with margins erose-ciliate. Ray florets 6–8, fertile, yellow, the ligules 5–6.5 mm long, 1.5–2 mm wide, irregularly 3-lobed, the corolla-tubes 5–5.5 mm long, the style branches linear, obtuse, 1–1.5 mm long, stigmatic to apex. Achenes obcompressed, cuneate, 3–4 mm long, 1 mm wide, sparsely ascending-strigose, with 5 white nerves. Disk florets 11–15, sterile, yellow, the corolla 7–9 mm long, the anthers 2.5–3 mm long, the style branches 1.5–2 mm long, linear, the puberulent appendage 1–2 times longer than the stigmatic part. Ovaries of the disk florets equalling those of the ray florets. Pappus of 40–50 scabrous, brownish bristles, 4–5.5 mm long.

Distribution. Locally common on bare, rocky slopes, on peaks S of the Sierra San Pedro Mártir, Baja California, Mex. (Fig. 1B); usually associated with species of *Juniperus, Quercus, Yucca,* and *Prunus* at 1150–1450 m; flowering May–Jun.

This taxon most closely resembles *H. enormidens* and *H. vernicosa,* differing primarily in the number and size of involucres. Of these three species, *H. odontolepis* is most like other members of *Hazardia* in its larger, subclasping leaves, in its larger heads with more numerous florets, and in the presence of stigmatic lines along the style branches of its disk florets.

3. **Hazardia enormidens** (Moran) Clark, comb. nov.—*Haplopappus enormidens* Moran, Phytologia 34:371. 1976.—TYPE: Mexico: Baja California: Ridge 5 km SW of San Isidoro (7.5 km by road), ca. 1170 m, SW foothills of the Sierra San Pedro Mártir (near 30°44′N, 115°34′W), 19 Jul 1975, *Moran and Reveal 22062* (Holotype: SD!; Isotypes: ASU!, SD!, to be distributed)

Glutinous shrublet 1–3 dm tall, much branched from a woody crown. Branchlets flexuous, light green, soon becoming tan, gray in age, 0.5–1 mm in diameter, 1.5 dm long, sparsely hispidulous, leafy throughout, with internodes averaging 3–6 mm, angled from leaf margins and midrib downward, mostly with small few-leaved fascicles in axils. Leaves sessile and subclasping-decurrent, elliptic to oblong, acute, 6–10 mm long, 2 mm wide at base to 3 mm wide above, coriaceous, glandular-pitted to heavily resinous, moderately hispidulous either mostly near margins or throughout, the midrib prominent abaxially, the lateral veins less prominent to obscure, the apex deflexed, tipped with a white spine to 0.5 mm long, the margins entire or with

1–9 spinose teeth 0.2–0.5 mm long, very irregularly spaced. Heads radiate, solitary at ends of branchlets or in cymose capitulescences with 2–4 heads on peduncles 1–12 mm long, from upper axils except when solitary. Involucres cylindric or subfusiform, shorter than disk, 9–12 mm high, 2–3 mm wide exclusive of squarrose tips; bracts 15–20, outer ones spiny-margined and graduating into leaves, inner ones subequal, linear, 1-nerved, acute, green to yellowish, 6–9 mm long, 1–2 mm wide, with margins erose-ciliate above. Ray florets 3–6, fertile, yellow, the ligules 3–4 mm long, 1–1.3 mm wide, scarcely toothed at apex, the corolla tubes 3–5 mm long, the style branches linear, obtuse, 0.6–1.4 mm long, stigmatic to apex. Achenes obcompressed, cuneate, 3–4 mm long, 1 mm wide, sparsely ascending-strigose, with 5 white nerves. Disk florets 5–11, sterile, yellow, the corolla slightly ampliate from the middle, 7–9 mm long, the anthers 2.5–3 mm long, the style branches 1–2 mm long, linear, puberulent throughout, lacking evident stigmatic lines. Ovaries of the disk florets equalling those of the ray florets. Pappus of 45–55 scabrous, brownish bristles, 4–6 mm long. Chromosome number, $n = 5$ (Moran, 1976).

Distribution. Locally abundant in open areas at the edge of chaparral, known only from the type locality and from about 40 km SSE, S of Rancho San Miguel, Baja California, Mex. (Fig. 1B); usually associated with species of *Juniperus, Adenostoma, Yucca,* and *Agave* at 975–1175 m; flowering Jul–Aug.

Hazardia enormidens is like *H. odontolepis* in leaf shape and relative size of disk ovaries and like *H. vernicosa* in having one-nerved bracts and in lacking stigmatic lines along the style branches of the disk florets. *Hazardia enormidens* has been suggested to form natural hybrids with *H. vernicosa* [Moran, 1976; cf. *Moran and Reveal 22607a & b* (ASU, SD)].

4. **Hazardia vernicosa** (Brandegee) Clark, comb. nov.—*Haplopappus vernicosus* Brandegee, Proc. Calif. Acad. Sci. II, 2:168. 1889.—non Reiche, Fl. Chil. 3:312. 1902.—TYPE: Mexico: Baja California: El Rosario, 20 May 1889, *Brandegee s.n.* (Holotype: UC!; Isotypes: GH!, NY!, US!)

Glutinous shrublet 2–3 dm tall, much branched from a woody crown. Branchlets light green to brown, gray with age, 0.5–1 mm in diameter, 1–2 dm long, glabrous, resinous and granular, leafy throughout, with internodes averaging 3–6 mm, angled from leaf margins and midrib downward, mostly with small, few-leaved fascicles in axils. Leaves with narrowed, petiole-like base, cuneate-obovate to cuneate-oblanceolate, acute, 6–9 mm long, 1 mm wide at base to 5 mm wide above, coriaceous, glandular-pitted, heavily resinous, sparsely hispidulous on midrib or glabrous, midrib prominent abaxially, the lateral veins obscure, the apex deflexed, tipped with a white spine less than 0.5 mm long, the margins with 4–6 spinose teeth to 0.5–1 mm long, irregularly spaced. Heads radiate, solitary at ends of branchlets or in cymose capitulescences with 2–3 heads on peduncles 1–10 mm long, from upper axils except when solitary. Involucres cylindric-turbinate, shorter than disk, 6–7 mm high, 2–3 mm wide exclusive of squarrose tips; bracts 15–20, outer ones spiny-margined and graduating into leaves, inner ones subequal, oblong to linear, 1-nerved, acute, green to yellowish with green tips, 4–6 mm long, to 1 mm wide, with margins mostly ciliate. Ray florets 3–5, fertile, yellow, the ligules to 3 mm long, to 1 mm wide, obtuse, the corolla tubes 2–4 mm long, the style branches linear, obtuse, 0.5–1.4 mm long, stigmatic to apex. Achenes to 2 mm long, to 0.5 mm wide, obcompressed, angled, truncate, densely silky. Disk florets 4–8, sterile, yellow, the corolla slightly ampliate from the middle, 4–5 mm long, the teeth 0.6 mm long, the anthers 2.5–3 mm long, the style branches 1–2 mm long, linear, acute, puberulent throughout, lacking evident stigmatic lines. Ovaries of the disk florets half as long as those of the ray florets. Pappus of 30–40 white to brownish, scabrous bristles, 3–4 mm long. Chromosome number, $n = 5$ (Keil and Pinkava, 1976).

Distribution. Usually abundant in many localities in the foothills from N of San Vicente to SE of El Rosario, Baja California, Mex. (Fig. 1B); sometimes associated with species of *Juniperus, Yucca, Agave,* and *Quercus* at 50–1200 m; flowering Jun–Jul.

Hazardia vernicosa is most closely related to *H. odontolepis* and *H. enormidens*. Of these three species, *H. vernicosa* is the most divergent from the other members of *Hazardia*. Its unique characters are smaller leaves with petiole-like bases, smaller heads with fewer and smaller florets, and ovaries of the disk florets half as long as those of the ray florets rather than of equal size. *Hazardia vernicosa,* like *H. enormidens,* has one-nerved bracts and lacks stigmatic lines along the style branches of the disk florets.

HAZARDIA Section HAZARDIA

Woody shrubs; outer involucral bracts with entire margins; disk florets fertile.

5. HAZARDIA BERBERIDIS (Gray) Greene, Erythea 2:112. 1894.—*Haplopappus berberidis* Gray, Syn. Fl. 1^2:126. 1884.—*Aster berberidis* (Gray) Kuntze, Rev. Gen. Pl. 1:317. 1891.—TYPE: Mexico: Baja California: All Saint's Bay, Jul 1882, *F. E. Fish s.n.* (Holotype: GH!; Photographs: NY!, UC!; Isotypes: K!, US!)

Haplopappus cruentus Greene, Pittonia 2:17. 1889.—*Hazardia cruenta* (Greene) Greene, Erythea 2:112. 1894.—TYPE: Mexico: Baja California: On the largest of the Coronado Islands, 4 Jun 1889, *C. F. Pond s.n.* (Holotype: ND-G; Isotype: ND-G)

Woody shrub 0.5–2 m tall, loosely branched. Branches brown to gray in age, 3–30 mm in diameter, 5–10 dm long, sparsely villous, leafy throughout, with internodes averaging 1–2.5 cm, striate, often with small few-leaved fascicles in axils. Leaves sessile, clasping, oblong to obovate or subspatulate, obtuse, 20–50 mm long, 3–10 mm wide below to 18 mm wide above, coriaceous, glabrous to sparsely hispidulous toward base of midrib, the midrib prominent abaxially, the lateral veins pinnate and impressed, the margins acutely to spinosely serrate throughout. Heads radiate, solitary at ends of branches or in racemose capitulescences, sessile, or on leafy peduncles to 3 cm long. Involucres broadly turbinate to campanulate, shorter than the disk, 1–2 cm high, 1–1.5 cm wide; bracts 30–60, imbricated in several series, rigidly chartaceous, glutinous, with darkened green apex 1–3 mm long and resinous-granular, oblong-obtuse to broadly acute, 3–10 mm long, 1–2 mm wide, with margins erose-ciliate. Ray florets 15–25, yellow or aging to dark red-purple, the ligules 6–9 mm long, 1.5–2 mm wide, minutely 3-lobed at the apex, oblanceolate, the corolla tubes 4–5 mm long, the style branches 1–1.5 mm long, linear, obtuse, 0.6–1.4 mm long, stigmatic to apex. Disk florets 30–60, yellow or aging to dark red-purple, the anthers 3–5 mm long, the style branches 1.5–2.5 mm long, linear, broadly acute, the puberulent appendage shorter than or equalling the stigmatic portion. Ray and disk achenes similar, compressed, 5–6 mm long, 0.5–1 mm wide, glabrous, 4-angled and striate between the angles. Pappus of 30–50 scabrous, brownish bristles, 6–9 mm long. Chromosome number, $n = 5$ (fide R. C. Jackson on labels of *Moran 13435, 21055*).

Distribution. Locally abundant from beaches to foothills from El Socorro N to Rosarito, Baja California, Mex., and on adjacent Coronados and Todos Santos Islands (Fig. 1B); usually associated with species of *Agave, Artemisia, Simmondsia, Opuntia, Rhus,* and *Atriplex* at 5–380 m; flowering Mar–Sep.

Hazardia berberidis is similar in habit and leaf morphology to the eradiate *H. squarrosa* and *H. rosarica.* It forms natural hybrids with the entire-leaved *H. orcuttii* (Hall, 1928; cf. *Clark 1099, 1101a–d, 1102a–d* (ASU, LL), *Hall 12253* (UC), *Moran 13441* (ARIZ, DS, MICH, RSA, SD), *Moran 14516, 14637* (SD), *Rose 60078, 60079* (CAS, NY, RSA)) and *H. ferrisiae* (cf. *Moran 14070* (DS, MICH, NY, RSA, SD, US)). *Hazardia berberidis* has many features in common with *Haplopappus* section *Polyphylla* of Chile, supporting previous suggestions that *Hazardia* and *Haplopappus* had a common origin (Hall, 1928; Turner, pers. comm.). Their present disjunction, between Baja California and Chile, suggests that one gave rise to the other, but the direction of evolution is not yet known.

6. HAZARDIA ORCUTTII (Gray) Greene, Erythea 2:112. 1894.—*Haplopappus orcuttii* Gray, Proc. Amer. Acad. Arts 20:297. 1885.—

TYPE: Mexico: Baja California: All Saint's Bay, 22 Sep 1884, *C. R. Orcutt 1230* (Holotype: GH!; Isotypes: A!, F!, MICH!, NY!, UC!, US!; fragments, UC!)

Resinous shrub 5–10 dm tall. Woody branches few and open to 30 mm in diameter below, 3–5 mm above, 3–8 dm long, glabrous and slightly resinous, leafy throughout, with internodes averaging 2–8 mm, minutely ribbed or angled from leaf midrib downward, occasionally with few and small-leaved fascicles in axils of much larger leaves. Leaves sessile and subclasping, spatulate-lanceolate to narrowly obovate, acute to occasionally obtuse below, mucronate, 20–50 mm long, 3–15 mm wide, coriaceous, resinous-punctate, glabrous, the midrib prominent, the lateral veins reticulate and inconspicuous, the margins entire or rarely few-toothed below. Heads radiate, in racemose or paniculate capitulescences from 5–15 cm in length, up to 50 cm, the peduncles reduced or absent above to 2 mm long below. Involucres turbinate, shorter than disk, 7–10 mm high, 4–6 mm wide exclusive of the squarrose tips; the bracts 30–40 in several series, linear, acute to obtuse, light green, with a resinous glandular-dotted apex, 4–6 mm long, to 1 mm wide, the margins scarious. Ray florets 8–12, fertile, yellow, the ligules 2–3 mm long, to 1.5 mm wide, broadly acute, the corolla tubes 3–4 mm long, the style branches linear, obtuse, 1–1.5 mm long, stigmatic to apex. Disk florets 10–20, fertile, yellow, glabrous, the corolla slightly ampliate from the middle, 5–7 mm long, the lobes broadly acute, to 0.8 mm long, the anthers 2–2.5 mm long, the style branches 1.5–2 mm long, sublanceolate, obtuse, the puberulent appendage nearly equalling the stigmatic portion. Ray and disk achenes similar, or those of rays slightly shorter, subcylindric but tapering slightly to the base, faintly ribbed, 3–4.5 mm long, to 1 mm wide, sparsely ascending-strigose. Pappus of 20–30 scabrous, brownish bristles, 4–5 mm long. Chromosome number, $n = 5$ (fide R. C. Jackson on label of *Moran 13440*).

Distribution. Locally common in open habitats, coastal plains and hills from Colonet to Tijuana, Baja California, Mex. (Fig. 1C); usually associated with species of *Agave, Artemisia, Simmondsia, Opuntia,* and *Rhus* at 10–200 m; flowering Aug–Sep.

Hazardia orcuttii probably hybridizes in nature with *H. ferrisiae* (cf. *Clark et al. 1097b-l* (ASU, LL); *Moran 14067* (DS, RSA, SD, US)).

7. **Hazardia ferrisiae** (Blake) Clark, comb. nov.—*Haplopappus ferrisiae* Blake, Proc. Biol. Soc. Wash. 48:171. 1935.—TYPE: Mexico: Baja California: Playa S of San Vicente, 13 Aug 1933, *W. S. Cooper 75* (Holotype: DS!; photograph and fragments, US!)

Glutinous shrublet 2–5 dm tall, much branched from a woody base. Branches brownish, 1–2 mm in diameter, 1–3 dm long, glabrous and resinous, leafy throughout, with internodes averaging 1–5 mm, angled from leaf margins and midrib downward, occasionally with small few-leaved fascicles in axils. Leaves sessile, oblanceolate to linear, acute, 10–15 mm long, 2–3 mm wide, coriaceous, glandular pitted to heavily resinous, glabrous, the midrib prominent to obscure, the lateral veins reticulate and impressed, the margins entire. Heads eradiate, or in cymose capitulescences with 3–15 subsessile heads crowded at ends of branches. Involucres narrowly turbinate, nearly equalling the disk, 5–7 mm high, 2–3 mm wide; bracts 10–15, the outer ones to 2 mm long and 0.8 mm wide, the inner ones to 8 mm long and 0.8 mm wide, with margins scarious and sparsely ciliate above, subulate to linear, acute, with a brown carinate glandular apex. Florets 7–12, yellow, the corolla slightly ampliate from the middle, 5–7 mm long, the teeth 0.6–0.8 mm long, the anthers 2.5–3 mm long, the style branches 0.9–1.5 mm long, the puberulent appendages equalling the stigmatic portion. Achenes obovate, 1.5–2 mm long, to 0.5 mm wide, ascending-strigulose, 5-nerved. Pappus of 30–40 scabrous, brownish bristles, 2.5–4 mm long. Chromosome number, $n = 5$ (fide R. C. Jackson on label of *Moran 1400*).

Distribution. Common on coastal plains and mesas in the region of Colonet, Baja California, Mex. (Fig. 1C); associated with species of *Agave, Opuntia, Rosa, Ambrosia,* and *Mesembryanthemum* at 25–150 m; flowering Jun–Aug.

8. **Hazardia rosarica** (Moran) Clark, comb. nov.—*Haplopappus rosaricus* Moran, Trans. San Diego Soc. Nat. Hist. 15:159. 1969.—TYPE: Mexico: Baja California: Locally common on N slope at 75 m, Arroyo del Campo Viejo, 2.3 miles SE of El Consuelo and 7.2 miles NNW of El Rosario (near 30°09′N, 115°46′W), 2 Jul 1967, *Moran 14020* (Holotype: SD!; Isotypes: ARIZ!, CAS!, GH!, KANU!, MICH!, MO!, NY!, RSA!, UC!, UCLA!, US!)

Glutinous shrub 2–9 dm tall, much branched from a woody base. Branchlets zigzag, slender, to 1 mm in diameter, 1–4 dm long, brown turning to gray in age, lower woody portions to 3 mm in diameter, glutinous to granular, leafy throughout, with internodes averaging 5–15 mm, angled from leaf margins and midrib downward, occasionally with small few-leaved fascicles in axils. Leaves sessile and subclasping to subpetiolate, obovate to spatulate, obtuse to rounded-acute, 10–25 mm long, 1–2 mm wide at base to 5–12 mm wide above, coriaceous, glandular-pitted to heavily resinous, glabrous, the midrib obscure or slightly protruding abaxially in lower portion, the lateral veins obscure, the margins dentate with 2–8 white, spinose-tipped, deltoid teeth, 0.5–1.5 mm long, regularly to irregularly spaced. Heads eradiate, solitary at ends of branchlets, or in thyrsoid capitulescences with 1–3 sessile or subsessile in upper axils. Involucres turbinate, shorter than disk, 8–12 mm high, 3.5–5 mm wide; bracts 30–60, imbricated in 5–8 series, erect or with tips slightly spreading, chartaceous with scarious margins and short herbaceous tips, abaxially and adaxially glandular near apex, erose and spinose-mucronate, to 1 mm wide, 2–7 mm long, oblong to linear-oblanceolate. Florets 15–25, yellow, corolla gradually ampliate from the middle, 5.5–6.5 mm long, the lobes erect, acute, 0.6–0.9 mm long, the anthers 1.5–2 mm long, the style branches 1–1.5 mm long, the appendage ovate, acute, puberulent, nearly equalling the stigmatic portion. Achenes subterete, narrowing at both ends but less so at apex, 3–3.5 mm long, 1–1.5 mm wide, dark to black, with 5 white nerves, sparsely appressed-pubescent. Pappus of 25–40 scabrous, white to brownish bristles, 4–6 mm long. Chromosome number, $n = 5$ (Moran, 1969; Keil and Pinkava, 1976).

Distribution. Locally abundant on N and E slopes and ridges, within 8 km of the sea, from NE of El Socorro to SE of El Rosario, Baja California, Mex. (Fig. 1B); usually associated with species of *Agave, Ambrosia, Aesculus, Dudleya,* and *Bergerocactus* at 75–475 m; flowering Jun–Oct.

9. HAZARDIA STENOLEPIS (Hall) Hoover, Vasc. Pl. San Luis Obispo Co. Calif. 296. 1970.—*Haplopappus squarrosus* ssp. *stenolepis* Hall, Publ. Carnegie Inst. Wash. 389:253. 1928.—TYPE: USA: CA: Fresno Co.: Parkfield Grade, 12 km from Coalinga, 13 Oct 1921, *Hall 11767* (Holotype: UC!; Isotypes: DS!, GH!)

Dense shrub 3–10 dm tall, very woody at the base. Branches whitish to brown or gray in age, 0.2–1.5 cm in diameter, 1–6 dm long, coarsely to finely scabrous, with internodes averaging 0.3–1.5 cm, striate, often with small few-leaved fascicles in axils. Leaves sessile, subclasping, oblong to obovate, obtuse, mucronate, 15–25 mm long, 7–12 mm wide, coriaceous, glabrous, resinous, the midrib prominent abaxially, the lateral veins obscure, the margins sharply serrate to dentate with mucronate teeth. Heads eradiate, in densely spicate capitulescences 3–15 cm long. Involucres very narrowly turbinate, shorter than the disk, 10–17 mm high, 3–6 mm wide; bracts 20–30, loosely imbricated in several series, chartaceous, glabrous, slightly glutinous at the apex, erect or slightly spreading, linear, acute, 3–23 mm long, to 1 mm wide. Florets 4–8, yellow, the corolla gradually ampliate from the middle, 9–11 mm long, the lobes erect, 0.7–1 mm long, the anthers 3.5–4 mm long, the style branches 2–2.5 mm long, linear, acute, the puberulent appendage equal to or slightly exceeding the stigmatic portion. Achenes compressed, 5–8 mm long, 0.5–1 mm wide, glabrous, 5-angled and striate between the angles. Pappus of 40–60 scabrous, red-brown bristles, 7–12 mm long. Chromosome number, $n = 5$ (Anderson et al., 1974).

Distribution. Locally common on serpentine or loose shale, dry soils of the Inner Coast Ranges, E Monterey, San Luis Obispo, and Santa Barbara cos. and W Fresno Co., CA (Fig. 1A); usually associated with species of *Quercus, Pinus, Ceanothus, Arctostaphylos, Heteromeles,* and *Artemisia* at 150–1200 m; flowering Sep–Nov.

10. HAZARDIA SQUARROSA (Hook. & Arnott) Greene, Erythea 2:112. 1894.—For synonymy and typifications see the varietal headings.

Multi-stemmed shrub 3–23 dm tall with a hard woody base to 4 cm in diameter. Branches tan to gray in age, 0.2–3 cm in diameter, 2–8 dm long, glabrate to tomentulose above, with internodes averaging 1–2.5 cm, striate, often with small few-leaved fascicles in axils. Leaves sessile, clasping, oblong to obovate or subspatulate, obtuse, 15–50 mm long, 10–20 mm wide, coriaceous to rigidly chartaceous, glabrous or puberulent on upper surface, sometimes resinous, the midrib prominent abaxially, the lateral veins obscure, the margins sharply serrate to dentate, sometimes mucronate. Heads eradiate, in racemose-spicate or glomerate-spicate capitulescences 4–20 cm long. Involucres turbinate, shorter than the disk, 8–15 mm high, 7–10 mm wide exclusive of the squarrose bracts; bracts 30–60, closely imbricated in several series, chartaceous at base, the apex glandular-pubescent or glabrous and resinous, erect, oblong to lanceolate, acute to obtuse, sometimes mucronate, 3–10 mm long, 1–2 mm wide. Florets 9–30, yellow or reddish, the corolla gradually ampliate from the middle, 9–11 mm long, the lobes erect or slightly spreading, 0.7–1.2 mm long, the anthers 3.5–4 mm long, the style branches 2.5–3 mm long, linear, acute, the puberulent appendage shorter than or nearly equal to the stigmatic portion. Achenes obovate, 5–8 mm long, 0.5–1.2 mm wide, glabrous, 5-angled and striate between the angles. Pappus of 40–60 scabrous, white to red-brown or tawny bristles, 7–12 mm long. Chromosome number, $n = 5$ (DeJong and Montgomery, 1963; Jackson, 1968, 1978; fide Jackson on labels of *Moran 13548, 13575, 13611*; fide Pinkava on label of *Clark 1105*).

Stems glabrate to sparsely pubescent above or scabrid and resinous; leaves glabrous, resinous; involucres 11–15 mm high; florets 18–30, the corollas 10–11 mm long; pappus tawny.
  Stems glabrate to sparsely pubescent above; bracts glandular-pubescent, obtuse to acute, squarrose. . . . . 10a. var. *squarrosa.*
  Stems glabrous to scabrid, resinous; bracts smooth resinous, obtuse to subtruncate, mucronate, erect or slightly spreading, never squarrose. . . . . 10b. var. *obtusa.*
Stems often tomentulose, especially near heads, not resinous; leaves often sparsely pubescent on upper surface, rarely resinous; involucres 8–12 mm high; florets 9–16, the corollas 9–10 mm long; pappus white to red-brown. . . . . 10c. var. *grindelioides.*

10a. HAZARDIA SQUARROSA var. SQUARROSA—*Haplopappus squarrosus* Hook. & Arnott, Bot. Beech. Voy. 146. 1833.—TYPE: USA: CA: Monterey Co.: Locality not definitely stated but probably in the vicinity of Monterey, exact date not stated, *Beechey Voyage s.n.* (Holotype: K!; photograph and fragments: UC!; photograph: US!)

Distribution. Locally abundant in foothills and coastal mountains, from Monterey to Santa Barbara and E in the mountains surrounding the Salinas Valley, CA (Fig. 1A); usually associated with species of *Quercus, Artemisia, Arctostaphylos, Ceanothus, Heteromeles,* and *Pinus* at elevations of 20–700 m; flowering Aug–Oct.

10b. HAZARDIA SQUARROSA var. OBTUSA (Greene) Jepson, Man. fl. pl. Calif. 1030. 1925.—*Hazardia obtusa* Greene, Fl. Franciscana 375. 1897.—*Haplopappus squarrosus* ssp. *obtusus* (Greene) Hall, Publ. Carnegie Inst. Wash. 389:253. 1928.—*Haplopappus squarrosus* var. *obtusus* (Greene) McMinn, Illus. man. Calif. shrubs 571. 1951.—TYPE: USA: CA: Kern Co.: San Emigdio Canyon, 2 Oct 1894, *Eastwood s.n.* (Holotype: ND-G; photograph and fragments: UC!; Isotypes: GH!, UC!)

Distribution. Locally common in dry canyons of mountains in W Kern Co. and adjacent Ventura Co., CA (Fig. 1B); usually associated with species of *Quercus, Eriogonum, Pinus, Arctostaphylos,* and *Ceanothus* at 600–1200 m; flowering Sep–Nov.

10c. **Hazardia squarrosa** var. **grindelioides** (DC.) Clark, comb. nov.—*Pyrrocoma grindelioides* DC., Prodr. 5:350. 1836.—*Aster grindelioides* (DC.) Kuntze, Rev. Gen. Pl. 1:316. 1891.—*Haplopappus squarrosus* ssp. *grindelioides* (DC.) Keck, Aliso 4:103. 1958.—TYPE: USA: CA: Exact locality and date not stated [probably in the vicinity of Santa Barbara, based on Douglas' itinerary; "1833" on label probably refers to date specimen was received in England since Douglas' California collecting was almost entirely during 1831–1832 (Jepson, Madroño 2:97. 1933)], *Douglas 60* (Holotype: G-DC; photograph and fragments: UC!)

Distribution. Locally common in foothills and coastal mountains and islands from Santa Barbara Co., CA, S into the interior of N Baja California, Mex. (Fig. 1A); usually associated with species of *Quercus, Pinus, Arctostaphylos, Rhus, Heteromeles, Adenostoma,* and *Ceanothus* at 100–1300 m; flowering Jul–Oct.

Hazardia squarrosa is the most variable species of *Hazardia,* diverging morphologically to form three varieties over a wide distributional range. Intermediates are found between var. *squarrosa* and var. *grindelioides* in some areas of Santa Barbara County, and intermediates between var. *grindelioides* and var. *obtusa* occur in a few locations in Ventura County. Raven (1963) reported that natural hybrids are formed between *H. squarrosa* var. *grindelioides* and *H. detonsa* on Santa Cruz Island, resulting in plants like that named *H. serrata* (see Excluded Names; cf. *Clark 1035, 1062* (ASU, LL), *Pollard s.n.* (CAS), *Raven and Smith 15285* (JEPS), *Wilken 8807* (UCSB)).

11. HAZARDIA CANA (Gray) Greene, Pittonia 1:29. 1887.—*Diplostephium canum* Gray, Proc. Amer. Acad. Arts 11:75. 1876.—*Corethrogyne cana* (Gray) Greene, Bull. Calif. Acad. Sci. 1:223. 1886.—*Haplopappus canus* (Gray) Blake, Contr. U. S. Natl. Herb. 24:86. 1922.—TYPE: Mexico: Baja California: Guadalupe Island, 28 Mar 1875, *Palmer 39* (Holotype: GH!; Isotypes: F!, GH!, MO!, NY!)

Haplopappus traskae Eastwood, Proc. Calif. Acad. Sci. ser. 4, 20:156. 1931.—TYPE: USA: CA: San Diego Co.: San Clemente Island, Jun 1903, *Trask 292* (Holotype: CAS; Isotypes: NY!, US!)

Open rounded shrub 6–20 dm tall, loosely branched. Branches irregular, 1–5 mm in diameter, 1–10 dm long, moderate to densely lanate-tomentose, lower woody portions to 3 cm in diameter with tomentum irregularly distributed and revealing light brown bark, leafy to capitulescence, with internodes averaging 5–20 mm, striate underneath the tomentum. Leaves subsessile or petiolate, the petioles to 1 cm long, oblanceolate, obtuse, 4–12 cm long, 1–4 cm wide, membranous, glabrate adaxially, densely short-tomentose abaxially, serrulate to subentire or occasionally closely serrate below, pinnately veined, the midrib prominent. Heads radiate, in large thyrsoid capitulescences. Involucres broadly turbinate, shorter than disk, 7–10 mm high, 5–8 mm wide; bracts 25–35, loosely imbricated in several series, the outer ones with a tuft of loose woolly pubescence at the apex, the inner ones glabrous or sparsely ciliate on the margins, 2–7 mm long, 1–1.5 mm wide, oblong, acute. Ray florets 6–14, inconspicuous, not exceeding the disk, yellow changing to red-purple in age, scarcely bilabiate to ligulate, the ligules to 1.8 mm long, to 0.6 mm wide, the corolla tubes 4–5 mm long, the style branches linear, obtuse, 0.5–1 mm long, stigmatic to apex. Disk florets 15–25, yellow changing to red-purple in age, the corolla slightly ampliate from the middle, 6–8 mm long, the lobes to 0.6 mm long, very sparsely puberulent in the lower portion, the anthers 2.5–3 mm long, the style branches ovate-appendaged, 1–1.5 mm long, the puberulent appendage much smaller than the stigmatic portion. Ray and disk achenes similar, fusiform, 3–4 mm long, to 1 mm wide, canescent, 4-nerved, striate. Pappus of 30–40 scabrous, brown or reddish-brown bristles, 4–7 mm long. Chromosome number, $n = 5$ (Raven, 1963).

Distribution. Sparse populations on rocky canyon walls, San Clemente Island, CA, and Guadalupe Island, Baja California, Mex. (Fig. 1C); associated with species of *Opuntia, Galium, Artemisia,* and *Heteromeles* at 200–500 m; flowering Jun–Sep.

12. HAZARDIA DETONSA (Greene) Greene, Pittonia 1:29. 1887.—*Corethrogyne detonsa* Greene, Bull. Torrey Bot. Club 10:41. 1883.—*Haplopappus detonsus* (Greene) Raven, Aliso 5:343. 1963. TYPE: In protologue, Greene referred to a "single rigid, leafy branch . . ." at CAS ". . . without a note to indicate whence or through whom it was obtained". He suggested, nevertheless, that the plant "may have come from some island of the Californian coast long ago". Fragments at GH, labelled by Greene and dated 5 May 1882, are undoubtedly from this specimen. (Holotype: CAS; Isotype: GH!)

Open irregular shrub 6–25 dm tall, loosely branched. Branches irregular, 1–8 mm in diameter, 1–12 dm long, densely lanate-tomentose, lower woody portions to 3 cm in diameter with tomentum irregularly distributed and revealing light brown bark, leafy to capitulescence, with internodes averaging 5–20 mm, striate underneath the tomentum. Leaves sessile to subpetiolate, subclasping, narrowly ovate to obovate, obtuse, 4–14 cm long, 1–5 cm wide, thick, subcoriaceous, densely short-tomentose adaxially densely lanate-tomentose abaxially, coarsely serrate to subentire, pinnately veined. Heads radiate, in compound, subcorymbose capitulescences. Involucres broadly turbinate to campanulate, 10–13 mm high, 10–13 mm wide; bracts 30–50, loosely imbricated in several series, the outer ones densely lanate-tomentose, the inner ones lanate-pubescent below with a tuft of woolly pubescence at the apex, 4–10 mm long, 1–2 mm wide, oblong, acute. Ray florets 6–14, inconspicuous, not exceeding the disk, yellow changing to red-purple in age, scarcely bilabiate to ligulate, the ligules to 2.2 mm long and 0.9 mm wide, the corolla tubes 5–6 mm long, the style branches linear, obtuse, 0.5–1 mm long, stigmatic to apex. Disk florets 30–40, yellow changing to red-purple with age, the corolla slightly ampliate from the middle, 8–10 mm long, the lobes to 1 mm long, very sparsely puberulent in the lower portion, the anthers 3.5–4.5 mm long, the style branches linear to narrowly ovate-appendages, 1.4–2 mm long, the puberulent appendage much shorter than the stigmatic portion. Ray and disk achenes similar, fusiform, 3–4 mm long, to 1 mm wide, pubescent, 4-nerved, striate. Pappus of 30–40 scabrous, brown or reddish-brown bristles, 6–9 mm long. Chromosome number, $n = 5$ (fide Pinkava on label of *Clark 1061*; Raven et al., 1960).

Distribution. Sparse populations on open rocky hillsides and canyon walls, Anacapa Island (fide Raven, 1963), Santa Rosa and Santa Cruz Islands, Santa Barbara Co., CA (Fig. 1C); often associated with species of *Pinus, Rhus, Mimulus, Arctostaphylos, Ceanothus,* and *Quercus* at 15–300 m; flowering Apr–Nov.

Hazardia detonsa is most closely related to *H. cana* of the southern islands; these have been considered conspecific by several authors (Greene, 1886; Hall, 1928; Munz, 1959). Raven (1963) re-established the specific status of *H. detonsa* and suggested that confusion between it and *H. cana* in the past has been caused by a lack of adequate material of the latter and the extreme variability of the former, due in part to hybridization with *H. squarrosa* var. *grindelioides.*

13. **Hazardia brickellioides** (Blake) Clark, comb. nov.—*Haplopappus brickellioides* Blake, Proc. Biol. Soc. Wash. 35:173. 1922.—TYPE: USA: NV: Nye Co.: Rocks, Ash Meadows, Sheep Mt., May–Oct 1898, *C. A. Purpus 6022* (Holotype: US!; Isotypes: NY!, UC!)

Rigid shrub 2–8 dm tall, much branched from hard woody trunk. Branches white-barked, aging to gray, 1–3 mm in diameter, 1–4 dm long, pilose to scabrid, some hairs thickened and tipped with yellow glands, leafy throughout, with internodes averaging 0.5–2 cm, straight to zigzag, angled from leaf margins and midrib downward. Leaves oval, elliptic or obovate-cuneate, acute, 10–35 mm long, 5–25 mm wide, coriaceous, pilose to scabrid, some hairs thickened and tipped with yellow glands, the midrib prominent, the lateral veins less prominent to obscure, reticulate, the apex tipped with a white spine 0.5–1 mm long, the margins dentate with 1–4 pairs of spinose teeth to 0.5 mm long, rarely entire. Heads radiate, solitary at ends of branchlets or in cymose capitulescences with 2–3 heads, peduncles 1–10 mm long from upper axils. Involucres cylindric to turbinate, shorter than disk, 6–7 mm high, 4–5 mm wide exclusive of the squarrose tips; bracts 15–25, in 4–5 series, lanceolate, 1-nerved, hispidulous and glandular, the tip greenish, squarrose or the inner ones erect, 3–7 mm long, 1–1.5 mm wide. Ray florets 5–8, yellow, inconspicuous, not exceeding the disk, the ligules 2–4 mm long, 0.5–1 mm wide, scarcely toothed at apex, the corolla tubes 4–5 mm long, the style branches linear, obtuse, 0.5–1.7 mm long, stigmatic to apex. Disk florets 8–12, yellow, the corolla slightly ampliate from the middle, 6–8 mm long, the lobes to 0.5 mm long, glandular-puberulent, the anthers 2.5–3 mm long, the style branches linear, 0.9–1.5 mm long, the appendage much shorter than the stigmatic portion. Ray and disk achenes similar, oblong, 2–3 mm long, 1 mm wide, silky pubescent, with 5 white nerves. Pappus of 20–30 scabrous, white to brownish bristles, 5–7 mm long. Chromosome number, $n = 6$ (Anderson et al., 1974; Jackson, 1966).

Distribution. Locally common on rock outcrops and cliffs, limestone mountains, in S Nye and Clark cos., NV, and in the Death Valley region of Inyo Co., CA (Fig. 1A); usually associated with species of *Atriplex, Eriogonum,* and *Brickellia* at 700–2100 m; flowering Jun–Oct.

Hazardia brickellioides was included in *Haplopappus* section *Belpharodon* by Hall (1928), based on the immature heads of the type collection. Jackson (1968) transferred it to section *Hazardia* because of the meiotic behavior of the chromosomes in artificial F_1 hybrids between *H. brickellioides* and *H. squarrosa* var. *squarrosa.* The chromosome number of *H. brickellioides, n* = 6, is anomalous in *Hazardia,* but all other characters support its inclusion in the genus.

EXCLUDED NAMES

Hazardia serrata Greene, Pittonia 1:30. 1887. = HAZARDIA DETONSA × SQUARROSA. [cf. Raven (1963)]. TYPE: USA: CA: Santa Barbara Co.: Santa Cruz Island, Jul–Aug 1886, *E. L. Greene s.n.* (Holotype: ND-G; Isotype: ND-G)

LIST OF EXSICCATA

More than 1500 herbarium specimens were examined during this study. Along with field observations these are the basis of my morphological and distributional data. A list of specimens examined is on file at ASU and has been distributed to herbaria cited below. Additional copies are available on request from the author.

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A NEW SPECIES OF OREONANA, A GENUS OF SNOW-ADAPTED UMBELLIFERAE

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Abstract

A new species, *O. purpurascens,* is described from California. A chromosome number of $n = 11$ is reported for each of the three species of the genus. Observations are recorded on the adaptation of the life cycle to conditions of heavy snowfall and the unique mode of seed dispersal. Comments on generic relationship and a key to the species conclude the paper.

Oreonana purpurascens Shevock & Constance, sp. nov.

Plantae perennes acaulescentes e radice palari, foliis et inflorescentia dense pubescentibus vel inflorescentia glabrata; vaginae longae, foliorum laminis anguste ovatis pinnatis bipinnatisectis, divisionibus ultimis lanceolatis oblongisve; petioli quam laminae plerumque breviores; inflorescentia crescens primum ante folia, umbellis maturis magnis globosis cinereo-hirsutis, pedunculis folia distincta excedentibus; radii quoquoversus radiantes ad basin versus breve dilatati, radiis exterioribus scarioso-alatis connatisque; umbellulae 1–3-floribus fertilibus et 15–30 floribus staminalibus sterilibusve obsitae; involucellum lobatum; flores albi umbellis post anthesin purpureis; sepala purpurea conspicuissima, pedicellis staminalibus sterilibusve dense hirsutibus fructum aliquantum excedentibus; fructus ovalis orbicularisve, superficie albo-hirsuta glabratave; vittae in intervallis et in commissuris plures; seminum superficies involuta (Fig. 1).

Plants perennial, acaulescent, 8–22 cm tall, the taproot massive and often branched, the leaf blades and petioles and the inflorescence densely short-grayish-hirsute, or the inflorescence ± glabrate; bladeless sheaths 3–6 cm long, the lamina of foliage leaves narrowly ovate, 5–10 cm long, 4–8 cm broad, obtuse at apex, truncate at base, pinnate and then bipinnatisect, the ultimate divisions lanceolate or oblong, mucronate, but not evidently cartilaginous-margined, 1–3 mm long, up to 1 mm broad; petioles 4–7 cm long, purple, persistently hirsute, mostly shorter than lamina; inflorescence appearing well before foliage leaves, the umbels globose, grayish-hirsute, 2.5–4.5 cm in diameter at maturity, the peduncles rather stout, 12–18 cm long, glabrous or glabrate, definitely exceeding leaves; rays 20–35, stout to slender, 5–15 mm long, spreading in all dimensions, the outer broadly scarious-winged and scarious-webbed, but all shortly dilated at base; umbellets of 1–3 fertile and 15–30 either staminate or entirely sterile flowers;

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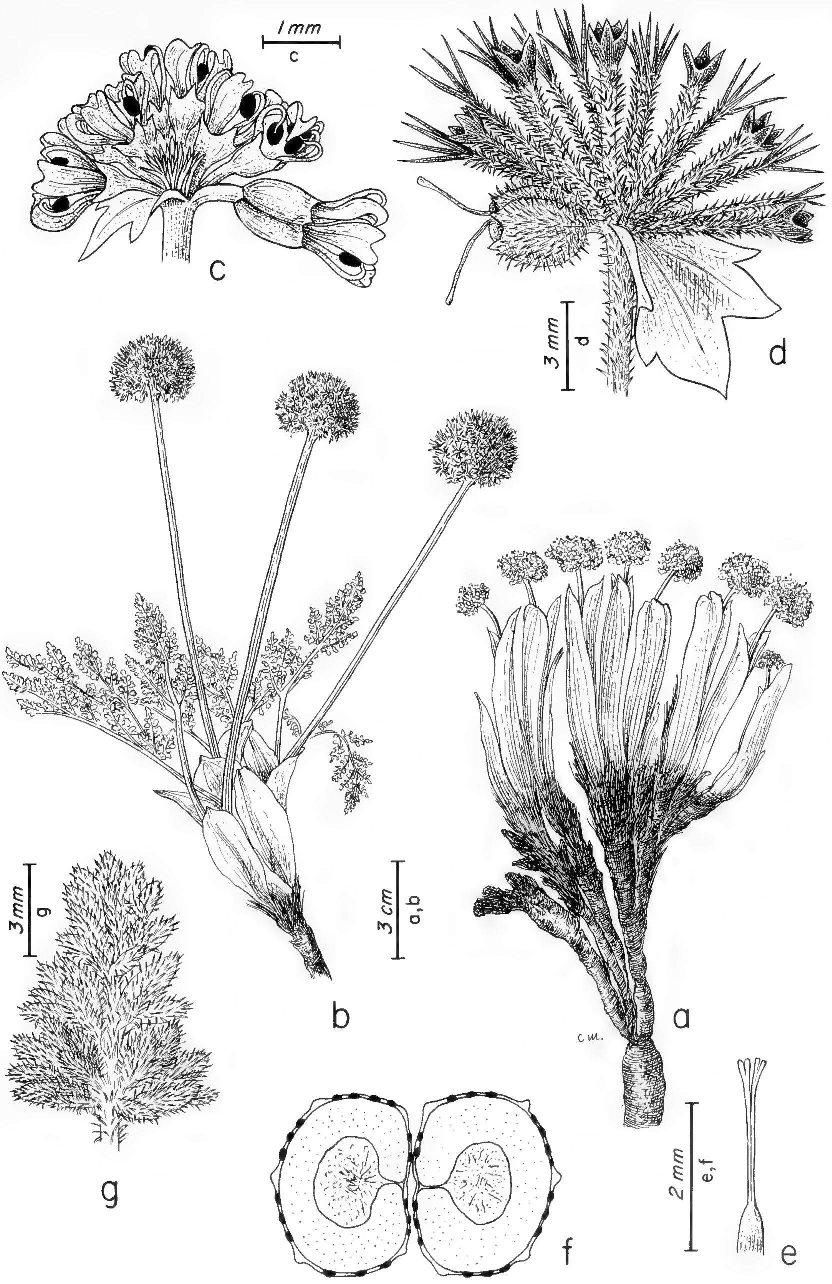

FIG. 1. *Oreonana purpurascens*. a. Flowering habit. b. Fruiting habit. c. Flowering umbellet (opened and some flowers removed). d. Fruiting umbellet. e. Carpophore. f. Fruit transection. g. Leaflet. All from *Shevock 5412, 5428*.

involucel with 5 or more irregular lobes, the lobes lanceolate-attenuate, mostly glabrate dorsally, scarious with prominent purple veins; flowers white, but heads turning purple after anthesis due to the purple sepals, the anthers purple; sepals usually 3 or 4, conspicuous, lanceolate to linear-subulate, mostly 1.5–3 mm long, those of staminate flowers joined at base to form a narrow cup, the sepals spreading-ascending and calyx hence somewhat stellate-spreading, the pedicels of staminate and sterile flowers 3–10 mm long, densely short-hirsute and considerably exceeding fruit when mature; petals usually 4, oblanceolate to obovate-spatulate, 1.5–2.5 mm long, early deciduous; styles 1.5–3 mm long; ovaries white-hirsute; fruit oval to orbicular, 4–5 mm in diameter, the surface short-white-hirsute to glabrate, the ribs filiform; vittae 3–5 in the intervals, 3–5 on the commissure; seed face involute.

TYPE: USA, CA, Tulare Co.: Slate Mt., T21S R32E S19, Sequoia Natl. Forest, 2690 m, 14 Jun 1977, *Shevock 5537*. Holotype: UC; Isotypes: COLO, F, GH, K, MO, NY, RSA, US.

Additional specimens examined: USA, CA, Tulare Co.: Weaver Lake trail, Jul 1946, *Buckalew s.n.* (UC); Big Meadows, 7 Jun 1952, *Buckalew s.n.* (FSC); Slate Mt., T21S R31E S25, 15 Jul 1976, *Shevock 5212* (CAS), T21S R32E S19, 19 Apr 1977, *Shevock 5411* (UC), T21S R31E S24, 19 Apr 1977, *Shevock 5412* (UC), T21S R32E S19, 26 Apr 1977, *Shevock 5428* (UC); summit trail between Mountaineer Cr. & Jacobsen Meadow, T20S R31E S3, 26 May 1977, *Shevock 5474* (UC). Nearly all populations so far discovered occur on open metamorphic ridge tops in Red Fir forest at 2625–2790 m, a habitat that appears to favor dispersal by wind and gravity. The plants are most common on rocky, sparsely vegetated ridges, considerably less abundant where the ripe fruits become lodged and germinate in pine mat manzanita, and very scarce among the red fir and white pine adjacent to the ridges.

Oreonana comprises a small group of montane herbaceous California Umbelliferae (Apiaceae) adapted to low-temperature environments and extensive winter snow cover. These belong to the ecological class of spring ephemerals, which grow from underground storage organs and develop rapidly both vegetatively and reproductively as the snow melts (Salisbury et al., 1973). Their life cycle appears to resemble that of *Orogenia linearifolia* Wats., in which "flowers were completely formed within an apical sheath while still beneath the soil surface and under snowy cover" (Kimball et al., 1973, p. 161). As stated by Billings, "Almost all alpine plants . . . produce flower primordia at least the year before flowering and sometimes 2 or 3 years before. These preformed flower buds insure that there is no delay in flowering after snowmelt and that there is time for seed-set, assuming all other environmental conditions are met. The preformed flower bud is a ubiquitous arctic-alpine adaptation" (1974, p. 126). In the case of *Oreo-*

nana, "Its acaulescent nature, with the small leaves and scapes arising directly from the root crown, contribute to its early blooming since time is not consumed in growing a main stem," as remarked by Buckalew (unpublished, 1956. Copies are available from L. C.).

The senior author has made extensive observations and numerous photographs of *O. clementis* and *O. purpurascens* during the course of their ontogeny. In *O. clementis* the flower buds emerge directly from the ground after or at the same time as the leaves, but never before them. There is no protective sheath surrounding the buds as they force their way up through the granitic gravel. Occasionally one may find a laggard bud working its way to the surface even after the majority of them has developed. In *O. purpurascens,* on the other hand, as soon as the snow melts, the mature flower buds push their way up through the large sheaths that extend well above the ground surface, presenting a display reminiscent of that of some of the small Sierran species of *Allium.* Once a sheath breaks the surface of the ground, no more buds emerge from that sheath. The foliage leaves emerge only after the flowers are fully expanded; only two leaves develop on each flowering stalk. As the white petals fall, the heads become quite purple from the deep color of the calyx; at the same time, the dark purple peduncles elongate markedly. Eventually, however, both heads and peduncles lose their purple coloring.

At the inception of this study, no cytological information was available for any species of *Oreonana.* We are now able to report chromosome counts on all three species (Table 1). We are most grateful to Tsan-Iang and Fei-mei Chuang of Illinois State University, Normal, for making these counts. The somatic count for *O. purpurascens* was obtained from root tips secured by germinating fruit soaked for 24 hours in a 1 percent solution of Clorox and kept for two months at a temperature of approximately 4°C. The meiotic counts were secured from buds fixed in the field.

Obtaining buds of *O. purpurascens* in the meiotic stage proved to be particularly difficult. In 1977, buds were collected while the snow was melting, but these proved to be too mature. Late in April, 1978, the senior author snow-shoed up Slate Mountain, dug down through 8–10 feet of snow and found purple anthers, an indication of pollen. On the basis of this experience, we concluded that flower buds must form at the end of the summer growing season and that meiosis must occur during late fall or winter. Bud-collecting trips were commenced in August, and very minute flower buds were detected at that time, but such buds showed very little enlargement even late into October. After the occurrence of three small snowstorms earlier in the month, however, buds which provided dividing pollen mother cells were secured on 27 November.

The mode of fruit/seed dissemination is also remarkable. Buckalew (loc. cit.) described it as follows: "The fruiting head, freed from the

TABLE 1. CHROMOSOME NUMBERS IN *Oreonana*.

Species	$n =$	$2n =$	Collection
O. clementis	11		Lloyd Meadows, Sequoia Natl. Forest, Tulare Co., 29 Mar 1977, *Shevock 5406*.
	11		Dome Rock, Sequoia Natl. Forest, Tulare Co., 19 Apr 1977, *Shevock 5408*.
O. purpurascens	11	22	Slate Mt., Sequoia Natl. Forest, Tulare Co., 14 Jun 1977 (27 Nov 1978), *Shevock 5537*.
O. vestita	11		Mt. Baldy notch, Angeles Natl. Forest, San Bernardino Co., 4 May 1977, *Shevock 5429*.

plant by the withering scape, is very light and quite round, so that it can be moved by a comparatively light breeze to shake out its seeds as it rolls." Wind dispersal (anemochory) is not unique in Umbelliferae. As quoted by Dawson (1967), Philipson and Hearn comment on a particular New Zealand scree plant: "As the seeds ripen on the female plants the thin base of the stem breaks and the whole visible part of the plant dries up and becomes stiff. This ball-like mass acts as a tumbleweed, being blown along the surface of the scree shedding seeds as it goes" (1962, p. 31). Van der Pijl cites instances from other families in which globular infructescences break off and roll along the ground (chamaechores), notably *Fedia* (Valerianaceae) from the Mediterranean region and *Spinifex* (Gramineae) from Australia and Indonesia, the so-called "wind-balls" (1969, p. 59). What is unique about *Oreonana,* however, is not only the abscission of the whole infructescence, but the fact that the pedicels of sterile and staminate flowers, which surpass those of fertile ones, become rigid and, with the aid of the persistent calyx, act like the spokes of a three-dimensional wheel, with the fruits carried near the hub until they are jarred loose—a true "tumble umbel"!

The genus *Oreonana* was proposed by Jepson to accomodate what he believed to be an undescribed plant (*O. californica* Jepson) from the Mount Whitney region of the Sierra Nevada, and *Deweya vestita* Wats., which had been named much earlier from the San Gabriel Range of southern California. *Oreonana californica* was subsequently shown to be conspecific with *Drudeophytum clementis* M. E. Jones. Jones (1912) referred to the instability of generic lines in this part of the family, as reflected in the synonymy of *O. vestita,* which has been placed at various times also in *Velaea* DC., *Deweya* Torr. & Gray, *Drudeophytum* Coult. & Rose, and *Tauschia* Schlecht. The vicissitudes of these genera need not concern us here. Mathias and Constance (1944, pp. 89–90) concluded that *Oreonana,* distinguished by its prominent and persistent sterile pedicels, deserved generic status, although it appears to be closely related to *Tauschia* and *Arracacia*.

The discovery that all three of its species are diploid and have a chromosome complement of $n = 11$ is not particularly helpful in determining the affinities of *Oreonana* within the family. Both *Tauschia* and *Arracacia* have a base number of $x = 11$, and four western American species of *Tauschia* (*T. arguta, T. glauca, T. hartwegii, T. parishii*) are diploid. All species of *Arracacia* and the Mexican species of *Tauschia* that have been investigated cytologically appear to be polyploid, but the chromosome numbers of most species have not yet been determined. Thus, a relationship of *Oreonana* to *Tauschia* is at least not precluded by the cytological data.

Key to *Oreonana*

Foliage and inflorescence grayish-hirsute with short stiff hairs; umbels globose, the rays spreading in all dimensions, the outer rays usually conspicuously scarious-winged; flowers white with purple anthers; sepals conspicuous, stellate-spreading; pedicels of staminate/sterile flowers 3–10 mm long.

  Inflorescence appearing simultaneously with or a little after foliage leaves; bladeless leaf sheaths 0.5–2 cm long; umbels 1–3 cm in diameter, the rays 5–15 (20), 2–8 mm long; flowers either perfect or staminate; sepals of staminate flowers yellow, mostly 0.5–1.5 mm long . . . . 1. *O. clementis* (M. E. Jones) Jeps.

  Inflorescence appearing well before foliage leaves; bladeless leaf sheaths 3–6 cm long; umbels 2.5–4.5 cm in diameter, the rays 20–35, 12–18 mm long; flowers perfect, staminate, or entirely sterile; sepals of staminate and sterile flowers deep purple, mostly 1.5–3 mm long. . . . . 2. *O. purpurascens* Shevock & Constance

Foliage and inflorescence densely white-tomentose with long silky hairs; umbels hemispherical, the rays spreading horizontally to ascending, the outer rays not scarious-winged; flowers mostly yellow or maroon with yellow anthers; sepals inconspicuous, not stellate-spreading; pedicels of staminate flowers 10–25 mm long. . . . . 3. *O. vestita* (S. Wats.) Jeps.

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PINUS COULTERI AND WILDFIRE ON MOUNT DIABLO, CALIFORNIA

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ABSTRACT

Wildfires burned stands of *Pinus coulteri* on Mt. Diablo, in west-central California, in 1931 and 1977. Trees in woodland vegetation survived the earlier burn but were largely destroyed by the more recent fire, perhaps because of fuel accumulations associated with fire suppression. Coulter pine in brush vegetation suffered mortality in both years. Reproduction of the trees was high after each burn, and little seeding occurred in brush environments except during years following the fires. Policies of fire suppression that lead to high intensity burns in both woodlands and chaparral seem detrimental to the species.

Wildfires typically promote the reproduction of pines (*Pinus*) and restrict the survival of competing species (Mirov, 1967). The relationship between wildfire and *Pinus coulteri* D. Don, a species restricted to central and southern California, however, appears unclear. Several authors have suggested that the range of coulter pine has been restricted by fire, or that the tree has increased with recent suppression of fires (Zobel, 1953; Wilson and Vogl, 1965; Wright, 1968; Griffin, 1976). By contrast, other evidence has indicated that reproduction of coulter pine may be unaffected, or even encouraged, by burning (Wright, 1970; Minnich, 1976; Vogl, 1976). The differing intensities of fires in years prior and subsequent to the initiation of fire suppression may in part account for these apparently contradictory responses (Vogl, 1976).

In the summer of 1976, I began sampling three stands of coulter pine on Mt. Diablo, in west-central California, to determine the effects on the species of a July, 1931, fire (Bowerman, 1944). In July, 1977, a fire again burned two of these areas, and I resampled all three stands in the summer of 1978. This paper evaluates the effects of both fires.

METHODS AND RESULTS

In 1976, the point-quarter method was used to sample the trees along a 900 m east-west traverse of the 30 ha woodland on the north slope of Twin Peaks (Fig. 1:A). The sizes and ages of the coulter pines indicated that the species occurred as an all-aged stand. Half of the 49 measured trees were less than 9 cm dbh, with each increasingly larger 10 cm diameter class represented by fewer individuals; the largest tree encountered had a dbh of 71 cm. Of the 27 coulter pines cored with an increment borer, 13 were more than 45 years of age, and thus had survived the 1931 fire; the oldest tree was more than 104 years of age. Only trees exceeding 28 cm dbh (about 50 years of age) had

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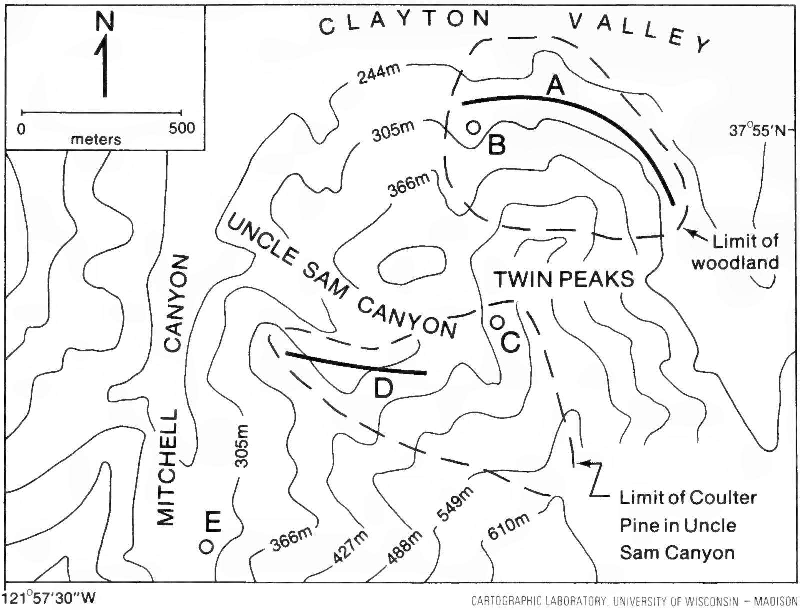

FIG. 1. Contour map of northwest edge of Mt. Diablo, indicating sample sites. A. Traverse of woodland sampled in 1976 and 1978. B. Area of light burn sampled in 1978. C. Area in brush sampled in 1976 and 1978. D. Traverse sampled in 1976. E. Grove sampled in 1976 and revisited in 1978.

heavily charred bark, typically extending 1 to 3 m up the trunks. All trees less than 28 cm dbh were free of charring, implying an absence of fires over the last 50 years. A strong correlation (r = 0.96) between size and age suggested that the stand had developed with little competition, and thus in an open woodland. By contrast, sampling showed that the woodland had an understory of *Pinus sabiniana, Quercus agrifolia,* and locally of *P. coulteri,* as well as scattered growth of smaller woody plants. The average distance between all trees in the woodland was 4.9 m, and the basal area per ha for coulter pines was 13.2 m^2 (for all trees, 21 m^2). In spite of dominating the overstory (importance values for tree species in the woodland were *P. coulteri* 140, *Q. agrifolia* 72, *P. sabiniana* 51 and *Q. douglasii* 38), coulter pine was not reseeding throughout the stand: seedlings were restricted to open areas.

The remaining 1976 sampling included coring of all coulter pines along a 350 m traverse of the scattered trees south of the bottom of Uncle Sam Canyon (Fig. 1:D), within a 2 m by 40 m quadrat near the head of that canyon (Fig. 1:C), and along a 50 m traverse of a grove of about 40 trees in Mitchell Canyon (Fig. 1:E). In each of these areas, the coulter pines were associated with heavy brush, notably *Hetero-*

meles arbutifolia, Ptelea crenulata, and *Toxicodendron diversilobum.* In both Uncle Sam and Mitchell canyons, coulter pines were even-aged. Forty of the 41 trees cored had germinated between 1932 and 1950, and one had germinated before 1932. Only two trees, both uncored seedlings in Uncle Sam Canyon, had germinated after 1950. These stands of coulter pine apparently became established shortly after the 1931 fire, which Bowerman (1944) reported as having destroyed most of the trees. For the 26 years after 1950, essentially no reproduction had occurred in these stands in heavy brush.

The 1977 fire swept through most of the Twin Peaks woodland and much of the stand in Uncle Sam Canyon. Unlike the 1931 burn, the recent fire killed most of the coulter pines on Twin Peaks. In June, 1978, sampling by the point-quarter method along the traverse of the woodland studied in 1976 (Fig. 1:A) found only 3 percent of the coulter pines alive. Essentially all of the dead trees retained brown needles, suggesting that the burn was a hot ground fire. The trunks of the trees were charred high into the canopy.

Several other areas on Twin Peaks, not sampled in 1976, were apparently subjected to less intense heat, and supported higher percentages of living trees. The least damaged portion of the woodland, with coulter pines charred but alive, was a strip 20–100 m wide along the northern edge of the stand where the woodland borders the grassland and savanna of Clayton Valley. Two additional areas of ca. 1 ha each, both within the woodland on northwest exposures, also supported many (25–75) living coulter pines. In one of these two small areas near the west edge of the woodland (Fig. 1:B), a survey found nine of 52 coulter pines (17 percent) alive; all trees larger than 40 cm dbh had survived, and all but one smaller than 40 cm dbh were dead. On the living trees, brown needles were restricted to the lower branches, and charred bark extended at most 10 m up the trunks.

Pine seedlings (species could not be identified in these recently-germinated seedlings) were much more common in the woodland after than before the fire. In 1978, they were found in 19 of 34 4m^2 quadrats examined along the traverse of the heavily burned section of the woodland, with an average of one seedling per 8 m^2. Contrarily, in two 40 m traverses within one of the areas of lighter burn, all of 14 samples contained pine seedlings, with an average of two seedlings per m^2. The intense heat in the heavily burned area may have destroyed seeds within the cones of the trees, but the less intense heat in the lightly burned area may have helped to open the cones without destroying the seeds. Seedlings were disproportionately located on sites with much exposed mineral soil; 88 percent of the quadrats with less than 25 percent coverage by organic litter or plants had pine seedlings, and only 29 percent of the quadrats with more than 75 percent of such coverage had pine seedlings.

The sampling indicated that 20 percent of the coulter pines in Uncle

TABLE 1. SUMMARY OF *Pinus coulteri* STAND DATA AFTER 1931 AND 1977 WILDFIRES.

Year	Twin Peaks woodland		Uncle Sam Canyon brush	Mitchell Canyon brush
	A	B		
1976	all-aged stand; mature trees developed without strong competition; seedlings restricted to open areas	not sampled	even-aged stand; trees germinated 1932–1950; very few seedlings	even-aged stand; trees germinated 1932–1950; no seedlings
1977	heavy burn	light burn	spotty burn	not burned
1978	3% of *P. coulteri* alive; seedlings common throughout stand, averaging 1 per 8m^2; seedlings on mineral soil	17% of *P. coulteri* alive; 7 trees larger than 40 cm dbh alive, and most smaller trees dead; seedlings abundant, averaging 2 per 1m^2; seedlings on mineral soil	20% of *P. coulteri* alive, but these mostly unburned; most burned trees dead; seedlings scattered, averaging 1 per 10m^2; seedlings on mineral soil	stand little changed; no healthy seedlings

Sam Canyon (Fig. 1:C) were alive in 1978. The surviving trees were scattered, and most were not burned, apparently reflecting spottiness of the fire. Most of the dead trees were heavily charred and without needles, suggesting an intense crown fire; such a burn is not surprising considering the tall brush and the small stature of the pines in the prefire vegetation. The coulter pines at the southern edge of the stand, however, were in a large area that escaped burning in 1977. Only five 4m^2 quadrats of 18 examined in the burned area had pine seedlings, with an average of one seedling per 10 m^2. Seedlings were restricted to quadrats in which at least 50 percent of the ground area was exposed mineral soil. The paucity of seedlings in Uncle Sam Canyon, even in areas with mineral soil, is a puzzle; it could be related to the destruction of seeds by the fire.

The grove in Mitchell Canyon (Fig. 1:E) was not burned in 1977 and remained a stand of coulter pine emerging above a dense understory of *Heteromeles arbutifolia* and *Quercus agrifolia*. The brush was sufficiently dense to make foot travel difficult. Many of the *Heteromeles* plants were dead but uncharred, suggesting that their deaths occurred after the 1931 fire; the shade cast by the oaks and pines may have been responsible for the shrub mortality. The ground surface within the stand was covered by a thick layer of pine needles and oak leaves. No pine seedlings were found in either 1976 or 1978, except for a few pale, poorly-developed individuals at one locale near the southern edge of the grove in 1978. These data and observations are summarized in Table 1.

CONCLUSIONS

This study led me to make several conclusions about coulter pine and wildfire on Mt. Diablo: (1) in the woodland on Twin Peaks, the 1977 fire was apparently much hotter and more destructive than that of 1931. The greater intensity of the more recent fire may have resulted from increased fuel loads caused by successful fire suppression in the years after 1931. This pattern of fire suppression, leading to accumulation of fuels and high intensity burns, is common in forests in the American West (e.g., Kilgore, 1973; Agee et al., 1978); (2) the fires killed coulter pines in the brushy environments in both 1931 and 1977, probably because of abundant fuels in each year. The intensity of fires in chaparral vegetation, as in woodlands or forests, may be greater since initiation of fire suppression (Parsons, 1976), and such hot fires may be responsible for reducing the distribution of certain tree species including *P. coulteri* (Wright, 1968; Vogl, 1976); (3) reproduction by coulter pine in both woodland and brushy vegetation is greatly enhanced by burning that exposes mineral seedbeds (cf. Minnich, 1976; Vogl, 1976); (4) the differential survival of large trees and the enhanced reproduction in less-intensely burned areas both suggest that frequent light fires may be beneficial to the species in woodland vegetation (cf. Griffin, 1976); and (5) the ecological behavior of coulter pine appears different in differing parts of its ecological range, presumably because of variations in environmental conditions and associated species.

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NOTEWORTHY COLLECTIONS

POLYGONUM HYDROPIPEROIDES Michx. (POLYGONACEAE).—Ecuador, Galápagos Ids., Indefatigable (Santa Cruz) I., S slope, 300 m, moist places, 7 Apr 1930, *Svenson 98* (BKL). Seen through courtesy of the Director, Brooklyn Botanical Garden.

Previous knowledge. Reported under this name by Svenson (Amer. J. Bot. 22:228. 1935): "South slope of the mountain, scattered in a moist ravine at 1000 ft." Erroneously ascribed to Isla Isabela in Wiggins and Porter (*Fl. Galápagos Ids*. 1971). Not otherwise known from the archipelago.

Diagnostic characters. Pl andromonoecious; lvs broad- to linear-lanceolate, ± glabrous except marginally; fls pink to rose; fr perianth oval, completely enclosing achene at maturity.

Significance. Abaxial surfaces of lvs of *Svenson 98* are covered with silvery pustules ("plate glands") typical of *P. opelousanum* Ridd. ex Small (Mitchell, Bull. N. Y. St. Mus. 431:53. 1978). Plate glands do not occur on *P. hydropiperoides*. *P. opelousanum*, more tropical in distribution than *P. hydropiperoides*, has been collected a number of times on Isla Santa Cruz in the general area where Svenson gathered his specimen. This is a single small plant with immature achenes that have not yet enlarged enough to become exserted from the perianth, as is typical for *P. opelousanum*. This character is generally used in keys to distinguish the two species. Thus, *P. hydropiperoides* should be deleted from the list of plants known to occur in the archipelago.—DUNCAN M. PORTER, Department of Biology, Virginia Polytechnic Institute & State University, Blacksburg 24061. (Accepted 28 Apr 1978.)

The following records are from the Arizona Strip, that portion of Arizona lying north and west of the Colorado River. Collections were made as part of a Bureau of Land Management inventory. Special acknowledgment is due Ralph K. Gierisch, BLM, who has generously provided many collections and field assistance.

For all taxa reported herein, herbaria consulted are ASU, ARIZ, ASC, and MNA; published sources are the following: Abrams, Illus. flora Pacific States. 1940–1960; Barneby, Mem. New York Bot. Gard. 13:1–1188. 1964; Beatley, Vasc. pls. Nevada Test Site. 1976; Benson, The cacti of Arizona, ed. 3. 1969; Cronquist et al., Intermountain flora. 1977; Davis et al., Flora of Idaho. 1952; Federal Register 40(127):27824–27924. 1975; Federal Register 41(117):24524–24572. 1976; Gillett, Canad. J. Bot. 50:1975–2007. 1972; Harrington, Man. pls. Colorado, ed. 2. 1964; Hitchcock and Chase, Man. grasses U. S. 1950; Hitchcock et al., Vasc. pls. Pacific Northwest. 1955–1969; Kearney et al., Arizona flora. 1960; Lehr, J. Ariz. Nev. Acad. Sci. 14:18. 1979; McDougall, Seed pls. Northern Arizona. 1973; McDougall and Stockert, Plateau 39:102–103. 1966; Muenscher, Poisonous pls. U. S., ed. 2. 1975; Munz, A flora of southern California. 1974; Munz, A California flora. 1959; Parker, An Illus. guide to Arizona weeds. 1972; Porter, A flora of Wyoming. 1962–1972; Raven, Contr. U. S. Natl. Herb. 37:161–396. 1969; Reveal, Phytologia 34:409–484. 1976; Shreve and Wiggins, Vegetation and flora of the Sonoran Desert. 1964; Tutin et al., Flora Europea. 1964; Welsh, Great Basin Naturalist 38:225–367. 1978; Welsh and Moore, Utah Plants, Tracheophyta. 1973; Welsh et al., Great Basin Naturalist 38:125–179. 1978.

BALSAMORHIZA HOOKERI Nutt. (ASTERACEAE).—Mohave Co.: Virgin Mts, E side Black Rock Mt, ca. 4 km W of Maple Spring, T39N R14W S13, basalt with *Juniperus, Pinus,* and *Artemisia tridentata,* 1900 m, 21 May 1978, *Brown 803 and Parfitt* (ASU).

Previous knowledge. NW WA to SW WY, S UT (Hitchcock), N CA (Munz). Absent from OR (Hitchcock).

Significance. First state record, representing a range extension from SW UT. *B. sagittata* (Pursh) Nutt. was recently reported from NE AZ (McDougall).

SOLIDAGO SPECTABILIS (D. C. Eaton) A. Gray. (ASTERACEAE).—Mohave Co.: near Littlefield, T40N R15W S4, along stream through desert shrub zone, 580 m, 21 Nov 1978, *Gierisch 4601* (ASU).

Previous knowledge. SE OR to UT, E-central CA (Munz).

Significance. First state record, representing a range extension from S UT.

STENOTUS ACAULIS (Nutt.) Nutt. (ASTERACEAE).—Coconino Co.: N end House Rock Valley, mouth of Burro Canyon, T39N R3W S4 NW¼, limestone, 1800–1950 m, 13 May 1978, *Brown 519 and Parfitt* (ASU); Buckskin Mts, T41N R2E S16 and 21, steep rocky limestone slope and ledges with *Cowania, Fallugia,* and *Artemisia,* 1990 m, 9 May 1978, *Gierisch 4285* (ASU).

Previous knowledge. Central OR (Abrams) to SASK (Davis), N-central CO (Harrington), N AZ (Kearney), Baja Calif. (Munz, 1974). Report from AZ based upon "doubtful evidence" (Kearney). Synonym: *Haplopappus acaulis* (Nutt.) A. Gray.

Significance. First definite state record, representing a range extension from adjacent UT.

Hutchinsia procumbens (L.) Desv. (**Brassicaceae**).—Mohave Co.: Buckhorn Spring ca. 8 km N of Lake Mead, T34N R16W S26, silty soil with *Larrea* and *Krameria,* 510 m, 19 Apr 1978, *F. Smith 934* (ASU). Cochise Co.: Croton Springs, Willcox Playa, 28 Mar 1962, *P. S. Martin s.n.* (ARIZ).

Previous knowledge. Brit. Columbia to WY, to W CO (Harrington), UT (Welsh and Moore), S CA (Munz), central Baja Calif. (Shreve), N AZ (Kearney); also Labrador to Newfoundland, in Europe, Asia, and Australia (Abrams).

Significance. Second and third state records; Croton Springs apparently the SE-most site in N.A. Last AZ collection from late nineteenth century at Pearce (Pierce) Spring, Mohave Co. (Kearney). We were unable to locate Pearce Spring on any maps.

Opuntia whipplei Engelm. & Bigelow var. **multigeniculata** (Clokey) L. Benson. (**Cactaceae**).—Mohave Co.: above Hurricane Rim, Navajo Trail, T39N R9W S8, rocky loam—limestone with *Cowania, Artemisia,* and *Chamaebatiaria,* 1615 m, 13 Sep 1978, *Gierisch 4509* (ASU).

Previous knowledge. Species from S NV to SW CO, to NW and W NM, N and central AZ (Benson). Variety from S NV to SW UT, NW AZ (Benson).

Diagnostic characters. Shrub with densely compact branching; joints up to 2 cm in diameter, usually shorter than 8 cm; spines 10 or more per areole, obscuring the stem; spine sheaths tan or yellowish-pink; fruit yellow, spineless; flowers greenish-yellow.

Significance. Second record of the variety in AZ. The previously reported locality is 116 km to the S. Proposed for threatened status throughout its range (Fed. Reg. 40).

Halogeton glomeratus (Bieb) Mey. (**Chenopodiaceae**).—Mohave Co.: E of Hurricane Rim near Antelope Springs, T41N R9W S23, desert scrub with *Atriplex, Chrysothamnus, Gutierrezia, Tetradymia,* and *Suaeda,* 22 Aug 1978, *Gierisch 4464* (ASU).

Previous knowledge. S ID to central WY (Porter), W-central CO (Harrington), UT, NV (Muenscher), S CA (Munz, 1974). Native to Eurasia (Porter).

Significance. First state record, representing a range extension from adjacent UT, and indicative of the continuing spread of this poisonous weed.

Astragalus acutirostris S. Wats. (**Fabaceae**).—Mohave Co.: 2.3 km SE of NV state line along road from Mesquite, NV to Lime Kiln Canyon, T38N R16W S9 NW¼, N-facing slope, sandy-rocky soil with *Larrea, Opuntia,* and *Yucca,* 790 m, 28 Apr 1978, *Brown 250 and Parfitt* (ASU). Identified by R. C. Barneby.

Previous knowledge. S and E CA to S NV, to Baja Calif. (Barneby), W-central AZ (Lehr).

Significance. Second record for the state and first record for Mohave Co. The Yavapai Co. locality (Lehr) is ca. 310 km SSE.

Trifolium kingii S. Wats. ssp. **macilentum** (Greene) Gillett. (**Fabaceae**).—Mohave Co.: Virgin Mts, Black Rock Mt, SE of Quaking Asp Spring, T39N R14W S10, 2060 m, 21 May 1978, *Brown 800 and Parfitt* (ASU). Identified by J. M. Gillett.

Previous knowledge. Species from S ID (Davis) to UT, E NV (Gillett), N AZ (Davis), W CO (Harrington). Subspecies from SW UT (Gillett, Welsh), E NV (Welsh). Because neither Gillett nor Welsh considered *T. kingii* ssp. *macilentum* to occur in CO or AZ, Harrington and Davis may have been working with misidentified specimens.

Diagnostic characters. Perennial to 35 cm tall with few leaves; leaflets thin, not fleshy, setose to dentate; heads conspicuously longer than broad; calyx sparsely pubescent, the lobes shorter than the tube.

Significance. First definite record for AZ, representing a range extension from adjacent SW UT.

PHACELIA CURVIPES Torr. (HYDROPHYLLACEAE).—Mohave Co.: Virgin Mts, Lime Kiln Canyon, T38N R16W S33 SE¼, E- and W-facing limestone slopes with *Juniperus, Pinus, Cowania,* and *Agave,* 1270 m, 28 Apr 1978, *Brown 265 and Parfitt* (ASU); Lime Kiln Canyon, T37N R16W S4, rocky and sandy SW slope with pinyon, juniper, *Quercus turbinella, Arctostaphylos,* and *Coleogyne,* 1430 m, 28 Apr 1978, *Gierisch 4232* (ASU).

Previous knowledge. S CA (Munz) to NV, SW UT (Welsh and Moore).

Significance. First state record, representing a range extension from SW UT and S NV. Its occurrence in AZ was anticipated by Kearney.

NAMA PUSILLUM Lemmon. (HYDROPHYLLACEAE).—Mohave Co.: Burro Study Area (Bureau of Land Management) ca. 8 km N of Lake Mead, T34N R16W S27, desert pavement with *Larrea, Ambrosia,* and *Opuntia,* 500 m, 27 Apr 1978, *F. Smith 983* (ASU).

Previous knowledge. SE CA (Munz) to S NV, W AZ (Kearney).

Significance. Second state record, representing a NNE disjunction of 162 km from the previously reported AZ locality at Fort Mohave, Mohave Co. Apparently the last AZ collection was made in 1884 (the type collection).

CAMISSONIA PARVULA (Nutt. ex T. & G.) Raven. (ONAGRACEAE).—Coconino Co.: W edge Paria Plateau, Corral Valley, along Corral Valley Road, T40N R4E S18 SE¼, deep sand with *Artemisia tridentata, Artemisia filifolia,* and *Juniperus,* 1860 m, 15 May 1978, *Brown 597 with Parfitt and Gierisch* (ASU). Identified by P. H. Raven.

Previous knowledge. S and central WA to W WY, to NW CO, UT, NV, E-central CA (Raven). Synonym: *Oenothera contorta* (Dougl.) Kearney var. *flexuosa* (A. Nels.) Munz, *pro parte.*

Diagnostic characters. Herbaceous annual to ca. 20 cm tall with one or more wiry stems, strigose to subglabrous, few glandular trichomes in inflorescence; leaves linear, definite basal rosette lacking; sepals reflexed singly, not in pairs.

Significance. First state record, representing a range extension from UT.

EREMOPYRUM TRITICEUM (Gaertn.) Nevski. (POACEAE).—Coconino Co.: ca. 1.6 km N of Fredonia on hwy 89A, T41N R2W S8 SE¼, hard gray clay with *Sarcobatus* and *Lycium,* 1430 m, 17 May 1978, *Brown 652 and Parfitt, Gierisch 4324* (ASU). Verified by F. W. Gould; N of Sedona, 1370 m, 1 Jun 1967, *Soil Conservation Service s.n.* (MNA).

Previous knowledge. E OR (Cronquist) to MT (Davis), to central CO (Harrington), W and central UT, N, NV (Cronquist). Native to Russia (Cronquist). Synonym: *Agropyron triticeum* Gaertn.

Significance. First state records, representing range extensions from W and central UT. Apparently continuing to spread.

POA NEVADENSIS Vasey ex Scribn. (POACEAE).—Mohave Co.: Virgin Mts, Lime Kiln Canyon, T38N R16W S33 SE¼, limestone with *Juniperus, Pinus, Cowania,* and *Agave,* 1270 m, 28 Apr 1978, *Brown 269b and Parfitt* (ASU). Verified by F. W. Gould.

Previous knowledge. AK (Cronquist) to MT (Hitchcock), to CO (Harrington), N AZ (McDougall), E-central CA (Munz).

Significance. Second definite locality for AZ and first record for Mohave Co., representing a disjunction of 280 km to the NW of the previously known AZ locality (Fort Valley Park, Coconino Co.).

SCHISMUS ARABICUS Nees. (POACEAE).—Mohave Co.: SW of St. George, flat SE of Black Knolls, with *Larrea, Lycium,* and *Krameria,* T41N R12W S18, 980 m, 20 May 1978, *Brown 757 and Parfitt* (ASU). Verified by F. W. Gould.

Previous knowledge. S CA (Munz, 1974) to S NV (Beatley), to S AZ (Kearney); also N AZ (Welsh et al.), SW UT (Cronquist), Chile (Hitchcock and Chase). Native to SW Asia (Munz) or Africa (Hitchcock and Chase).

Significance. Second record for N AZ, representing a disjunction of 185 km W of the site of the first N AZ record. These records, and a report of the species in extreme SW UT, add to the documentation of the continuing spread of *S. arabicus* throughout the range of *S. barbatus* as suggested by Parker.

ERIOGONUM DARROVII Kearney. (POLYGONACEAE).—Mohave Co.: near Ide Valley Spring, T39N R13W S31, rocky clay loam with *Pinus, Juniperus, Rhus,* and *Gutierrezia,* 19 Jul 1978, *Coombs and Bundy 2631* (ASU); near Ide Valley Spring, T38N R13W S6, gravelly loam in woodland with pinyon, juniper, and *Rhus,* 18 Aug 1978, *Gierisch 4453 and Bundy* (ASU); verified by J. L. Reveal; vicinity of Mt Trumbull, gravelly loam with *Juniperus, Cowania,* and *Artemisia,* 2 Jun 1978, *Gierisch 4375* (ASU); Parashont Wash, T34N R12W S10, rocky loam along roadside with *Juniperus* and *Artemisia,* 1740 m, 24 Aug 1978, *Coombs, Gierisch and Bundy 2695* (ASU); 0.8 km S of Pigeon Tank, T33N R12W S6, gravelly loam in road, 1740 m, 7 Sep 1978, *Coombs and Bundy 2753* (ASU). Verified by J. L. Reveal.

Previous knowledge. White Pine Co., NV and Kaibab Plateau, Coconino Co., AZ (Reveal).

Diagnostic characters. Low, spreading annual, leafy throughout; outer tepals fan-shaped and hooded.

Significance. First records for Mohave Co., representing disjunctions of 80–130 km W of previously reported localities. Proposed for endangered species status (Fed. Reg. 41). However, these collections show the species is rather widespread on the Strip.

RANUNCULUS TESTICULATUS Crantz. (RANUNCULACEAE).—Coconino Co.: ca. 1.6 km N of Fredonia along hwy 89A, T41N R2W S8 SE¼, hard gray clay with *Lycium,* 1430 m, 17 May 1978, *Brown 654 and Parfitt* (ASU); Coconino Co.: Oak Creek Canyon, May 1973, *Theroux 495* (MNA); Apache Co.: Canyon de Chelly National Monument, *Halse 756, 776, 791, 803, 843* (ARIZ); 6.4 km NW of Ganado along hwys 63 and 264, picnic area, 20 Apr 1979, *K. Rill 5018* (OSH, ASU).

Previous knowledge. E WA (Abrams) to NE WY (Porter), to W CO (Harrington), UT, N AZ (McDougall), NV, OR (Hitchcock). Native to SE and E-central Europe (Tutin). Synonym: *Ceratocephalus testiculatus* (Crantz) Roth.

Significance. Second, third, fourth, and fifth state records, representing the spread of the species throughout much of N AZ. May be expected to invade Mohave Co. which is ca. 1 km W of the Fredonia site. First report was from Grand Canyon Village, 110 km SSE of Fredonia (McDougall and Stockert).

GALIUM BIFOLIUM S. Wats. (RUBIACEAE).—Mohave Co.: E side Virgin Mts, Maple Spring in Maple Canyon, T39N R13W S17 and 20, steep N-facing slope, limestone with *Acer* and *Quercus,* 1680 m, 21 May 1978, *Brown 784 and Parfitt* (ASU).

Previous knowledge. S Brit. Columbia (Hitchcock) to MT, to W-central CO (Harrington), N AZ (Kearney), S CA (Munz, 1974).

Significance. Second state record and first Mohave Co. record, representing a disjunction of 170 km NW of the previously reported locality (Greenland Lake on N rim of Grand Canyon).—BRUCE D. PARFITT, GREGORY K. BROWN, and ELINOR LEHTO, Department of Botany and Microbiology, Arizona State University, Tempe 85281. (Accepted 30 Apr 1979).

PLASTICITY IN THE GERMINATION OF CALIFORNIA *Fragaria* SEEDS.—In two recent studies, substantial genetic variability was found in adults of *Fragaria chiloensis* and *F. vesca* for 25 quantitative traits and three enzyme systems (Hancock and Bringhurst, Amer. J. Bot. 65:795–803. 1978; Amer. J. Bot. 66:367–375. 1979). Most of these characters were shown to be significantly associated with various soil and climatic conditions, suggesting ecotypic differentiation. The purpose of this study was to determine if the germination responses of these species have also undergone ecotypic differentiation.

Eight diverse sites encompassing a broad range of environmental conditions were selected for study. These were McKinleyville (MK): near jct of Murray and Kelly roads N of McKinleyville; Pelican Beach (PB): 4 km S of the Oregon border; Dry Lagoon (DL): 6.4 km S of Redwood Creek Park; Enderts Beach (EB): along trail at end of Bluff Road; Pacifica Hilltop (PH): near jct of Copeland and Fassler avenues; Hecker Pass (HP): near Mt. Madonna along hwy 129; Point Sur (PS): headland north of Point Sur along hwy 1; and Año Neuvo (AN): beach at Año Nuevo Point.

From 15 Jul to 18 Aug 1975, runner plants were taken from at least 50 separate clones at each site, planted in 2000 cm^3 pots containing a sandy loam, and placed in a single greenhouse. They were fertilized, irrigated with deionized water, and protected from various pests and diseases as needed.

From the start of anthesis in March until its termination in August, pollen was transferred every three days among all open flowers in each population using a camel hair brush. Care was taken to keep the pollen of the various populations separate. As fruits ripened, they were squashed between two paper towels and their seeds were removed after drying for three days at room temperature. Seeds from at least 50 fruits of each population were mixed together and stored dry in envelopes at 5°C until the germination studies began six months later.

At equidistant points along the same transects used for plant collection, five soil samples were gathered from 5 cm beneath the soil surface and were stored at room temperature in open glass jars. The five soil samples from each collection site were blended to produce 8 bulked soil types. These soils were poured 1 cm deep into petri plates and three replicates of 50 seeds from each population were placed on each soil. A single soil and seed population was tested in each plate. The soils were saturated with water, covered with cellophane and randomly arranged in a growth chamber maintained between 20°C at night and 28°C at day, with 1300 ft-c and a 14 hr day/10 hr night photoperiod. Germination was recorded every two days for a total of 30 days (radicle emergence was used as the criterion for germination). Mean values for germination percentage and rate were calculated for each population. Significant groups at the 5 percent level were determined using a Duncans Multiple Range Test (Steel and Torrie, *Principles and procedures in statistics*. 1960). An arcsine transformation was performed prior to analysis of the germination percentage data.

The methods employed in the collection, storage, and germination of seeds generally resulted in high proportions of germinated seed. The ranges for each seed population on the various soils tested were: *F. chiloensis*: AN (.47–.90); PS (.50–.72); PH (.52–.92); MK (.57–.97); DL (.62–.97); and PB (.52–.95). *F. vesca*: PS (.67–.97); PH (.52–.97); EB (.72–1.00); and HP (.35–.82).

The results, however, offered little evidence of ecological differentiation for germination characteristics. The seed populations generally sorted into two to four significantly different groups with several populations often belonging to the same group. On their "native" soils, only 50 percent of the *F. chiloensis* and 75 percent of the *F. vesca* populations were in the group with the highest germination percentages, while 66 percent of the *F. chiloensis* and 50 percent of the *F. vesca* populations were in the fastest germinating group. These results were not far from what could be expected by chance. Furthermore, only 16 percent of the *F. chiloensis* and 25 percent of the *F. vesca* germinated more rapidly on their "native" soil than any other, while only 55 percent of the *F. chiloensis* and 50 percent of the *F. vesca* populations had higher germination percentages on their native soils than others.

It is possible that little ecological differentiation was observed in our seed populations, because a critical selective factor was eliminated in the way we handled our soils. Parameters such as soil litter, temperature, soil surface microstructure, and allelochemicals are probably important and may have also affected the results.

We do know, however, that the lack of discrimination between the populations arose in spite of substantial variation in soil pH, salinity, and organic carbon content (Hancock and Bringhurst, op. cit.). After storage, the various soils had salinities ranging from 371–832 ppm, while pH varied from 5.11–7.20, and percent organic carbon values ranged from 0.13–5.97 percent. It seems likely, then, that the germination requirements of California populations of *Fragaria* are quite plastic for at least these parameters.

We thank several anonymous reviewers who insisted on making us see the truth.—JAMES F. HANCOCK, Department of Biology, University of South Carolina, Columbia 29208 and R. S. BRINGHURST, Department of Pomology, University of California, Davis 95616. (Accepted 28 Apr 1979.)

REVIEWS

A Primer of Ecological Principles: Book One. By RICHARD J. VOGL. 1978. xiii + 172 pp. Pyro Unlimited, Cypress, CA. $4.95.

A casual perusal of the table of contents might lead one to decide that this is yet another addition to the recent proliferation of texts on ecological theory. From the title alone one might be tempted to place this book on the shelf alongside Wilson and Bossert's *A Primer of Population Biology*. Both title and table of contents are, in this sense, misleading. This is not a run-of-the-mill ecology text. It is an attempt to present basic ecological principles—and their management implications—in clear concise language and in an interesting, light-hearted fashion. It is to Vogl's credit that he emphasizes the role of this volume as a supplement to field experience, which he, along with most practicing ecologists, considers the backbone of our science.

In format the book alternates pages of briefly-described ecological principles with pages of more or less apt quotations from a wide range of sources. This is initially a refreshing approach. The book is replete with quotable quotes (e.g., "Many scientists use statistics the way that drunkards use lamp posts; that is, they use them more for support than for illumination.") and offers many insights that will elicit knowing chuckles from experienced ecologists. The book is punctuated by rather charming and sometimes whimsical drawings—often with a strong American Indian influence. It is, however, a treatment with a viewpoint, and as such may not be well received by those not already of Vogl's primarily preservationist persuasion. Unfortunately, the businessman, rancher, miner, developer, for whom this book, in part, is intended, may consider this a radical treatise rather than a source of solid ecological information.

The introductory chapter presents a balanced perspective on the field of ecology. In addition to the standard definition of ecology, Vogl presents several "alternate definitions" that should hit close to home for many readers. An example: Ecology is "The study that takes natural things that are easy to comprehend and translates them into languages . . . that few can understand." There is an emphasis on the holism of ecology, on the importance of synthesis, interpretation, and speculation to meaningful ecological research. There follows an exhaustive listing of the branches of ecology. That many of these categories overlap might be unclear to the beginning student. The introduction to this section is overly critical of those who specialize within ecology.

Perhaps the most illuminating statement in Chapter II (General Ecological Principles) is that "there are no absolute principles or universal ecological laws other than those that govern the physical . . . and biological worlds . . . . When generalizations are made in ecology . . . there are always variations and usually exceptions." Although this chapter lists most principles found in more classic ecology texts, there is no suggestion of relative importance. Five pages are spent on Shelford's and Liebig's "laws", but the concepts of food and energy chains and Gause's principle are each relegated to one sentence. Attempts to simplify occasionally lead to inaccurate definitions (ecotypes, p. 46). Vogl presents an enlightened, balanced view of succession and of species diversity-stability concepts. Unfortunately, his discussion ends with the proclamation, "Natural diversity should be preserved and restored, and not destroyed and replaced with monotonous monocultures that invite unnatural catastrophes." Many of Vogl's non-ecologist readers are likely to close the book in disgust at this statement. Throughout the later chapters of the book, this occasional confusion of principles with opinions, unfortunately, persists.

Chapters II–VI contain principles relative to resource management, the role of man, and energy. Most of the principles presented are sound and basic. Environmentalists will find here a great deal of support for their views. Unfortunately, principles are not presented persuasively or supported adequately enough to convince a non-believer. These chapters would profit greatly by the inclusion of occasional examples—one example might be worth a thousand principles!

The final chapter, "Ecological Comments", contains a series of vignettes summarizing Vogl's views on many topics ranging from wilderness to chemicals to education. The thrust of this section is that the long-term survival of our civilization will require a basic alteration in the value systems by which many of us live. With this, I wholeheartedly agree! This chapter is thought-provoking and contains much excellent fuel for discussion.

The concept of a book designed to present ecological principles in a format that will make them accessible to people of a wide range of backgrounds and persuasions is laudable. Vogl's approach to ecology is refreshing and generally well-balanced. Unfortunately, the lack of hierarchal arrangement and organization left this reviewer, at some points in the book, with the feeling that she was working her way through something akin to a shopping list. Keeping principles to minimum statements helps simplify a subject best when principles themselves are kept to a minimum. Blank spaces and pages (ostensibly to facilitate marginal comments by the reader) make up approximately 20 percent of the book. The concepts presented might be better remembered if these spaces contained examples, which are notably lacking throughout. A book so rooted in natural resource management ought really to fill the pages with print and expect the reader to provide notepaper as needed!

This book should find its best use in high school and introductory ecology classes as a relatively painless means of introducing principles and generating discussion. Outside readings and laboratory and field experience would add much needed depth to the material presented. It will provide enjoyable recreational reading for practicing ecologists and excellent quotations for the frontispieces of doctoral dissertations. One can't help but wonder what is forthcoming in Book Two!—SUSAN G. CONARD, Department of Botany, University of California, Davis 95616.

Flora of Barro Colorado Island. By THOMAS B. CROAT. ix + 943 pp., 571 photographs + maps and graphs. Stanford University Press, Stanford, CA. 1978. ISBN 0-8047-0950-5. $55.00.

When Gatun Lake, in the Panama Canal Zone, was created in 1911-14, through deliberate flooding by the builders of the Canal, a taller than usual group of hills, largely covered with remarkably natural semi-evergreen moist tropical forest, was cut off as Barro Colorado Island. The forest was set aside as a nature reserve in 1923 and, after a period of administration by the Institute for Tropical Research (under the direction of the National Research Council), the Smithsonian Institution set up its Tropical Research Institute (STRI) on the island. Thus, there began intensive study of the forest and its animal inhabitants. It would be expected that with the restricted area (15.6 km^2) and the number of taxonomists and ecologists who have studied the plants over more than half a century, the flora would have been comprehensively treated some time ago, but this was not the case.

A list of plants was made by P. C. Standley in 1927 (with supplements in 1929 and 1933) and was followed by the same author's *Flora of the Panama Canal Zone* in 1928, but both of these floras were based almost entirely on herbarium material in the United States National Herbarium. The difficulty of relating such literature to the usually nonflowering material encountered in the field was partly overcome by Dennis H. Knight's key to the trees in sterile condition in his *Field Guide to the Trees of Barro Colorado Island* in 1970. But in 1967, the production of a full-scale flora was begun. The location of its author on the staff of the Missouri Botanical Garden was particularly appropriate in view of the concurrent production there of the multitudinous parts of the *Flora of Panama* by a number of specialists.

Dr. Croat has responded magnificently to the challenge to produce a flora of the island, and he enjoyed the backing of the Missouri Botanical Garden, the Smithsonian Institution and, not least, the National Science Foundation. He acknowledges assistance, over the years, from 81 specialists in particular families and 34 others who gave advice. The result is a flora that is comprehensive and modern in every way.

The Introduction of more than 60 pages covers the climatic characteristics, the geological and soil types, the vegetation types and their habitats (with photographs), the growth forms, the floristic characteristics, "sexual" characteristics and geographical affinities of the flora. Historical and recent changes in the flora are noted and no less than 20 pages are devoted to its phenological characteristics. A history of the Panama Canal Zone is provided with an account of the botanical studies that have been carried out there.

In the Flora itself, there are maps, keys for both floriferous and sterile material and, *mirabile dictu,* 553 well-reproduced photographs of the essential parts of a great many species. There is an index of common names as well as the index of scientific names. About 375 literature references are listed. The classification systems used are those of Scagel and collaborators for the vascular cryptogams, and Engler for the phanerogams. The genera are alphabetized within families, and species are similarly treated within genera. Adventive species are included as well as natives.

The treatment of the individual species (1369 of them) is thoroughly up-to-date and, considering the large number of specialists who gave advice, is surely authoritative. The usual morphological description of each species is supplemented by habitat information, phenological data, seed-dispersal information, and quite detailed information about geographical distribution beyond the Island. For those species where it is known, there is information about pollinators.

Considering the fabulous amount of information contained in this huge book, and its beautiful packaging, its price is extremely reasonable. It may well serve as a model for future floras of intensively studied areas elsewhere in the tropics, and I prophesy that much use will be made in other parts of the neotropics of the information in it about widespread species. All concerned with the production of this magnificent book are to be congratulated.—HERBERT G. BAKER, Department of Botany, University of California, Berkeley 94720.

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LICHEN VEGETATIONAL GRADIENTS IN RELATION TO THE PACIFIC COAST OF BAJA CALIFORNIA: THE MARITIME INFLUENCE

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Abstract

In central and south-central Baja California lichen communities change with increasing distance from the Pacific coast. Total lichen cover decreased from 15 percent on the coast to less than 0.5 percent at inland sites, and species richness decreased from 15–25 at coastal sites to three or fewer species inland. On *Fouquieria diguetii* lichen cover exceeded 60 percent at the coast and decreased to less than 1 percent inland. The presence of this rich lichen community is related to higher atmospheric moisture conditions along the coast. Two lichens absorbed water rapidly and lost water relatively slowly. In preliminary studies the coastal dominant species of this pair maintained a high rate of photosynthesis from 40 to 100 percent saturation whereas the inland dominant exhibited a narrower photosynthetic peak at 30–40 percent saturation. It is inferred that the coastal species is adapted to moister conditions.

Although the higher-plant vegetation of Baja California is relatively well known (Shreve, 1951; Shreve and Wiggins, 1964; Hastings et al., 1972; Humphrey, 1974), the lichen vegetation is rather poorly known. A study of lichens at San Quintín (Rundel et al., 1972) is the only published quantitative description of this lichen flora. From our extensive lichen collections throughout Baja California we have observed that lichen abundance and species richness decrease with increasing distance from the Pacific coast. Fruticose lichens grow luxuriantly on desert vascular plants near the coast from just south of Ensenada to the tip of the peninsula 1200 km to the south-southeast. These large lichens are apparently adapted to the maritime microclimate of the coast. One conspicuous component of this microclimate is the presence of frequent fogs, formed where cold ocean currents flow adjacent to the warm desert land. The climate becomes more continental at inland sites where fruticose lichens disappear.

In this study we have quantified the relative cover and species richness of lichens and vascular plants with distance from the coast and have initiated physiological studies to explain the observed distribution patterns.

Methods

Vegetation. Selection of sites for sampling in Baja California was constrained by lack of accessibility in most areas. Choice of two tran-

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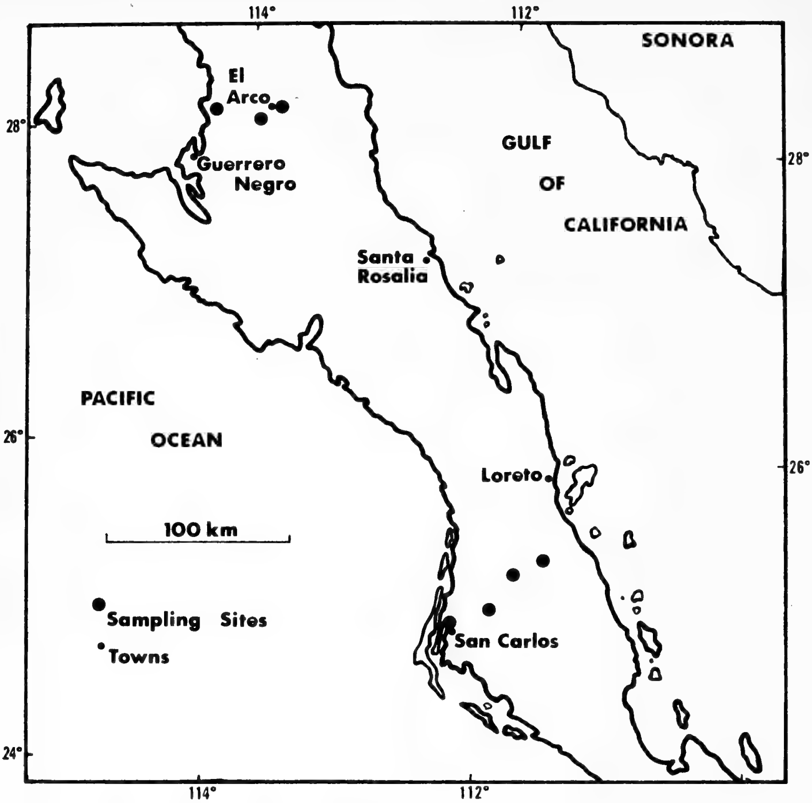

FIG. 1. Location of sampling sites in southern Baja California.

sect lines for sampling (Fig. 1) was in part dictated by the presence of roads. The San Quintín study (Rundel et al., 1972) was restricted to the north central coast, whereas our two transects include inland as well as coastal sites and are in the central and south-central portions of the peninsula. The transect from just north of Guerrero Negro to El Arco lies at approximately the midpoint of the peninsula (28°N) along the boundary of Baja Califfornia and Baja California Sur. The transect from San Carlos inland (25°N) lies approximately 300 km northwest of the southern tip of the peninsula.

These two transects have little topographic complexity. In this portion of the peninsula there is a broad coastal plain and a ridge of mountains, the Sierra de la Gigante, rising to approximately 2000 m, along the Gulf of California coast to the east. From the coastal plain to the base of the mountains the topography rises gradually as a bajada, composed of colluvial and alluvial materials eroded from the mountains.

Each transect began near sea level and rose gradually to approximately 300 m on the bajada at the terminal sites. Sampling sites were selected at 15–30 km intervals along the gradient from the coast until mountains were encountered (Fig. 1). Agricultural areas were avoided. At each site both lichens and vascular plants were sampled for cover using a m^2 frame. Cover was estimated to the nearest 0.1 percent (10 cm^2) in 50 quadrats per site that were positioned randomly along two parallel 125 m transect lines. These were 50 m apart and ran perpendicular to the nearest road.

Because lichens may exhibit substrate specificity (Barkman, 1958), the potential effect of heterogeneity due to vascular plant variation was eliminated along the southern transect by also estimating lichen cover on *Fouquieria diguetii* (van Tiegh.) I.M. Johnston, a shrub common to all the sites. In this case cover was visually estimated to the nearest 1 percent on the *Fouquieria* shrub located closest to each quadrat.

Biomass estimates for lichen and vascular plants were also obtained at sites near the coast. Within each quadrat two 1-dm^2 subquadrats were nested randomly and the column of lichen and vascular plant tissue above the subquadrat was harvested. Lichens and vascular plants were separated by species, air dried in the field, oven dried (60°C for 24 hours) in the laboratory, and weighed to the nearest 0.1 g.

Physiology. Samples of a coastal dominant lichen *Roccella babingtonii* Mont. and an inland dominant lichen *Ramalina complanata* (Sw.) Ach. were also collected, air dried, and returned to the laboratory for subsequent physiological work.

Because CO_2 exchange by lichens is strongly dependent upon water content (Lange, 1954), the ability of these two species to absorb and retain water was investigated. To determine the rate of water absorption, five specimens of each species were submersed sequentially in distilled water at 23°C for periods of 0.17, 0.5, 1, 2, 5, 10, 30, and 120 minutes. At the end of each time period the lichens were removed from the water, shaken briefly to remove external water, and weighed. After the lichens were saturated (2 minutes in the case of *Roccella* and 30 minutes in the case of *Ramalina*), they were allowed to air dry under laboratory conditions of 23°C and approximately 40 percent relative humidity. The samples were reweighed after drying periods of 0.5, 1.0, 1.5, 2, 3, 4, 7, and 9 hours.

To measure the gross photosynthetic rate of these lichens at different water contents, a series of measurements was made using $^{14}CO_2$ incorporation following the procedure of Shimshi (1969). Pieces of each species (6–10 mg) were submerged in distilled water for 2 hours to ensure saturation, then removed and allowed to air dry. Three replicate exposures were made at approximately 10 percent moisture intervals between saturation and air dry conditions. Exposures to $^{14}CO_2$

TABLE 1. MEAN COVER (PERCENT) AND NUMBER OF SPECIES OF LICHENS AND HIGHER PLANTS ALONG TWO TRANSECTS AWAY FROM THE PACIFIC OCEAN. Data are from 50 1-m^2 quadrats randomly placed on two sampling lines per site. Standard deviations calculated from the means for the two sampling lines are given in parentheses. + = observed but not sampled.

	Lichens				Vascular Plants		
			El Arco Transect (28°N)				
Kilometers from ocean:	0	31	45		0	31	45
Dendrographa				*Euphorbia misera*	10.7(3.4)	–	0.5(0.5)
leucophaea	4.6(2.6)	–	–	*Lycium californicum*	5.7(1.5)	3.0(3.8)	3.0(3.2)
Niebla				*Ambrosia magdalenae*	3.9(2.4)	0.9(1.2)	4.0(2.2)
pulchribarbara	2.6(0.9)	–	–	*Prosopis juliflora*	–	5.4(2.4)	–
Roccella babingtonii	2.3(0.1)	–	–	*Machaerocereus*			
Niebla ceruchis	4.7(3.5)	3.3(1.2)	–	*gummosus*	–	4.3(1.4)	4.1(0.0)
Buellia oidalea	0.1(0.1)	0.7(0.7)	<0.1 –	*Fouquieria diguetii*	+ –	1.7(1.0)	2.1(2.0)
Teloschistes			<0.1 –	*Bursera microphylla*	–	–	8.1(3.5)
chrysophthalmus	–	0.2(0.2)	0.1(0.1)	Other species	9.3	11.1	2.2
Anaptychia erinacea	–	–	–				
Other species	0.7	1.5					
Total cover	15.0	5.7	0.2	Total cover	29.6	26.4	24.0
Number of species	15	16	3	Number of species	7	15	13

TABLE 1. Continued.

San Carlos Transect (25°N)

Kilometers from ocean:	0	30	50	70
Dendrographa leucophaea	2.0(0.9)	–	–	–
Roccella babingtonii	4.8(3.0)	<0.1 –	–	–
Niebla ceruchis	2.2(0.4)	3.1(1.7)	–	–
Graphidiaceae sp.	1.7(0.2)	0.5(0.2)	–	–
Buellia oidalea	0.6(0.2)	0.3(0.1)	0.2(0.2)	<0.1 –
Teloschistes chrysophthalmus	+ –	0.4(0.5)	+ – 0.2(0.0)	–
Ramalina complanata	–	0.1(0.0)	0.5	+
Other species	3.9	1.9		0.1
Total cover	15.2	6.3	0.9	0.1
Number of species	25	21	9	2

	0	30	50	70
Euphorbia californica	10.0(6.3)	2.1(1.2)	2.3(1.3)	0.1(0.1)
Fouquieria diguetii	9.3(1.5)	0.8(1.1)	2.7(0.4)	0.4(0.5)
Lycium andersonii	4.4(0.9)	–	4.0(1.1)	–
Machaerocereus gummosus	3.1(2.2)	8.1(3.4)	7.3(4.2)	+ –
Acacia constricta	–	4.2(1.4)	5.2(1.2)	7.8(0.3)
Bursera microphylla	–	–	5.2(3.9)	5.3(2.5)
Atamisquea emarginata	3.9(1.8)	–	–	3.8(1.7)
Other species	8.2	2.7	18.7	27.7
Total cover	38.9	17.9	45.4	45.1
Number of species	12	9	17	16

were made for approximately 22 seconds in a small plexiglass chamber at 4400 lux under fluorescent lighting at 26°C. Immediately after the exposure the samples were placed in scintillation vials on ice to reduce respiratory release of the $^{14}CO_2$. Subsequently the samples were dried at 100°C for 24 hours, weighed and then combusted in an oxygenated atmosphere following the technique of Tieszen et al. (1974). The released $^{14}CO_2$ was trapped in 5 ml of absorbing solution (3:3:5 absolute methanol:B-phenethylamine:toluene). After adding 10 ml of scintillation cocktail, emission of beta particles was counted by a Nuclear Chicago liquid scintillation counter (Tri-Carb Model 3220). After correcting for background radiation with controlled unexposed lichen samples, the data were converted to CPM/mg thallus and the data plotted in relation to the percent thallus saturation.

RESULTS

Vegetation. In contrast to the vascular plants, the lichens exhibited marked gradients in species richness and abundance along the transects (Table 1). For the Guerrero Negro transect lichen species richness per site decreased from 15 or 16 in the coastal plain sites to 3 at the inland bajada site. For the San Carlos transect species richness decreased from a high of 25 species at the coastal site to a low of 2 species at the interior sites. A parallel decline in lichen cover was found along the two transects from 15 percent cover to 1.2 percent cover and from 15.2 percent cover to 0.1 percent cover respectively for the Guerrero Negro and San Carlos transects.

Species richness for the vascular plants exhibited lower overall variability and no obvious gradients along the transects. Vascular plant cover was fairly constant within the respective transects, varying from 24 to 30 percent for the Guerrero Negro transect and from 38 to 45 percent for the San Carlos transect except for the 30 km site on the San Carlos transect. In the course of sampling, the latter site was found to be disturbed by tree and shrub cutting activity, and consequently community cover estimates for both lichens and vascular plants were low. The higher cover values on the San Carlos transect reflect the fact that to the south the desert grades into a thorn forest community where cover exceeds 100 percent.

We found marked shifts in lichen species along the transects. Several of the dominant species, including *Dendrographa leucophaea* (Tuck.) Darb., *Niebla pulchribarbara* (Rundel & Bowler) Rundel & Bowler, and *Roccella babingtonii,* and many of the less abundant species, including *Graphis* sp., *Lecanora pacifica* Tuck., *Ochrolechia pallescens* (L.) Mass., *Pertusaria* sp. and *Ramalina denticulata* Nyl., exhibited very restricted coastal distributions. Several other species exhibited somewhat broader distributions, extending from the coastal sites to one or more of the adjacent interior sites. These included the less abundant *Buellia oidalea* (Nyl.) Tuck. and *Niebla ceruchis* (Ach.) Rundel & Bowler and the less abundant species *Caloplaca* cf. *californica* Zahlbr., *Dirinaria* sp., *Haematomma puniceum* (Sm. *ex* Ach.) Mass. and *Lepraria candelaris* (L.) Fr. A third group of species, including *Candelaria concolor* (Dicks.) B. Stein, *Parmelia caperata* (L.) Ach., *P. hypotropa* Nyl., *Ramalina crinita* Tuck., *R. menziesii* Tayl., *Teloschistes chrysophthalmus* (L.) Th. Fr. and *Xanthoria parietina* (L.) Th. Fr., show affinities for the midportion of the transects. Only five species, *Anaptychia erinacea* (Ach.) Trev., *Buellia oidalea, Physcia stellaris* (L.) Nyl., *Ramalina complanata,* and *Teloschistes chrysophthalmus* were found at the most interior sites and all of these had low cover values.

Niebla pulchribarbara was the only terricolous lichen sampled. All the other species were corticolous. Saxicolous lichens that are typical of northwestern Baja California were absent due to a scarcity of rocks.

Almost all of the lichen species were found on both transects. Exceptions included *Niebla pulchribarbara,* which apparently was at the southern end of its range at Guerrero Negro, and *Ochrolechia pallescens, Ramalina complanata,* and *Xanthoria parietina,* which were collected only on the southern transect. This is the first report of *Xanthoria parietina* in western North America.

Among sampling sites within a transect the vascular plants did not exhibit the marked variation in species composition found among the lichen species; however, there was considerable variation in vascular plant species between transects (Table 1). *Euphorbia* spp. were the only dominant vascular plants that exhibited a restricted coastal distribution. *Bursera microphylla* A. Gray was the only dominant restricted to the interior bajada sites. *Bursera microphylla, Fouquieria diguetii,* and *Machaerocereus gummosus* (Engelm.) Britt. & Rose were the only vascular plant species that were dominant on both transects. In addition, *Lycium californicum* (Nutt.) A. Gray and *Euphorbia misera* Benth. were dominant on one transect, but present in reduced abundance on the other transect. Dominant species restricted to one transect were *Acacia constricta, Ambrosia magdalena* (Brandegee) Payne, *Atamignea emarginata* Miers, *Lycium andersonii* A. Gray, and *Prosopis juliflora* (Sw.) DC.

The patterns for less important species were similar to those for the dominant species. Only five of these species [*Jatropha cinerea* (C. G. Ortega) Muell. Arg., *Lophocereus schottii* (Engelm.) Britt. & Rose, *Pedilanthus macrocarpus* Benth., *Tillandsia recurvata* L., and *Yucca valida* Brandegee] were found in common between the two transects. Two of the most conspicuous vascular plants because of their height were *Yucca valida* in the Guerrero Negro transect and *Pachycereus pringlei* (S. Wats.) Britt. & Rose in the San Carlos transect, but they contributed little to total community cover.

In general the patterns of cover and species richness of lichens on

TABLE 2. MEAN LICHEN COVER (PERCENT) AND NUMBER OF SPECIES ON *Fouquieria diguetii* ALONG A TRANSECT EAST FROM SAN CARLOS. Estimates are based on 50 shrubs per site. Standard deviations calculated from the means for the two sampling lines are given in parentheses.

Kilometers from ocean:	0	30	50	70
Roccella babingtonii	35.7(2.7)	4.2(0.9)	–	–
Dendrographa leucophaea	2.8(2.1)	0.3(0.2)	–	–
Parmelia hypotropa	1.6(0.1)	0.8(0.2)	–	–
Niebla ceruchis	11.0(3.6)	37.3(5.6)	<0.1 –	–
Ramalina denticulata	4.3(2.6)	0.3(0.1)	0.1(0.0)	–
Buellia oidalea	0.8(0.1)	0.6(0.1)	<0.1 –	–
Teloschistes chrysophthalmus	+ –	2.9(1.3)	+ –	–
Ramalina complanata	0.1(0.1)	1.1(0.1)	2.2(0.1)	0.3(0.2)
Physcia stellaris	–	–	1.4(0.1)	0.4(0.2)
Other species	9.0	9.1	1.0	–
Total cover	65.3	56.6	4.7	0.7
Number of species	27	27	13	2

Fouquieria diguetii (Table 2) parallel those obtained from the general community sampling. Species richness declined from 27 near the coast to 2 at the site farthest from the coast. Total lichen cover decreased from 65 percent to 0.7 percent. Lichen community dominance shifted from *Roccella babingtonii* at the coastal site to *Niebla ceruchis* at the 30 km site to *Ramalina complanata* at the interior sites. *Dendrographa leucophaea, Parmelia hypotropa,* and *Ramalina denticulata* all exhibited peak abundance at the coastal site. *Teloschistes chrysophthalmus* showed peak abundance at the 30 km site; *Physcia stellaris* dominated at the 50 km site.

Maximum lichen biomass values of approximately 120 g/m^2 (Table 3) were obtained at the coastal sites where the lichen to vascular plant biomass ratio was approximately 1:3. At interior sites this ratio was lower, reflecting the decreased proportion of lichens in the community.

TABLE 3. MEAN ABOVE-GROUND BIOMASS (g/m^2) OF LICHENS AND VASCULAR PLANTS. Sites are specified by distance from the Pacific Ocean. Means are based on 50 1-dm^2 quadrats from two sampling lines. Standard deviations are given in parentheses. Values at 50 and 70 km sites on the San Carlos transect were not obtained because of the scarcity of lichens.

Location	Lichens	Vascular Plants	L/VP ratio
El Arco transect			
0 km	121.2(14.7)	343.6(40.3)	.352
31 km	19.5(8.3)	105.3(59.5)	.185
45 km	1.6(1.6)	230.1(62.4)	.007
San Carlos transect			
0 km	112.3(67.2)	303.4(62.4)	.370
30 km	18.9(5.2)	185.8(107.3)	.096

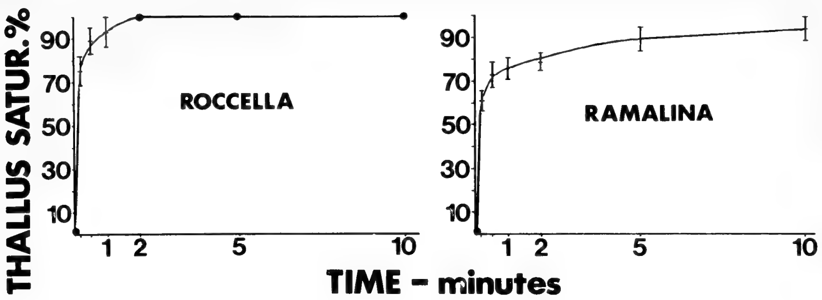

FIG. 2. Water absorption by *Roccella babingtonii* and *Ramalina complanata* as a function of submersion time in distilled water at 23°C. Intervals of ±1 S.D. are constructed about the means.

Physiology. The uptake of water by the two species tested was extremely rapid (Fig. 2). Within 10 seconds thalli were more than 60 percent saturated. Complete saturation of *Roccella babingtonii* occurred after submersion for 2 minutes whereas *Ramalina complanata* took up to 30 minutes to become saturated. Loss of water occurred similarly for both species: approximately 50 percent in the first 1.5 hours, 80 percent in 3 hours, and 96 percent in 9 hours (Fig. 3).

Relative photosynthesis as a function of thallus saturation (Fig. 4) yielded very different curves for the two species. In both species photosynthesis was zero when the thallus was dry; appreciable photosynthesis occurred when thallus saturation was 20 percent of maximum. In *Ramalina complanata* maximum photosynthesis occurred in the 30–

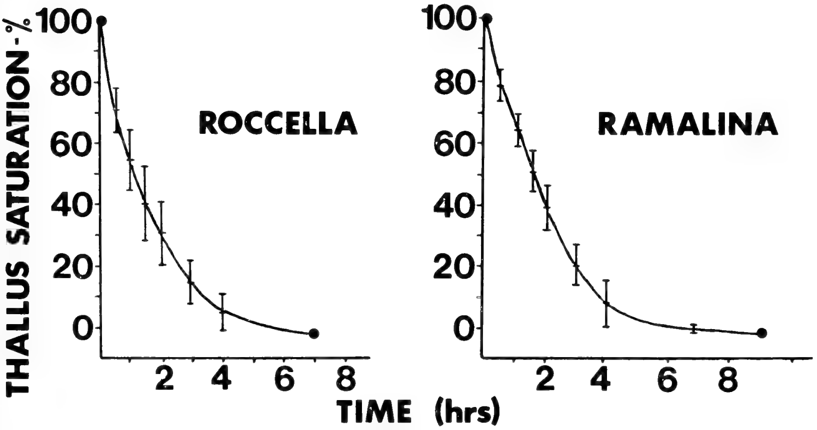

FIG. 3. Water loss as a function of time by *Roccella babingtonii* and *Ramalina complanata* under laboratory conditions of 23°C, 40 percent relative humidity, and 1000 lux. Intervals of ±1 S.D. are constructed about the means.

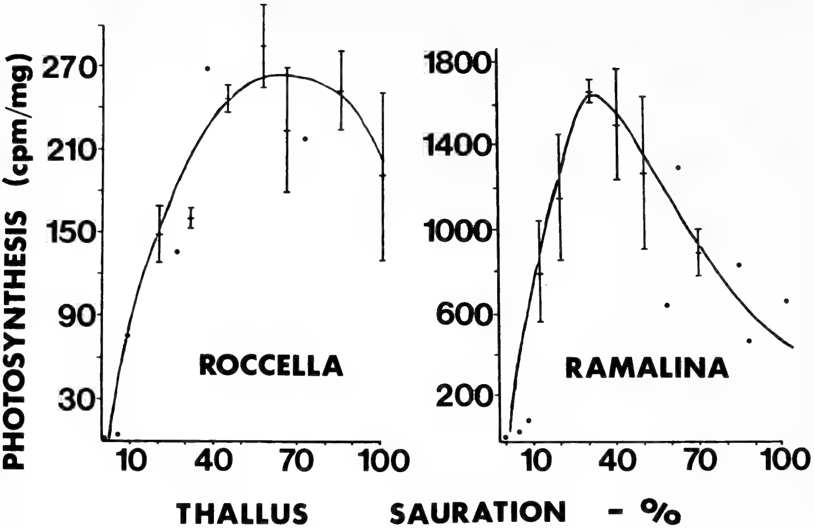

FIG. 4. Rate of photosynthesis by *Roccella babingtonii* and *Ramalina complanata* as a function of percent saturation as measured by $^{14}CO_2$ incorporation at 26°C and 4400 lux. Intervals of ±1 S.D. are constructed about the means.

40 percent saturation range and declined to values less than 50 percent of maximum when 90–100 percent saturated. Linear regression showed that this decline was highly significant ($p < 0.01$). In contrast, the rate of photosynthesis of *Roccella babingtonii* was almost maximal for all measurements between 40–100 percent saturation. There is a slight drop in mean photosynthetic rate for *Roccella* above 40 percent saturation, but this was not significant ($p \simeq 0.20$) when tested by linear regression.

DISCUSSION

The Pacific coastal lichen communities of Baja California together with a smaller zone along the southern coast of Sonora and northern Sinaloa form a unique component of the Sonoran Desert lichen flora. The abundance of the large fruticose species in the genera *Dendrographa, Niebla, Ramalina, Roccella,* and *Teloschistes* is one of the most conspicuous aspects of the coastal community. These genera are absent from eastern Baja California and from almost all mainland areas of the Sonoran Desert. In contrast, interior desert regions are dominated by crustose lichen species in the genera *Acarospora, Caloplaca, Dermatocarpon, Lecanora, Peltula,* and the foliose species in the genus *Parmelia* subg. *Xanthoparmelia* (Nash, 1975; Nash et al., 1977). The absence of the latter group of species from the Baja California transects was due to lack of available substrates. Almost all of the interior Sonoran Desert lichens are saxicolous and terricolous. Rocks were absent from most of our sampling sites and the sandy soils of the coastal plain are probably so unstable that terricolous lichens cannot become established. In the northern Pacific coast of Baja California, where rock outcrops and firmer soils do exist, saxicolous and terricolous lichens can be found in abundance. Many of these species are restricted to the coastal habitat.

A second aspect of the southern coastal Baja California lichen communities is the preponderance of corticolous species. All but one of the lichens sampled (*Niebla pulchribarbara*) grew epiphytically on shrubs or small trees. In contrast, corticolous lichens are almost completely absent from the mainland Sonoran Desert areas, where the few species are restricted to more humid locations along permanent sources of water (Nash, 1975; Nash et al., 1977). Furthermore, lichen abundance is much greater in coastal Baja California than at interior Sonoran Desert sites. Estimates of lichen cover (0.03–8.1 percent) and biomass (0.02–38.3 g/m^2) at US IBP Desert Biome sites (Nash et al., 1977) are far lower than those found near the coast of Baja California.

The ecology of the large fruticose lichens found at the coastal sites is not fully understood. Many of the species are known to range from the tip of Baja California north into southern California (Hale, 1969). In addition, we have found a small area in southern Sonora where several of the species also occur. One common denominator for all locations is the presence of a maritime influence that results in higher atmospheric moisture conditions. Because of the desert environment of Baja California, high atmospheric moisture conditions are not continually present. We hypothesize that one important variable may be the periodicity of dry and moist conditions. For example, Ahmadjian and Heikkilä (1970) have demonstrated that alternating dry and wet conditions are necessary for the maintenance of symbiosis in *Endocarpon pusillum*. Furthermore, these species do not occur in northern California where fog is more continually present. A better understanding of the distribution patterns will require study of more variables, including temperature.

On a world-wide basis the coastal Baja California lichen community is not unique. Galun (1963) reported the occurrence of different *Ramalina, Teloschistes,* and *Xanthoria* species in the Negev Desert where dew, apparently from moist air from the Mediterranean Sea, allows these large lichens to survive in otherwise arid conditions. Other fog-induced lichen communities are known from the Namib Desert of South Africa (Walter, 1937; Vogel, 1955) and the Atacama Desert of South America (Follman, 1967; Thomson and Iltis, 1968). The common denominator for all of these communities is apparently high atmospheric moisture as dew or fog.

At this time it is difficult to quantify appropriate moisture parameters that may account for the presence of the lichen dominated coastal community of Baja California. It is clear from the literature and from data presented here that, to be active physiologically, lichens must imbibe water. However, the pattern of increased lichen abundance and species richness near the coast does not reflect greater precipitation on the coast. In fact, the precipitation patterns reported by Hastings and Humphrey (1969) are opposite to expectations of greater precipitation correlated with greater lichen community development. Thus, for the northern transect (28°N), a coastal site at Vizcaíno receives 8 cm and the inland site at El Arco receives 14 cm per year. Likewise, farther south (26°N) the coastal site of La Poza Grande receives 6 cm and the inland site at Comondu receives 14 cm per year.

Although precipitation is lower on the coast, atmospheric moisture is undoubtedly higher on the coast because of the maritime influence and this factor probably accounts for the lichen abundance. Lange (1969; Lange et al., 1970a, 1970b) has shown that the fruticose desert lichen *Ramalina maciformis* (Del.) Bory is capable of maintaining a positive photosynthetic balance in the Negev Desert where dew is the major water source. Even on nights when dew does not occur, sufficient water may be imbibed under high relative humidity conditions to allow brief periods of photosynthetic activity immediately after sunrise.

Unfortunately, in Baja California we cannot cite data on the frequency of occurrence of fog or dew. However, we have experienced both phenomena personally while traveling the Pacific Coast of Baja California and it is reasonable to infer from our general climatic knowledge that both must occur frequently. The prevailing northwest winds that occur along the entire Pacific coast of Baja California (Humphrey, 1974) bring relatively cool, moist air onto the coastal regions because they flow across the relatively cold California Current prior to reaching the peninsula (Mosiño Alemán and Garcia, 1974). Presence of this maritime air over land is inferred from the fact that temperature means are lower by 2–3°C at coastal sites compared with corresponding locations inland. In relation to our northern transect (28°N), Hastings and Humphrey (1969) reported that the mean annual temperature at coastal Vizcaíno is 18.8°C whereas the inland site at El Arco has a mean annual temperature of 20.6°C. Likewise, to the south (26°N) the coastal site of La Poza Grande has a mean annual temperature of 20.0°C whereas Comondú, the corresponding location inland, has a mean of 22.8°C. With radiative cooling, which occurs during the night, moist air will reach the condensation point and dew or ground fog will form. Such ground fogs are typical of southern California's maritime province (Bailey, 1966) at least as far south as Vizcaíno (Humphrey, 1974). Furthermore, the presence of fog will reduce solar radiation at ground level and thus result in lower temperatures. The extent of maritime influence inland from the coast is not known exactly but it is germane that the width of the maritime climatic zone delimited by Bailey (1966) in southern California is approximately as broad as the zone of lichen abundance along the coast of Baja California.

The saturation curves (Fig. 2) demonstrate the capacity of two Baja Californian lichens to absorb water rapidly, a phenomenon characteristic of many lichens (Ahmadjian, 1967). The submersion technique is not directly analogous to the response of a lichen to fog or dew, but we have observed that lichens sprayed with a water mist also imbibe water rapidly. Rapid water imbibition would be advantageous to lichens in environments where fog and dew are important water sources. Sufficient imbibition of water to activate photosynthesis and respiration should occur in Baja Californian lichens that are exposed to light fogs. In our personal experience we have repeatedly observed lichens at San Carlos to be fully saturated at dawn, with water dripping from the thalli. In contrast to water absorption, water loss from these lichens occurs more slowly (Fig. 3). The rate of water loss will, of course, vary with ambient conditions, being relatively slow on cool, overcast days and relatively rapid on warm, clear days. But whenever these lichens are partially moistened during daylight hours, a positive photosynthetic pulse is predicted, based on Lange's work cited earlier. These papers and unpublished data of the senior author show that for several desert lichens, respiration rates are independent of thallus saturation above 20 percent. Although we have no data on respiration of *Roccella* or *Ramalina,* the shapes of their net photosynthetic curves should be similar to the gross photosynthetic curves derived here.

We assume that in the absence of nonmarine water sources the intensity of foggy conditions should be reduced inland. If this assumption is correct, the photosynthetic curves (Fig. 4) may reflect adaptations that are functionally important in the ecological segregation of the species along the lichen gradient (*Roccella* coastal and *Ramalina* inland). Photosynthesis of *Ramalina* is markedly reduced at 100 percent saturation compared with photosynthesis at 30–40 percent saturation but photosynthesis of *Roccella* is essentially unchanged as 100 percent saturation is reached. *Ramalina* occurs in an environment where saturation probably occurs less frequently. Even in the same environment, *Ramalina* would reach saturation less frequently because the water absorption rate is slower (Fig. 2). If the observed differences in rates of relative gross photosynthesis between *Ramalina* and *Roccella* (Fig. 4) represent true population differences (variable densities of algal cells among lichen samples lead to widely disparate photosynthetic values), then *Ramalina* will be able to fix an equal amount of photosynthate in a shorter time period and should be expected to survive better in the drier portion of the transect where it is found.

The observed photosynthetic differences (Fig. 4) probably also reflect anatomical differences. *Ramalina* has a relatively thick cortex whereas *Roccella* has a relatively thin one. Saturation of the extracellular air spaces in the *Ramalina* combined with its thick cortex would impede CO_2 exchange more effectively.

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HIGH-ELEVATION SPECIES CLUSTERS IN THE ENCHANTMENT LAKES BASIN, WASHINGTON

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ABSTRACT

Subalpine and alpine vegetation from the Enchantment Lakes Basin was analyzed by species classification methods (Q-mode or inverse analysis) to determine groups of species that cooccur. It was possible to make environmental interpretations of these groups consistent with the known habitat preferences of each species within the group. Eleven groups were identified in the subalpine. Three indicate different forest conditions; two indicate wet, open forests; three suggest different rocky, open, low-elevation habitats; and three indicate krummholz habitats. In the alpine 14 groups fall into five categories: one indicates acid soils; three indicate wet to mesic meadows; four indicate seasonally dry meadows at various elevations; three indicate mesic to dry fell-fields; and three indicate xeric fell-fields and talus. Species composition of each group is given. It is concluded that species classification is a useful tool even when not combined with stand classification (R-mode or normal analysis). It enhances the investigator's ability to detect species valuable as indicators and is useful in experimental design.

The high elevations of the east-central Cascades are receiving increasing recreational stress. The creation of the Alpine Lakes Wilderness Area will intensify impact in fragile high-elevation ecosystems by making the region and its qualities better known to hikers, yet the vegetation of the alpine portions of this region remains little known. Douglas (1972) studied subalpine vegetation of the mesic North Cascades, while Douglas and Bliss (1977) studied high-elevation meadow vegetation across the North Cascades. They described a number of communities similar to those in the Enchantment Lakes Basin. Data from their Table 2 (Douglas and Bliss, 1977, p. 120–123) provide a partial basis for assessment of some of my results.

The present objectives are to identify natural groups of species, to relate the species to habitats, and to suggest the basis for ecological group affinities. This analysis facilitates ecological interpretations of plant communities, identifies indicator species, is useful for subsequent research design, and provides information for management.

Inverse analysis has been used in many studies since its introduction by Williams and Lambert (1961). Typically it is used in conjunction with site classification (normal analysis) and when the two are combined, the approach is analogous to the differential tables produced by the Zurich-Montpellier methods (Westhof and van der Maarel, 1978; Holzner et al., 1978). The use of inverse analysis alone, henceforth termed "species classification", has not been widely reported, yet it offers an efficient tool to develop species groups with predictive value.

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METHODS

Field studies. The study area is located in the Wenatchee Mountains, a southeast-trending spur of the Cascade Range dominated by Mt. Stuart, a granodiorite batholith reaching 2889 m. The vegetation of portions of montane and subalpine slopes in this region has been described by del Moral (1974, 1975; del Moral et al., 1976; and del Moral and Watson, 1978). The Enchantment Lakes Basin is on the southeastern shoulder and contains eight large lakes and many ponds. Elevations range from 2060 m in the lower basin to over 2600 m on the peaks surrounding the upper basin. Forest and meadow vegetation interdigitate in response to physiographic factors. The vegetation is described elsewhere (del Moral, 1979).

The growing season becomes progressively shorter with increasing elevation, but is controlled locally by snow accumulation, melt patterns, exposure, wind, and frost. No climatic records exist for this basin; year-to-year fluctuations are large and are affected by the amount of winter snow and the frequency and amount of summer rain. The vegetation was in excellent condition and nearly all species were reproductive at the time of this survey. The Mt. Stuart granodiorite is the parent material of all soils in this basin. Soils differ in maturity and organic matter in response to drainage and erosion patterns.

The vegetation was sampled for species presence in 199 plots. Approximate plot locations were determined from topographic maps and aerial photographs, but the exact location was determined subjectively in the field to maximize within-plot homogeneity. The plots were distributed on the landscape so as to encompass the full range of accessible habitat variability. Forest plots were 10 × 20 m and meadow plots were 10 × 10 m. All vascular plant species within the plots were recorded (nomenclature follows Hitchcock and Cronquist, 1973). Plot location, elevation, slope, aspect, and soil characteristics were recorded. Moisture status of each site was estimated on a five-point scale from topographic, edaphic, and location factors. Exposure to wind and proximity to persistent snow banks were factors of major importance.

Analytical methods. Species classification reveals groups of species with similar local distributions that may reflect similar ecological or physiological properties. It is a procedure reciprocal to vegetation classification. Species classification has been termed inverse analysis (Williams and Lambert, 1961) and Q-mode analysis (cf. Mueller-Dombois and Ellenberg, 1974). The R-Q notation is fraught with interpretational difficulties and is best avoided.

Species classification can be affected by measures of abundance or dominance. Therefore, I used only presence-absence data in this study.

The 199 plots were divided into 113 with tree species (subalpine) and 86 lacking trees (alpine) and were analyzed separately.

Species were classified into groups with similar distribution patterns using two cluster methods. DIVINF divides species into groups based on their mutual occurrences in key plots (Williams, 1976) and therefore may mis-associate a species characteristic of one habitat that fortuitously occurs in a plot diagnostic of another habitat type. MULTBET merges a pair (or group) of species with the most similar distributional pattern in a series of agglomerative steps (Lance and Williams, 1967). Species with only one occurrence were eliminated. Because the results of the two algorithms were similar, I report a synthesis of the two, drawing upon the works cited below to resolve ambiguities. Of species classified by both methods, 73 percent of the subalpine and 74 percent of the alpine species are in identical groups, while only 5.5 percent and 4.5 percent, respectively, indicate different habitats. These seven discrepancies involve rare species. The remaining cases indicate similar habitat conditions.

Ecological interpretations of the species groups are inferred from Hitchcock and Cronquist (1973), Franklin and Dyrness (1973), del Moral (1974, 1975, 1979), del Moral et al. (1976), Douglas and Bliss (1977), del Moral and Watson (1978), and from the habitat characteristics of plots in which the species cooccur, especially diagnostic plots identified by DIVINF.

RESULTS

A total of 101 species could be grouped by the analytical procedures. The more useful species groups are those that consist of species with moderately wide distributions. These groups indicate fairly precise habitat conditions yet are sufficiently widespread to have meaning beyond the narrow confines of the study area. Groups consisting of very widely distributed community dominants are less informative.

Subalpine

Eighty-one of 102 species in the subalpine were classified into 11 groups. Those not classified are rare and have little indicator value. Parenthetical numbers after each species are the number of occurrences. An asterisk indicates a species whose habitat characterization agrees with that of Douglas and Bliss (1977) and a plus indicates a disagreement with those authors.

Group A. *Picea engelmannii* (25), *Ledum glandulosum* (22), *Saxifraga ferruginea* (22), and *Pedicularis ornithorhyncha* (8): cold wet forests around 2300 m in which standing or running water can be found.

Group B. *Pinus albicaulis* (104), *Larix lyallii* (90), *Abies lasiocarpa* (86), **Vaccinium myrtillus* (70), *Luzula hitchcockii* (66), **Cassiope* *mertensiana* (61), **Phyllodoce empetriformis* (58), **Luetkea pectinata* (43), **Vaccinium deliciosum* (13): and *Kalmia microphylla* (4): cool, mesic forest conditions on acid soils. These conditions are widely encountered in the closed forests of the lower basin below 2300 m.

Group C. **Phlox diffusa* (45), **Carex spectabilis* (43), **Veronica cusickii* (36), **Erigeron peregrinus* (33), *Lupinus polyphyllus* var. *burkeii* (33), and **Hieracium gracile* (31): poorly defined, but appears to be unified by species found on warm, moist, low-elevation forest margins in deep soils, often near low-elevation lakes.

Group D. **Carex nigricans* (12) and *Lewisia triphylla* (6): near lakes in wet meadows with scattered conifers.

Group E. *Arnica latifolia* var. *gracilis* (26), *Ligusticum grayii* (9), *Gentiana calycosa* (5), *Cassiope tetragona* (2), and **Valeriana sitchensis* (2): lush subalpine meadows in forest openings below 2200 m; completely lacking in dry meadows.

Group F. **Lupinus lepidus* var. *lobbii* (38), **Phyllodoce glanduliflora* (34), *Poa gracillima* (26), **Arenaria obtusiloba* (22), *Juniperus communis* var. *montanum* (21), *Saxifraga bronchialis* (20), *Carex rossii* (16), *Luzula campestris* var. *multiflora* (8), *Senecio canus* (6), *Festuca ovina* var. *brevifolia* (3), and **Trisetum spicatum* (3): open, dry, rocky sites, often at the margins of sites occupied by Group A.

Group G. **Juncus parryi* (72), **Antennaria alpina* (62), *Poa cusickii* (56), *Penstemon davidsonii* var. *menziesii* (55), *Sedum divergens* (51), and *Lewisia columbiana* (30): rock crevices and on the edges of dry forests; both *Sedum* and *Lewisia* often extend onto dry, sandy soils.

Group H. *Senecio cymbalarioides* (9), *Saxifraga integrifolia* var. *apetala* (3), *Cystopteris fragilis* (2), and *Epilobium latifolium* (2): infrequent, occurring in well-drained soils or rock crevices that remain wet for much of the growing season due to melting snows.

Group I. *Carex proposita* (47), **Penstemon procerus* var. *tolmiei* (35), **Erigeron aureus* (34), *Arabis lyallii* (29), *Artemisia trifurcata* (27), **Arenaria capillaris* var. *americana* (25), *Aster alpigenus* (22), *Spraguea umbellata* var. *caudicifera* (20), and **Eriogonum pyrolaefolium* var. *coryphaeum* (17): exposed, open forests above 2300 m. Most are prostrate, glaucous, or hirsute and have xeromorphic leaves.

Group J. **Carex nardina* (11), *Castilleja elmeri* (10), *Polemonium pulcherrimum* var. *calycinum* (10), *Phlox pulvinata* (9) **Agoseris glauca* var. *dasycephala* (6), **Silene acaulis* var. *exscapa* (6), *Draba paysonii* var. *treleasii* (5), *Campanula scabrella* (4), **Erigeron compositus* var. *discoideus* (4), **Smelowskia calycina* (4), *Eriogonum umbellatum* var. *hausknechtii* (3), *Polemonium elegans* (3), *Potentilla gracilis* var. *glabrata* (3), *Senecio pauperculus* (3), and *Eriogonum ovalifolium* var. *nivale* (2): primarily alpine species confined to krummholz and granite outcrops generally above 2300 m. Sites are characterized by early snow melt, extreme temperatures, and high wind.

Group K. *Polygonum minimum* (10), **Sibbaldia procumbens,* (7), *Hieracium albertinum* (6), *Castilleja miniata* (5), and **Arctostaphylos nevadensis* (3): dry, open, rocky sites that fail to receive significant snow melt.

Alpine

Analysis of the alpine vegetation grouped 84 species into 14 groups. Eighteen species were not classified. Drought and snow-melt patterns help govern the species patterns in these meadows and fell-fields.

Group L. **Phyllodoce empetriformis* (35) and **Cassiope mertensiana* (30): low-elevation, dry forest margins and progressively wetter sites at higher elevations.

Group M. *Kalmia microphylla* (11), *Saxifraga ferruginea* (10), *Pedicularis groenlandica* (8), *Ledum glandulosum* (7), **Sedum roseum* (7), *Castilleja miniata* (4), *Dodecatheon jeffreyi* (4), and *Ligusticum grayii* (3): very wet to boggy or muddy meadows; *Kalmia, Dodecatheon, Ledum,* and *Pedicularis* require moist soil throughout the growing season.

Group N. **Lupinus lepidus* var. *lobbii* (68), **Erigeron aureus* (49), *Sedum divergens* (41), *Artemisia trifurcata* (40), *Phyllodoce glanduliflora* (39), *Carex proposita* (32), *Luzula campestris* var. *multiflora* (32), and +*Vaccinium caespitosum* (8): generally widespread, occurring in relatively dry subalpine to alpine, deep-soiled meadows.

Group O. **Erigeron peregrinus* (41), **Veronica cusickii* (31), **Salix cascadensis* (27), and *Pedicularis ornithorhyncha* (18): lush meadows above 2300 m.

Group P. *Penstemon davidsonii* var. *menziesii* (24), *Oxyria digyna* (20), **Trisetum spicatum* (16), *Poa gracillima* (15), **Festuca ovina* var. *brevifolia* (14), *Phacelia sericea* (14), **Achillea millefolium* var. *alpicola* (13), *Senecio pauperculus* (13), *Epilobium alpinum* (10), **Saxifraga tolmiei* (9), *Cryptogramma crispa* (3): rock outcrops or gravelly soils that receive snow melt. *Cryptogramma* and *Oxyria* are confined to crevices.

Group Q. **Hieracium gracile* (22), **Luetkea pectinata* (22), *Aster alpigenus* (12), *Lomatium brandegei* (7), *Arnica latifolia* (6), *Lewisia columbiana* (5), and *Polemonium pulcherrimum* (4): low elevation, mesic meadows and rock margins. Several of these species are aggressive colonizers and indicate moderately disturbed sites.

Group R. **Carex nigricans* (22), *Gentiana calycosa* (17), *Lupinus polyphyllus* var. *burkeii* (14), *Senecio cymbalarioides* (13), *Lewisia pygmaea* (12), *Phleum alpinum* (12), and *Potentilla flabellifolia* (12): seasonally wet meadows, dry hummocks within ever-wet meadows, and along stream margins. The habitat is therefore moist for most of the growing season.

Group S. **Penstemon procerus* var. *tolmiei* (44), **Phlox diffusa* (33), *Arenaria capillaris* var. *americana* (25), **Eriogonum pyrolifolium* var. *coryphaeum* (25), *Castilleja elmeri* (23), *Campanula scabrella* (17), and *Carex scirpoidea* (4): rocky margins of graminoid-dominated, high elevation, mesic meadows. The species are somewhat xeromorphic.

Group T. **Antennaria alpina* (73), **Carex spectabilis* (65), *Poa cusickii* (63), **Juncus parryi* (54), and *Luzula hitchcockii* (44): widespread, but most common in high-elevation, sparsely vegetated meadows where snow often persists until August. However, they will cooccur wherever vegetation cover is low.

Group U. **Erigeron compositus* var. *discoideus* (19), *Carex rossii* (10), *Saxifraga caespitosa* (7), and *Juniperus communis* var. *montana* (6): dry, rocky meadows, except that *Saxifraga* is confined to moister microsites in such places.

Group V. *Heuchera cylindrica* var. *alpina* (6), *Erigeron compositus* (undescribed variant) (5), *Epilobium angustifolium* (4), and *Polygonum minimum* (4): relatively rare species, in dry, rocky sites showing evidence of recent disturbance (as from rock fall and avalanches). Probably the best indicators of physical disturbance.

Group W. **Carex nardina* (13), **Smelowskia calycina* (8), and **Dryas octopetala* (4): extreme alpine fell-fields above 2400 m with thin soils and low nutrients levels.

Group X. *Saxifraga bronchialis* (17), *Phlox pulvinata* (16), *Potentilla gracilis* var. *glabrata* (14), **Sibbaldia procumbens* (11), **Silene acaulis* var. *exscapa* (10), *Saxifraga integrifolia* var. *apetala* (9), *Geum rossii* (8), *+Carex breweri* var. *paddoensis* (7), and *Eriogonum umbellatum* var. *hausknechtii* (3): high-elevation fell-fields, particularly in exposed sites. Except for the sedge, they are low rosette or mat-forming species.

Group Y. *Arabis lyallii* (36), *Senecio canus* (23), *Draba paysonii* var. *treleasii* (21), and *Eriogonum ovalifolium* var. *nivale* (14): high, xeric fell-fields; prostrate, rosette-forming species adapted to drought and a short growing season, these species fail to occur in more productive meadows where competition presumably is more severe.

Discussion

Species comparisons. There is good agreement between habitat descriptions in Hitchcock and Cronquist (1973), the interpretations of Douglas and Bliss (1977), and those inferred here from species classification.

There are 66 species assigned to both subalpine and alpine groups Of these, 27 occur in relatively less severe habitats in the alpine than they do in the subalpine (e.g., *Antennaria alpina, Artemisia trifurcata, Carex proposita, Erigeron aureus,* and *Veronica cusickii*). Such a trend is common in ecological studies (Whittaker, 1967; del Moral and Watson, 1978) and it is reassuring that species classification reveals this general trend. Nine species (e.g., *Arenaria obtusiloba, Phlox dif-*

fusa, and *Senecio canus*) occur in drier habitats in the alpine than in the subalpine. Such shifts may reflect ecological compensation, in that relatively drier habitats at high elevation may provide as much effective moisture as wetter habitats in warmer sites. None of these shifts is pronounced. Many species of distinctly wet habitats (e.g., *Ledum glandulosum* and *Pedicularis ornithorhyncha*) and of dry habitats (e.g., *Carex nardina, Draba paysonii* var. *treleasii,* and *Poa cusickii*) do not change their relative positions.

There are 37 species classified in this study for which Douglas and Bliss (1977) record prominence values. There are only two cases in which my interpretations disagree with theirs. *Carex breweri* var. *paddoensis,* which I characterize as a species of dry meadows, is viewed by Douglas and Bliss as a species of concave slopes that become dry only at the end of the growing season. These interpretations may be compatible. *Vaccinium caespitosum* is too rare and variable in my study to give weight to my interpretation. The remaining 35 species are characterized in a way consistent with the results of Douglas and Bliss. Only presence/absence data were required.

Comparisons of the classifications. The smaller number of groups (from a larger number of plots) in the subalpine suggests that trees reduce habitat variability. In the alpine plots, relatively subtle microtopographic features result in significant habitat changes. Alternatively, species may display broader ecological amplitudes in the subalpine than in the alpine.

Species composition of groups changes substantially from subalpine to alpine, but these changes usually do not result in grossly different juxtapositions of species. For example, *Artemisia trifurcata* occurs with eight species in the subalpine and nine in the alpine, only two of which (*Carex proposita* and *Erigeron aureus*) occur in both groups. However, the remaining species indicate generally similar habitat conditions.

The subalpine plots fall into four broad ecological categories: forest sites (groups A, B, C); wet forest openings (groups D, E); rocky, open, low-elevation habitats (groups F, G, H); and rocky, xeric, krummholz habitats (groups I, J, K). The alpine groups fall into five categories: shrub-dominated acid meadows (group L); wet to mesic meadows (groups M, N, O); seasonally dry meadows (groups P, Q, R, S); alpine fell-fields (groups T, U, V); and xeric, alpine fell-fields and crevices (groups W, X, Y).

These results can be extended with caution beyond the study area provided that physiographic and physiognomic conditions remain similar and biogeographic effects do not become important.

Evaluation. The interpretations presented in this paper result from a largely unconscious interplay between the analytical results and the author's experience. Habitat characteristics of many of these species are well known to any field ecologist familiar with the region. However the numerical procedures serve to formalize what is known intuitively, to add species to the list of those formally or informally categorized, and to sharpen distinctions between and indicator value of the species in question.

Species groups are abstract collections of ecologically compatible species. In highly variable topography, it is often not possible to rely on a single species for ecological indications, so that the presence of a collection of species adds weight to the determinations. Species groups can and do show overlapping distributions and members of several groups can occur in a single plot (Williams and Lambert, 1961; Webb et al., 1970; Mueller-Dombois and Ellenberg, 1974). In such cases, the group indicating the most restricted set of conditions will provide the most information.

Species classification can be used for several phytosociological purposes. These include: 1) to determine characteristic plots on which to focus experimental work; 2) to clarify the indicator value of particular species; 3) to suggest indicator value of additional species; 4) to identify species with similar adaptive modes; and 5) to select typical or characteristic species for detailed experimental study.

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EXTRADITION OF SANVITALIA TENUIS TO ZINNIA (COMPOSITAE—HELIANTHEAE)

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ABSTRACT

Consideration of morphological similarities and differences suggests that the most recent addition to *Sanvitalia* should be transferred to *Zinnia*. These considerations together with taxonomic synopses of *Sanvitalia* and *Zinnia* sect. *Mendezia,* including keys, revised morphological circumscriptions, and updated geographic distributions, are abstracted.

Sanvitalia tenuis and members of *Zinnia* L. sect. *Mendezia* (DC.) Hoffm. (cf. Torres, 1963) share many characteristics, including the following: 1) resinous/glandular punctae on abaxial surfaces of leaves and ray corolla laminae; 2) receptacular paleae apically scarious, obtuse to acute; 3) ray corollas comprising an orbicular to oblong lamina inserted on a short tube; 4) anther appendages linear-subulate; 5) ray achenes dorsi-ventrally flattened (weakly triquetrous or with an adaxial mid-nerve in some zinnias), epappose to bicornute (some zinnias); and 6) hairs on achenes all straight. In contrast, all other sanvitalias (cf. Torres, 1964) have: 1) no resinous/glandular punctae on leaves or ray corollas; 2) receptacular paleae apically acuminate to a hard, sharp point; 3) ray corollas lacking a tube, laminae inserted directly on achenes; 4) anther appendages deltoid; 5) ray achenes rounded-triquetrous to subterete, pappus of three stout to subulate awns; and 6) hairs on achenes uncinate. In view of these and other similarities and differences, the following transfer to *Zinnia* sect. *Mendezia* seems timely:

Zinnia tenuis (S. Wats.) Strother, comb. nov.—*Sanvitalia tenuis* S. Wats., Proc. Amer. Acad. Arts 23:277. 1888.—TYPE: Mexico, Chihuahua, Sierra Madre, Sep 1887, *C. G. Pringle 1304*. (Holotype: GH!; Isotypes: NY!, UC!,US!)

Having thus altered *Sanvitalia* Lam. and *Zinnia* sect. *Mendezia* as treated by Torres (1963, 1964), it is appropriate to note further differences in circumscriptions. I treat *Sanvitalia angustifolia* as conspecific with *S. procumbens* and agree with McVaugh (1972) in including *Zinnia greggii* in *Z. angustifolia*. I resegregate *Z. palmeri* from *Z. maritima*. The following keys and diagnoses summarize these changes, correct minor errors in descriptions, update distribution records, summarize chromosome numbers, and outline salient similarities

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and differences among the taxa treated. Chromosome numbers included here have all been published; original sources are listed in papers cited here or in standard indices of plant chromosome numbers. Many were originally reported as "*n*" numbers; all are given here as "2*n*" numbers to facilitate comparison.

Key to *Sanvitalia*

Phyllaries 12–20, 2–4-seriate; ray achenes clearly 3-faced, adaxial faces often 2–3-nerved.
  Annuals, perhaps persisting; leaves all entire.
    Disc achenes strongly dimorphic within single heads: the outermost wingless, the innermost clearly 1–2-winged. . . . . *S. procumbens*
    Disc achenes essentially monomorphic: 4-angled to laterally compressed but not strongly winged.
      Leaf blades ovate to obovate, length mostly 1–2 times width; ray corollas 1.5–2.5 mm long; awns of ray achenes 2–3 mm long; disc pappus of 0(–2) awns. . . . . . *S. ocymoides*
      Leaf blades lance-ovate to lance-linear, length mostly 2–5 times width; ray corollas 2.5–4.5 mm long; awns of ray achenes 1.5–2.5 mm long; disc pappus of (0–)2–4 awns. . . . . *S. versicolor*
  Perennial suffrutices; larger leaves irregularly toothed or lobed. . . . . *S. fruticosa*
Phyllaries 8–11, 1–2-seriate; ray achenes subterete, obscurely trigonous, sulcate on each angle and on abaxial face. . . . . . *S. abertii*

Diagnoses of sanvitalias

Sanvitalia abertii A. Gray: erect annuals 0.5–2.9 dm high; leaf blades lance-linear, 2–4(–6) cm long, 2–6(–12) mm wide; heads stoutly pedunculate to sessile, solitary; phyllaries 8–11, subequal; ray corollas 2–5 mm long; ray achenes 2.5–3.5 mm long, awns stoutly conical, mostly less than 0.5 mm long; disc achenes essentially monomorphic, 4-angled, laterally compressed, the innermost nearly flat, all tuberculate, epappose; $2n = 22$. Southern California across Arizona and New Mexico into trans-Pecos Texas, south into Baja California Norte, Sonora, Chihuahua, and Coahuila.

Sanvitalia fruticosa Hemsl.: suffruticose perennials to 3 dm high; leaf blades lance-elliptic to lance-linear, the larger ones few-toothed or lobed, 9–26 mm long, (2–)4–12 mm wide; heads nearly to quite sessile, solitary; phyllaries ca. 12–18, graduate; ray corollas 5–7 mm long; ray achenes 3 mm long, awns to 3 mm long; outer disc achenes 4-angled, slightly laterally compressed, tuberculate, epappose, inner disc achenes more flattened, one or both margins narrowly winged, pappus of 1–2 slender awns; chromosome number unknown. Known only from s. Puebla and adjacent Oaxaca.

Sanvitalia ocymoides DC.: sprawling to procumbent annuals, mostly 1–2 dm high; leaf blades ovate to oblanceolate or obovate, cuneately narrowed at base onto petiole, 12–35 mm long, 7–16 mm wide; heads sessile, solitary or in 3's; phyllaries 12–20, subequal; ray corollas 1.5–2.5 mm long; ray achenes 4 mm long, awns 2–3 mm long; disc achenes 4-angled, the innermost slightly laterally compressed but not winged, all strongly tuberculate at maturity, 3.3–3.8 mm long, 0–2 awned; $2n = 32$. Known from s. Texas, Coahuila, Nuevo León, and Tamaulipas (to Jalisco and Querétaro fide Torres 1964).

As indicated in key and diagnoses, differences between *S. ocymoides* and *S. versicolor* are insubstantial. The two population systems may represent bicontinental disjunction within a single species.

Sanvitalia procumbens Lam.: sprawling procumbent to erect annuals to ca. 1 dm high, 3 dm across; leaf blades ovate to lance-linear, 1–2(–6) cm long, 4–13(–31) mm wide; heads sessile, solitary; phyllaries 13–21, graduate; ray corollas (2–)4–9 mm long; ray achenes 2.5–3.5 mm long, awns 1–3 mm long; outer disc achenes weakly 4-angled, laterally compressed, tuberculate, epappose, inner disc achenes laterally flattened, one or both margins winged, pappus of 1–2 slender awns; $2n = 16, 32$. Common, widespread, often ruderal, ranging from Chihuahua and Durango to Tamaulipas, Guerrero, Yucatán, and Costa Rica; adventive in California at Riverside and in trans-Pecos Texas in Chisos Basin (J. Henrickson, pers. comm.).

Ray corollas shorter than awns plus relatively narrow leaves have historically distinguished *S. angustifolia* Engelm. ex A. Gray from *S. procumbens*. But, many plants with longer ray corollas have narrowly lanceolate leaves (e.g., *L. R. Stanford et al. 722, T. F. Stuessy 986, B. L. Turner II 46*). Further, length of ray corolla ranges from 2 to 9 mm and awn length ranges from 1 to 3 mm. Because variation in both foliar and floral characters is considerable, continuous, and extends over a broad geographic area, it seems preferable to recognize a single species.

Sanvitalia versicolor Griseb.: erect to spreading annuals to 2 dm high; leaf blades lance-ovate to lance-linear, 14–32 mm long, 6–11 mm wide; heads sessile, solitary; phyllaries 12–16, subequal; ray corollas 2.5–4.5 mm long; ray achenes ca. 4 mm long, awns 1.5–2.5 mm long; disc achenes 4-angled, the innermost slightly laterally compressed, none winged, all strongly tuberculate, 3.9–4.5 mm long, (0–)2–4-awned; $2n = 32$. Known only from s. Bolivia and n. Argentina.

Key to *Zinnia* sect. *Mendezia*

Receptacular paleae metallic yellow to bright, coppery orange distally, rarely also purple-tinged.

  Ray corollas coppery orange to golden yellow (rarely white in *Z. angustifolia*) or pale with an orange spot at base (in *Z. tenella*), laminae mostly 6–15 mm long.

Usually perennials; ray corollas not bicolored; disc corollas ca. 5 mm long. . . . . *Z. angustifolia*

Annuals; ray corollas bicolored (look close for spot at base); disc corollas ca. 3 mm long. . . . . *Z. tenella*

Ray corollas uniformly pale greenish yellow to white, not orange at base, laminae mostly 4–9 mm long.

Peduncles 2–4 cm long in fruit; ray achenes 3–5 mm long; disc achenes pectinate-winged and ciliolate. . . . . *Z. bicolor*

Peduncles 3–6 cm long in fruit; ray achenes ca. 3 mm long; disc achenes scarcely winged, evenly ciliolate. . . *Z. leucoglossa*

Receptacular paleae deep purple to blackish brown distally or stramineous to tip.

Leaves narrowly triangular to linear, length mostly >3 times width, widest near base.

Leaves more than 4 mm wide; heads pedunculate.

Ray corollas 5–11 mm long, uniformly yellow to orange; disc achenes entire-winged. . . . . *Z. palmeri*

Ray corollas 2–4 mm long, often with purple spot at base; disc achenes pectinate-winged. . . . . *Z. purpusii*

Leaves 1–3 mm wide; heads sessile. . . . . *Z. tenuis*

Leaves oblong to lance-elliptic, length mostly <3 times width, widest near middle.

Annuals (perhaps persisting but not woody); peduncles 1–5 cm long in fruit; disc corollas orange to yellow distally . . . . *Z. littoralis*

Perennials, often suffrutescent; peduncles 7–10 cm long in fruit; disc corollas purple distally. . . . . *Z. maritima*

Diagnoses of zinnias

Zinnia angustifolia H.B.K.: perennial herbs or suffrutices, sometimes behaviorally annual, 1–3(–5) dm high; leaves petiolate to subsessile, blades narrowly lanceolate to lance-linear, 2–4(–7) cm long, 3–6(–9) mm wide, base truncate to cuneate; peduncles 1–3 cm long in fruit; paleae coppery orange distally, rarely turning black; ray lamina iridescent coppery orange to golden yellow (rarely white), ovate to oblong, 6–12(4–15) mm long; disc corollas distally coppery orange, rarely turning black, ca. 5 mm long; ray achenes 2.8–3.5 mm long, 1.3–1.6 mm wide; $2n = 22, 24$. Common from Sonora and Chihuahua to San Luis Potosí, Nayarit, and Michoacán.

Perennial habit and yellow to white ray corollas have historically distinguished *Z. greggii* Robins. & Greenm. from *Z. angustifolia,* usually characterized as annual with orange ray corollas. McVaugh (1972) noted that all these plants are perennials that may behave as annuals at times and that the different ray colors may be found in single populations. He further said that orange-rayed plants are more widely distributed and the pale-rayed plants are commonest in the Pacific portions of the coastal states from Sinaloa to Michoacán. He recognized two varieties: var. *angustifolia* and var. *greggii* (Robins. & Greenm.) McVaugh.

Olorode (1970) crossed all six pairings of *Z. angustifolia, Z. greggii, Z. littoralis,* and *Z. leucoglossa,* using plants from a single population of each. Color of ray corollas segregated 21:23 in F_1 of *Z. angustifolia* × *Z. greggii,* suggesting simple genetic control of the color differences and supporting conspecificity. In fact, pollen stainabilities (76–99 percent) and percentage of "plump seeds" (85) in all the F_1's suggest that these four nominal species are perhaps all conspecific. Unfortunately, we do not have results of intraspecific crosses or crosses involving other members of *Z.* sect. *Mendezia.*

Zinnia bicolor (DC.) Hemsl.: annuals (rarely persisting?) to 3 dm high; leaves petiolate to subsessile, narrowly lance-elliptic, 2–4 cm long, 4–9 mm wide, base broadly to narrowly cuneate; peduncles 2–4 cm long in fruit; paleae orange distally, sometimes faintly tinged with purple; ray lamina white to pale yellow, suborbicular to oblong, 5–9 mm long; disc corollas red-orange distally, 3–4 mm long; ray achenes 3–5 mm long, 1.2–2.2 mm wide, disc achenes mostly pectinate-winged and ciliolate; $2n = 22$. Scattered, local populations in San Luis Potosí, Nayarit, Jalisco, and Guanajuato.

Zinnia leucoglossa S. F. Blake: perennial or annual herbs, sometimes weakly suffrutescent, 2–4 dm high; leaves subsessile to short-petiolate, blades narrowly lanceolate, 2–4 cm long, 3–8 mm wide, base truncate to subcordate; ray lamina whitish to pale yellow, suborbicular to ovate, 4–6 mm long; disc corollas coppery orange distally, purple-tinged, sometimes turning black, 4–5 mm long; ray achenes 2–3 mm long, 1.0–1.2 mm wide, disc achenes not pectinate-winged, evenly ciliolate on margins; $2n = 22$. Very local in Sinaloa and Nayarit.

Zinnia littoralis Robins. & Greenm.: sprawling to erect annuals or short-lived perennials, stems to 3 dm long; leaves petiolate, lance-elliptic to oval, length mostly 2–4 times width, 12–35 mm long; peduncles 1–5 cm long in fruit; paleae stramineous throughout or sometimes orange to brown at very tip; ray lamina white to greenish or sulphur yellow, usually drying yellow, orbicular to oblong-elliptic, 5–11 mm long; disc corollas distally golden yellow to orange, 4.1–5.5 mm long; ray achenes 3–4 mm long, 1.4–2.1 mm wide; $2n = 22$. Endemic to environs of Mazatlán, Sinaloa.

In protologue, Robinson and Greenman (1896) cited collections as follows without designating herbaria of deposit: "Collected at Mazatlan by *Th. Coulter,* and rediscovered on dry hills of the coast at the same point by *W. G. Wright,* January, 1889, no. 1201 (distributed as *Z. maritima*?); also by *F. H. Lamb* on dry rocky cliffs at same place, 26 December, 1894, no. 325 (distributed as *Z. maritima*)." Of these, I have seen *Coulter* at GH; *Wright* at GH, UC, and US; and *Lamb* at GH, NY, and US (2). Torres (1963) cited as type, "T: . . ., *Lamb 325* US! Isotypes: MO! NY!". Neither on the specimens nor in print did Torres indicate that he had seen any of the snytypes at GH. Considering the wording of the protologue and the association of Robinson and Greenman with GH, I reject Torres' lectotypification and instead here designate as lectotype of *Zinnia littoralis* Robins. & Greenm.: *Th. Coulter 335* at GH.

Zinnia maritima H.B.K.: perennials, often suffrutescent (flowering first year?), stems to 3+ dm long; leaves petiolate, oblong to elliptic, length mostly less than 2.5 times width, 6–48 mm long; peduncles 2–10 cm long in fruit; paleae purple distally; ray lamina pale to golden yellow, orbicular to elliptic, 4–9 mm long; disc corollas purple distally, 3.5–4.5 mm long; ray achene body 3–4 mm long, 0.9–1.3 mm wide, apically attenuate and continuous with base of corolla tube; $2n = 26$. Endemic to environs of Acapulco, Guerrero.

Zinnia palmeri A. Gray: annuals (rarely persisting?), 2–4 dm high; leaves short-petiolate to sessile, blades mostly narrowly deltoid to linear-triangular, length mostly 3–7 times width, 2–5 cm long, 4–12(–21) mm wide at the truncate to subcordate-clasping base, margins often obscurely serrate; peduncles 2–15 cm long in fruit; paleae purple distally; ray lamina yellow, suborbicular to oblong, 5–11 mm long; disc corollas purple to blackish distally, 3–4 mm long; ray achene body 1.8–2.8 mm long, 1.1–1.3 mm wide, apically attenuate and continuous with base of corolla tube; $2n = 24$. Locally common in Nayarit, Jalisco, Colima, and Guerrero.

Torres (1963) treated *Z. palmeri* as conspecific with *Z. maritima,* which he characterized as annuals with "variable" leaves. He also said, "*Z. maritima* consists of intergrading races, probably ecotypes . . . ." After consideration of specimens at GH, LL, NY, TEX, UC, and US, including an isotype (*Palmer 386,* US) plus many topotypes (Tequila, Jalisco) of *Z. palmeri* and topotypes (Acapulco, Guerrero) plus photograph of holotype (*Bonpland 3874,* P) of *Z. maritima,* I have concluded that, in spite of considerable morphological variation, two distinct modes are discernable and distinguishable by differences given in the diagnoses.

Zinnia purpusii Brandegee: slender, erect annuals to 3 dm high; leaves sessile or nearly so, blades linear-triangular, mostly 2–5 cm long, (3–)4–7 mm wide at the truncate to subcordate-clasping base; peduncles 1–3 cm long in fruit; paleae purple distally; ray lamina pale yellow, sometimes with spot of purple at base, broadly ovate to orbicular, 2–4 mm long; disc corollas purple to blackish distally, ca. 2.5 mm long; ray achene body broadly elliptic, ca. 2.5 mm long, 1.5 mm wide, apically bicornute and continuous with the stout corolla tube; $2n = 24$. Known from few, isolated populations in Jalisco, Guerrero, and Chiapas.

Zinnia tenella Robins.: erect, rarely spreading annuals to 2 dm high; leaves petiolate, lance-elliptic to lance-linear, mostly 15–35 mm long, 4–8(–14) mm wide; peduncles 1–3 cm long in fruit; paleae coppery orange distally; ray lamina bright to pale yellow with an orange spot at very base, ovate to suborbicular, 6–9 mm long; disc corollas distally golden yellow to red-orange, ca. 3 mm long; ray achenes ca. 4 mm long, 2.2 mm wide, strongly tuberculate; $2n = 22$. Uncommon; Durango, Zacatecas, and Jalisco.

Zinnia tenuis (S. Wats.) Strother: erect annuals to 2 dm high; leaves linear, 6–28 mm long, 1–3 mm wide; heads sessile or nearly so; paleae stramineous to tip or purple-tinged distally; ray lamina pale yellow, ovate to orbicular, 2–3 mm long; disc corollas distally golden yellow, 1.5–2.2 mm long; ray achenes ca. 3 mm long, 1.8 mm wide; $2n = 18$. Known only from Sierra Madre of Chihuahua.

As indicated above, chromosome numbers reported for members of *Zinnia* sect. *Mendezia* are $2n = 18$, 22, 24, and 26. For sanvitalias, $2n = 16$, 22, and 32 are known. So, the chromosome number of *Z. tenuis* (Torres, 1966) is just as novel in *Zinnia* as in *Sanvitalia.*

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I thank staff at GH, LL, NY, TEX, and US for loans and, especially, J. Henrickson for helpful discussions, encouraging goadings, and *Sanvitalia* savvy.

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LYCIUM AROCHAE (SOLANACEAE), A NEW SPECIES FROM CENTRAL COAHUILA, MEXICO

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ABSTRACT

Lycium arochae is a distinctive new species known from a single population in central Coahuila, Mexico, where it is a codominant species in extensive alluvial flats surrounding the playa of Laguna Colorada. The species shows relationships to *Lycium berlandieri* Dunal and *L. pallidum* Miers.

Recent field work by Wendt and Lott in conjunction with the Chihuahuan Desert flora project and toward a floristic and vegetational survey of central Coahuila, Mexico, has revealed a number of rarities and novelties. Among these is a new species of *Lycium*.

Lycium arochae Chiang, Wendt, & Lott, sp. nov. a *L. berlandieri* Dunal et *L. pallido* Miers habitu compactiore, staminibus valde exsertis, filamentis in parte libera glabris, et praeterea a *priore* foliis glaucis, a *posteriore* floribus et foliis parvioribus recedit (Fig. 1).

Much branched, thorny shrubs 0.5–1.5 m tall. Young branches with ashy gray bark, turning brownish at maturity. Thorns slender, straight, 8–10 mm long. Leaves in fascicles of 3–6, glabrous, glaucous, bluish-green, semisucculent, obovate or oblong, mostly rounded at the apex, sessile, (2.5) 5–10 (12) mm long, (1.5) 2–3.5 mm broad. Flowers solitary at the leaf fascicles; pedicels slender, (5) 7–10 mm long, glabrous. Calyx campanulate to ovoid, 1.0–1.6 mm long; lobes 5, deltoid, subequal, 0.5–0.6 mm long, sparsely pubescent at the apex. Corolla 7 mm long; tube narrowly obconic, 5 mm long, glabrous; lobes 5, 2 mm long, violet, ovate, rounded at the apex, spreading or recurved, the margins sparsely ciliolate. Stamens unequal in length, often strongly exserted, surpassing the corolla lobes; filaments affixed to the corolla tube about 2 mm from the base, adnate to the tube for 1 mm, sparsely pilose where adnate, glabrous elsewhere. Style exserted. Fruit a many-seeded, ovoid, orange-red berry, 5–8 mm in diameter.

TYPE: Mexico, Coahuila, ca. 14.5 km SSE of Rancho Zacatosa (R. Arocha) in Laguna Colorada area, just north of Tanque El Revés

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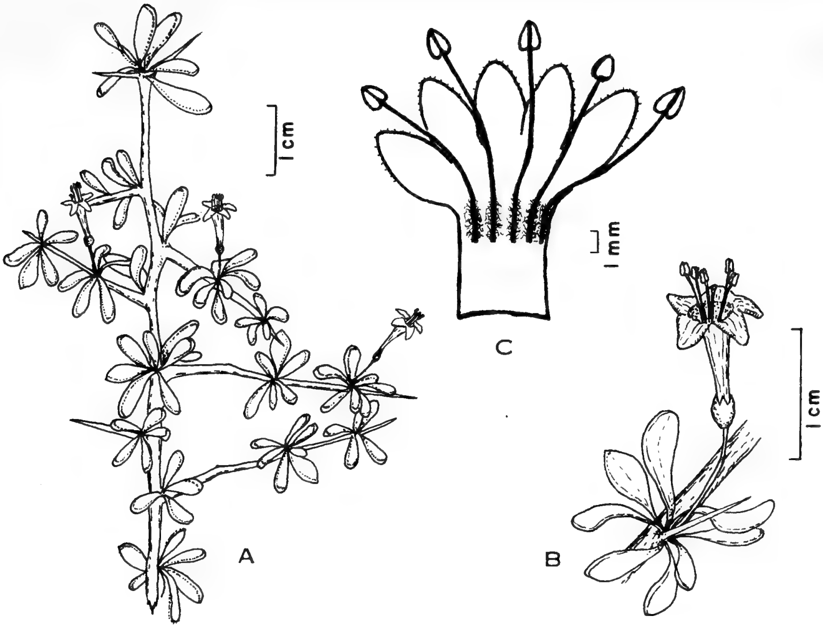

FIG. 1. *Lycium arochae*. A. Flowering branch. B. Enlargement of flower. C. Dissection of corolla.

(26°55′45″N, 102°41′05″W), desert scrub, 1100 m, 27 Oct 1976, *T. Wendt and E. J. Lott 1903* (Holotype: LL. Isotypes: MEXU, ENCB, and to be distributed).

Additional specimens examined: Mexico, Coahuila: road from Zacatosa southeasterly to Puerto Colorado, via Tanque Colorado, bottom of large valley SE of Zacatosa, common bush, 31 Aug 1941, *I. M. Johnston 8644* (GH, LL), *8644A* (GH, LL); ca. 13.2 km S of Rancho Zacatosa, W of Laguna Colorada, 3 Oct 1976, *T. Wendt, E. J. Lott, and M. Mispagel 1886* (LL); ca. 11.0 km SSE of Rancho Zacatosa, 27 Oct 1976, *T. Wendt and E. J. Lott 1902* (LL).

The epithet honors Sr. Leopoldo Arocha Treviño of Rancho Zacatosa (R. Arocha) in appreciation for friendship, hospitality, and assistance during numerous trips to the area.

The combination of small, glabrous, glaucous leaves; long-exserted stamens with filaments entirely glabrous in the free portion; and short-lobed, campanulate to ovoid calyx distinguishes the new species from other North American *Lycium* species. *L. arochae* is similar to *L. berlandieri* in flower size and corolla shape and approaches that species in leaf size and shape, but it differs in its strongly glaucous leaves, more compact habit, and long-exserted stamens glabrous in the free portion. In its glaucous leaves *L. arochae* is similar to *L. pallidum,* but differs in leaf size (2–12 mm long in *L. arochae* versus 10–40 mm in *L. pallidum*), flower size (ca. 5–8 mm long versus 14–25 mm long), habit, and details of the stamens. Although populations of both *L. berlandieri* and *L. pallidum* occur within several kilometers of the single known population of *L. arochae,* the origin of the latter species from hybridization between these two species seems unlikely, because *L. arochae* differs from both in habit and details of the stamens. For the present, *L. arochae* must be considered a quite distinct but very local species.

Lycium arochae is known only from alluvial flats surrounding the lakebed of Laguna Colorada, where it is abundant over several thousand hectares. The Laguna Colorada basin, also known as the "Barreal del Junco", is a small, relatively high, internal-drainage basin (ca. 1250 km^2 total potential watershed, playa elevation 1100 m) about 55 km west of the town of Cuatro Ciénegas, Coahuila. It lies in the immediate rainshadow of the 3000 m Sierra de la Madera to the north and northeast and the 2250 m Sierra de la Fragua to the east and southeast. Although no rainfall records are available for the basin, personal experience and information from local ranchers indicate that the average rainfall is probably less than that of the Cuatro Ciénegas area, which averaged 183.1 mm annually over 29 years (García, 1973). While the bajada and limestone slope vegetations are in many cases similar to those described by Pinkava (in press) for the adjacent Cuatro Ciénegas region, the basin floor is quite different, lacking entirely the springs and natural permanent water, as well as gypsum dunes and flats, characteristic of Cuatro Ciénegas. The small lakebed fills only in years of unusually high and intense precipitation, and the water table is very low, according to local sources. The soils in and near the playa are mostly fine-grained, light-colored alluvium derived from the predominating Cretaceous limestones of the area, but in some areas are quite reddish-brown due in part to sandstone-derived alluvium from the Colorada Formation, the type locality and only outcrop of which lies in the southern part of this basin (Charleston, 1974). These soils are not highly saline, as evidenced by general aspect and plant species composition (compare with lists in Henrickson, 1977), probably owing largely to the combination of very low rainfall, low water table, and small area of the drainage basin.

The central playa is quite sparsely vegetated with occasional *Prosopis glandulosa* Torr., *Koeberlinia spinosa* Zucc., and *Larrea tridentata* (DC.) Cov. Surrounding this is a zone of varying width composed of *Sericodes greggii* A. Gray, *Lycium arochae,* and *Atriplex obovata* Moq., several grasses including *Scleropogon brevifolius* Phil. and the annual *Bouteloua barbata* Lag., and scattered or local *Parthenium incanum* H.B.K., *Prosopis glandulosa, Opuntia leptocaulis* DC., and *Echinocereus enneacanthus* Engelm. The gray aspect of this zone contrasts sharply with the olive-green of the surrounding typical Chihuahuan Desert lowland scrub, which here includes *Larrea tridentata, Flourensia cernua* DC., *Parthenium incanum, Cordia parvifolia* DC., and *Prosopis glandulosa.* A fairly narrow zone of intergradation is present. Although *Lycium arochae* is abundant in the "gray zone", it is quite uncommon in the *Larrea-Flourensia* zone, being found in association with these species only in small pockets or peninsulas surrounded by *Sericodes-Lycium-Atriplex* vegetation.

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HEDEOMA TODSENII (LABIATAE), A NEW AND RARE SPECIES FROM NEW MEXICO

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ABSTRACT

Hedeoma todsenii is described from two populations in the San Andres Mountains of southcentral New Mexico. It is morphologically similar to *Hedeoma apiculatum.*

Hedeoma is a genus of 43 taxa (Irving, 1979) distributed principally in the southwestern United States and northern Mexico. Many of its taxonomic subgroups are composed of widespread and somewhat weedy annuals and perennials. In these the phenetic relationships of the species, as well as the naturalness of the various units themselves, are more or less apparent. The subgenus *Ciliatum,* however, comprises a small number of endemic species and, due to their relatively wide morphological discontinuities, relationships are difficult to discern and naturalness of the group is far from clear. A recent field survey of the San Andres Mountains of south-central New Mexico has resulted in discovery of a new species that greatly improves our understanding of species relationships within subgenus *Ciliatum.* For the first time the purported naturalness of *Ciliatum* can begin to be perceived.

Hedeoma todsenii Irving, sp. nov.

Herbae perennes suffruticosae ad 12 cm altae, caulibus numerosis. Folia sessilia, coriacea et integra, 8–14 mm longa, 2–4 mm lata, lanceolata-elliptica; apices obtusi vel mucronati. Flores singulares, axillares. Calyx 11–12 mm longus; annulus in parte centrali tubi situs. Corolla aureorubens ad 35 mm longa non annulata (Fig. 1).

Suffrutescent caespitose perennials 10–18 cm high. Stems numerous, simple and canescent or puberulent with hairs retrorsely curling. Leaves coriaceous, entire, lanceolate-elliptic, subsessile 8–14 mm long, 2–4 mm wide; apex obtuse to retuse; midrib and margins slightly hispidulose-tuberculate; lower surface deeply glandular-punctate, the upper less so. Flowers solitary and well-spaced in the upper portions of the stems; peduncles ca. 1.5 mm long; pedicels ca. 3–5 mm long, canescent; bracteoles lanceolate, longer than pedicels. Calyx 11–12 mm long (base to tip of teeth), tubular-funnelform, not gibbous, minutely scabrous on the nerves and glandular-punctate between; upper teeth partially connate forming a conspicuously recurved upper lip, lobes lanceolate, ca. 1 mm wide, 1.5 mm long, sparsely ciliate; lower

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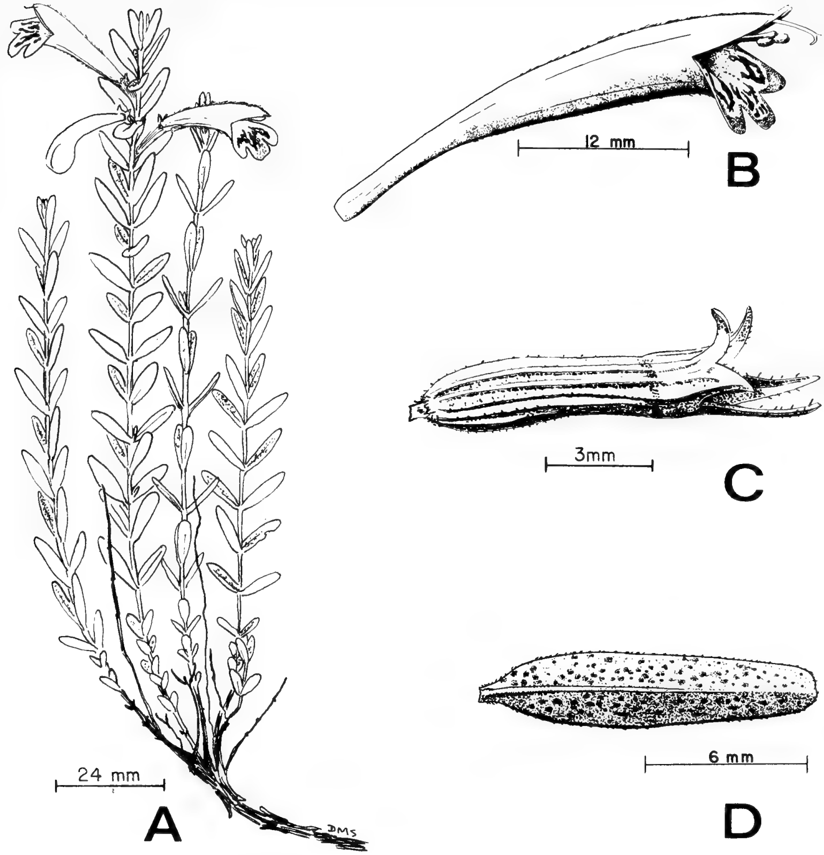

FIG. 1. Drawing of isotype (TEX) of *Hedeoma todsenii* Irving. A. habit; B. corolla; C. calyx; D. leaf undersurface.

teeth ascending, deltoid-aristate, 3.0–3.5 mm long, sparsely hirsute-ciliate; annulus ca. 1 mm wide, included and seated ca. 2 mm below juncture of upper and lower teeth. Corolla showy, up to 35 mm long, 6 mm wide at throat, sparsely pubescent in the tube but not annulate; the upper lip deeply obcordate, erect, up to 5 mm long, red in color on interior margins; lower lip streaked with red, recurved, the similar rounded lobes ca. 3.5 mm long, 3 mm wide; anthers exserted. Nutlets ca. 2 mm long, 1 mm wide, dark brown in color and weakly glaucous. Chromosome number unknown.

TYPE: USA, New Mexico, Sierra Co., San Andres Mountains, "On a steep north-facing gravelly gypseous limestone hillside in open pinyon, 2 km S of Hardin Ranch in Section 34 R2E, T12S," 2000 m, 18 Aug 1978, *T. K. Todsen SA 1–78* (Holotype: NY. Isotypes: US, TEX, NMC).

The discovery of *H. todsenii* adds a fifth species to a group of closely related endemics that form subgenus *Ciliatum* (Irving, 1979). *Hedeoma ciliolatum* and *H. pusillum* are restricted to gypsum outcrops near Galeana, Nuevo León, Mexico; *H. pilosum* has been collected only once from the calcareous summit of Old Blue Mountain in Trans-Pecos Texas; and *H. apiculatum* is known from only the protected canyons of the Guadalupe Mountains of Texas and New Mexico. Within this group, *H. todsenii* is most closely allied to *H. apiculatum.* The suffruticose, caespitose habit; the overall patterns of pubescence; the coriaceous, entire, lanceolate leaves; and the large tubular calyx with its deep-seated annulus are some of the morphological attributes that are common to both taxa.

Hedeoma todsenii and *H. apiculatum,* despite their obvious morphic similarities, differ in a number of characteristics. The most conspicuous is the large (up to 35 mm) yellow-red corolla of *H. todsenii* compared with the smaller (19–20 mm) lavender corolla of *H. apiculatum.* The calyces of *H. todsenii* are also longer than those of *H. apiculatum,* 11–12 mm and 9–10 mm, respectively. The leaves of *H. todsenii* are largely obtuse, and the anthers are exserted. In contrast, the leaves of *H. apiculatum* are apiculate at the apex and the anthers are included.

The morphological relationships between *H. todsenii* and *H. apiculatum* parallel those displayed by *H. ciliolatum* and *H. pusillum. Hedeoma pusillum* is the diminutive counterpart of *H. ciliolatum* with the most conspicuous difference being the large orange-red corolla of *H. ciliolatum* and the small lavender corolla of *H. pusillum.* Similarly, *H. apiculatum* can be viewed as a somewhat smaller form of *H. todsenii* with also the primary difference residing in the size and color of the corolla.

Within *Hedeoma* large corollas and exserted anthers foster outbreeding and are considered primitive traits; smaller corollas with anthers included facilitate autogamy and are considered derived characters. Thus, we can speculate that both *H. pusillum* and *H. apiculatum* are derived from their larger-flowered counterparts, *H. ciliolatum* and *H. todsenii. Hedeoma apiculatum* has a diploid chromosome number of $2n = 144$, which also indicates a derived position within *Hedeoma* ($x = 9$; Irving, 1976).

In addition to its close affinity with *H. apiculatum, H. todsenii* shares a number of morphological similarities with *H. ciliolatum,* and thus *H. ciliolatum, H. pusillum, H. apiculatum,* and *H. todsenii* are tied into a coherent and natural unit. Of these similarities, the most salient is morphology of the corolla. Corolla size and color are nearly identical in *H. todsenii* and *H. ciliolatum.*

Hedeoma todsenii is known from two small populations and, because of its highly restricted distribution, should be identified as an endangered or threatened species.

The specific epithet honors Dr. Thomas K. Todsen, Research Associate in Biology, New Mexico State University, who discovered the species during his continuing survey of the flora of the San Andres Mountains.

ACKNOWLEDGMENTS

I thank Dr. David Sutherland for his illustrations.

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(Accepted 22 Jun 1979.)

NOTEWORTHY COLLECTIONS

DRABA BOREALIS DC. (BRASSICACEAE).—USA, WY, Teton Co.: Sheep Creek (T41N R115W S16 SW¼), 5 Jun 1977, *R. W. Lichvar 253,* RM; Gros Ventre Canyon (T41N R115W S1 SE¼), 27 Jun 1977, *R. W. Lichvar 505,* RM. Common in moist soil along streams. Associates include *Actaea rubra, Salix boothii, Smilacina racemosa,* and *Trifolium pratense.* Verified by G. A. Mulligan, DAO, Apr 1978.

Previous knowledge. e. Asia, Aleutian Ids., and s. to mts. of B.C. and s.w. Alberta; in lower U.S. known only from CO. (Herbaria consulted: COLO, RM: published sources: Hultén, Fl. Alaska and Neighboring Terr. 1968; Lichvar, Fl. Gros Ventre Mts., M.S. thesis, Univ. WY. 1979; Scoggan, Fl. Canada 1978; Weber et al., Phytologia 41:486–498, 1979).

Diagnostic characters. Keys to *D. praealta* Green in Dorn (Man. Vasc. Pls. Wyo. 1977, p. 540) but is perennial to 5.5 dm high, caudex simple or branched; basal leaves 0.6–5 cm long, 0.3–1.8 cm wide, oblanceolate; cauline leaves 0.4–4 cm long, 0.2–1.8 cm wide, ovate to elliptic, toothed or entire; calyx 2–3 mm long; petals 4–6 mm long, white; fruits lanceolate, pubescent, 7–14 mm long, 2–4 mm wide; styles to 1 mm long.

Significance. First report for WY.

SILENE DICHOTOMA Ehrh. (CARYOPHYLLACEAE).—USA, WY, Teton Co., Teton Valley Ranch along Gros Ventre River (T42N R115W S1 SE¼), 21 Aug 1977, *R. W. Lichvar 1291,* RM. Frequent in marshy area on rocky bank. Associates include *Helianthella uniflora* and *Prunus virginiana.* Verified by R. L. Hartman, RM, Oct 1977.

Previous knowledge. Scandinavia, central Europe to w. Siberia; introduced into N.A., spreading from Quebec to B.C., s. to NC, MO, and CA. Known in ID and MT. (Herbarium consulted: RM; published sources: Hitchcock et al., Vasc. Pls. Pacific Northwest. 1964; Fernald, Gray's Man. Bot., 8th ed. 1950; Hitchcock and Maguire, Univ. Wash. Publ. Biol. 13:1–73. 1947; Lichvar, op. cit.).

Diagnostic characters. Keys to *S. noctiflora* L. in Dorn (op. cit., p. 198) but is annual to 8 dm high; leaves lanceolate to oblanceolate, 3–8 cm long, 0.3–3.5 cm wide, the lower petioled; calyx 10–15 mm long; petals white to reddish, bifid; styles usually 3; capsule 3-celled.

Significance. First report for WY. Not spreading as of June, 1979.

EPIPACTIS GIGANTEA Dougl. ex Hook. (ORCHIDACEAE).—USA, WY, Teton Co., Gros Ventre River on Teton Valley Ranch (T42N R115W S1 SW¼), 27 Jun 1977, *R. W. Lichvar 507, 581,* RM. Common in moist, dark soil. Associates include *Carex nebraskensis, Juncus tracyi,* and *Salix boothii.*

Previous Knowledge. B.C. to Baja Calif. and most of w. U. S. to SD, OK, and central Mex. Known in ID and MT. (Herbaria consulted: COLO, RM; published sources: Correll, Native Orchids of N.A. 1950; Cronquist et al., Intermt. Fl. 1977; Lichvar, op. cit.; Dorn, op. cit.). Dorn, (op. cit., p. 1013) gives WY distribution as Big Horn Co., based on a single 1896 collection from Shell Creek (*C. L.* & *C. E. Moore s.n.,* RM).

Significance. New to Teton Co. The population at Shell Creek could not be located in July, 1979.—ROBERT W. LICHVAR, Wyoming Natural Heritage Program, The Nature Conservancy, 1603 Capitol Ave., No. 325, Cheyenne, WY 82001. (Accepted 19 Jul 1979.)

APONOGETON DISTACHYUS L. f. (APONOGETONACEAE).—USA, CA, San Diego Co., Kearny Mesa (32°50′N, 117°10′W), within 100 m of n. end of Kearny Mesa Rd. at s. edge of Miramar Naval Air Station and Miramar Mounds Natural Landmark, 20 Dec 1978, *J. Keeley 7269* (LOC); 22 Mar 1979, *J. Keeley 7270, 7274* (LOC), *7271, 7273* (RSA), *7272* (LAM). Rooted floating aquatic, occasional in undisturbed vernal pools, abundant in deeper pools and marshes created by a stream. Tuberous rhizomes may allow it to survive dry periods. Flowers Dec–Apr. Verified by C. Davidson (LAM) and R. Thorne (RSA).

Previous knowledge. Native to s. Africa, commonly cultivated in parks. Reported as an escape in San Mateo Co. (Munz, Supplement to a Calif. fl. 1968). Herbaria consulted: RSA, LAM.

Significance. New plant family for S CA. In some deeper pools *A. distachyus* is an aggressive colonizer, further endangering native vernal pool flora.

STANLEYA PINNATA (Pursh) Britton (BRASSICACEAE).—USA, CA, Ventura Co., Conejo Valley (34°10′N, 118°50′W), 2.9 km n. of hwy 101 and 0.7 km w. of Westlake Blvd., ca. 350 m, 29 Apr 1979, *J. Keeley 7148–49* (LOC). Widely scattered suffrutescent shrubs forming a conspicuous part of dense undisturbed Coastal Sage Scrub with *Salvia leucophylla, Encelia californica,* and *Artemisia californica.* Only on s.-facing slopes. Verified by C. Davidson (LAM).

Previous knowledge. "Seleniferous soil, desert slopes and washes, 1000–7500 ft.; Creosote Bush Scrub to Pinyon-Juniper Wd.; Santa Rosa mts. to Cuyama V. and Inyo Co.," e. to ND, KS, and TX (Munz, A fl. of s. Calif. 1974, p. 302). Herbaria consulted: RSA, LAM. A specimen (RSA-127995) collected in 1958 in coastal sage along "coast hwy [hwy 1] near Malibu Creek" (ca. 25 m) apparently has been overlooked heretofore.

Significance. These specimens extend the distribution of *Stanleya pinnata* to the coast, to lower elevation, and to another plant community. Other shrubs with both coastal and desertic distributions include *Eriogonum fasciculatum, Euphorbia miseri,* and *Atriplex canescens.*—JON E. KEELEY, Department of Biology, Occidental College, Los Angeles, CA 90041 and STERLING C. KEELEY, Department of Biology, Whittier College, Whittier, CA 90608. (Accepted 19 Jul 1979.)

PILOSTYLES THURBERI A. Gray (RAFFLESIACEAE).—USA, NV, Nye Co., W. Frenchman Flat, s. slope Pink Holes Hill (36°44′35″N, 116°01′40″W), 22 Nov 1976, *Williams et al. 287* (NTS, RSA, CAS, US). Rare. Observed on the stems of six shrubs of *Psorothamnus polydenius* (Torr.) Rydb. on talus of sandstone-tuff at s. base of a small hill, *Atriplex canescens-Larrea tridentata* dominated vegetation, 1020 m. Parasite with 2 mm long, brownish flowers protruding from stems of host.

Previous knowledge. Known from CA (San Diego, Imperial, and Riverside cos.) and from AZ (Yuma Co.), all on *Psorothamnus emoryi* (A. Gray) Rydb.; NM and TX; n. Mex. (Herbaria consulted: UC, CAS, RSA, RENO, LV, US; published sources: Armstrong, Fremontia 5:20–22. 1977; Rowell and Blassingame, Sida 3:77–81. 1967; Rutherford, Aliso 7:263–288. 1970; Munz, A fl. of s. Calif. 1974; Kearney and Peebles, Arizona fl. 1960; Shreve and Wiggins, Veg. and fl. Sonoran Desert. 1964; Kuijt, Biol. parasitic fl. pls. 1969.)

Significance. New to Nevada. Northward disjunction of 400 km. First documentation of *Psorothamnus polydenius* as host plant. Does not appear to differ from parasites on *P. emoryi.*—MICHAEL P. WILLIAMS, E.G. & G., Inc., 130 Robin Hill Road, Goleta, CA 93017 and RICHARD C. CASTETTER, 1409 W. Picacho, Las Cruces, NM 88001. (Accepted 10 Aug 1979.)

NOTES AND NEWS

REEVALUATION of *Pyrus hoffmannii* (ROSACEAE) FROM THE PLEISTOCENE CARPINTERIA ASPHALT DEPOSIT, CALIFORNIA.—Chaney and Mason (Publ. Carnegie Inst. Wash. 415:45–79. 1933) proposed the name *Pyrus hoffmannii* for a flower, an immature fruit, and a leaf from the Late Pleistocene flora of the asphalt deposit near Carpinteria, Santa Barbara Co., CA. Recent radiocarbon dates indicate an age of greater than 50,000 years for this flora (Miller and Peck, Trans. San Diego Soc. Nat. Hist. 19:85–106. 1979), but some fossils from the deposit may be younger. Chaney and Mason (op. cit.) believed these specimens to represent an extinct species related to *Pyrus rivularis* Dougl. However, reevaluation by Dr. D. I. Axelrod of the type specimens (Santa Barbara Museum of Natural History Paleontology Collection Specimens *277–279*) reveals that they are *Amelanchier pallida* Greene (= *A. alnifolia* of authors).

The secondary and tertiary venation of the type leaf is not shown accurately in the original sketch (Chaney and Mason, op. cit., Fig. 13). Microscopic examination of the leaf (Fig. 1) shows venation inseparable from leaves of *A. pallida.* The thinly scattered filamentous curled hairs on the pedicels of the type fruit and flower agree with those of *A. pallida,* as does the basic floral morphology. Therefore, *P. hoffmannii* is a later synonym of *A. pallida. A. pallida* still occurs in the region (Smith, A fl. Santa Barbara Reg. Calif. 1976), is common and widespread in California, and fits well into previous

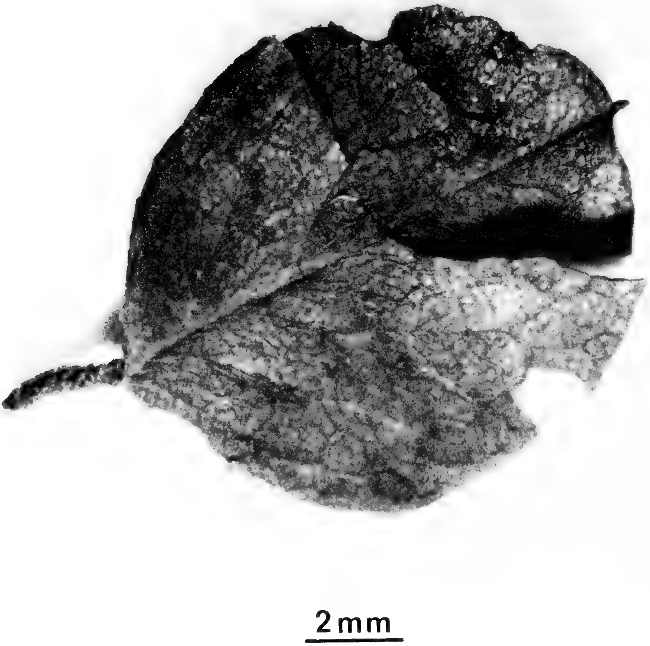

FIG. 1. Venation of *Amelanchier pallida* Greene (= *Pyrus hoffmannii* Chaney and Mason), Santa Barbara Museum of Natural History Paleontology Collection Specimen *279.*

paleoecological interpretations of the fossil biota of the Carpinteria asphalt deposit (Chaney and Mason, op. cit.; Wilson, Publ. Carnegie Inst. Wash. 440:59–76. 1933; DeMay, Publ. Carnegie Inst. Wash. 530:61–76. 1941). With the identity of *P. hoffmannii* resolved, all members of the Carpinteria fossil flora (and all Late Pleistocene floras in California) are believed to represent living taxa.

D. I. Axelrod and C. F. Smith assisted in the preparation of this note.—SCOTT E. MILLER, Santa Barbara Museum of Natural History, Santa Barbara, CA 93105. (Accepted 28 Apr 1979.)

CHROMOSOME NUMBER FOR *Calochortus tiburonensis* (LILIACEAE).—*Calochortus tiburonensis* Hill from the type locality was found to have ten pairs of chromosomes in PMCs at metaphase 1. The aceto-carmine squash technique was used. Drawings of the chromosomes have been attached to *Ornduff 70816* (JEPS) collected in 1973 on Ring Mt., Tiburon Peninsula, Marin Co., CA. No further voucher was collected because of the distinctiveness and rarity of this species, which is known only from this location. *Calochortus luteus* Dougl. ex Lindl. and *C. umbellatus* Wood, which are also found on Tiburon Peninsula (Howell, Man. fl. pls. ferns Marin Co., Calif. 1970), are not sympatric with *C. tiburonensis*. The species is listed as both very rare and endangered (Powell, ed., Inventory rare endang. vasc. pls., Calif. Native Pl. Soc. Special Publ. 1. 1974) and has been proposed for designation as "Endangered" under the federal Endangered Species Act of 1973 (Fed. Reg. 41:24552. 1976). It was listed as "Endangered" by the California State Fish and Game Commission on 6 Oct 1978.

In his description of *C. tiburonensis,* Hill (Madroño 22:100–104. 1973) discussed the sectional relationships of this species using Ownbey's taxonomy of the genus (Ann. Missouri Bot. Gard. 27:371–561. 1940). Ownbey divided the genus into three sections primarily on bulbcoat and capsule morphology. Differences in chromosome number mostly parallel these delimitations. The fibrous-reticulate bulbcoat and nonwinged capsule of *C. tiburonensis* would place it in sect. *Cyclobothra.* Hill questioned this association with reference to other traits, most notably gland morphology, which more closely resembles sect. *Calochortus.* The chromosome number $n = 10$ also aligns the species with sect. *Calochortus,* where $x = 10$. On the basis of four species, sect. *Cyclobothra* has $x = 9$ (Beal and Ownbey, Bot. Gaz. 104:553–562. 1943; Cave, Univ. Calif. Publ. Bot. 57:1–58. 1970). Counts should be made for the remaining 11 species in sect. *Cyclobothra* before assessing the sectional status of *C. tiburonensis* on the basis of chromosome number.

I thank Dr. Robert Ornduff and Dr. Marion S. Cave for their technical assistance and Dr. James W. Bartolome for his editorial comments.—MITCHEL P. MCCLARAN, Department of Forestry and Conservation, University of California, Berkeley 94720. (Accepted 1 July 1979.)

Malacothrix clevelandii COMPLEX (COMPOSITAE—LACTUCEAE) REVISITED.—In 1962 *Malacothrix clevelandii* A. Gray was divided into four species by Davis and Raven (Madroño 16:258–266). One of the proposed new species was *M. similis,* a tetraploid ($2n = 28$) whose pollen is significantly larger than that of the diploid *M. clevelandii* ($p < 0.01$, Student's t-test). A second new species, *M. stebbinsii,* also was found to have larger pollen than *M. clevelandii* and it was conjectured that the chromosome count of $2n = 28$ reported by Stebbins et al. (Univ. Calif. Publ. Bot. 26:401–430. 1953) for "*M. clevelandii*" from Tucson, AZ (for which no voucher could be found) could be referred to *M. stebbinsii.* On a collecting trip through Arizona in 1973, I found a population of *M. stebbinsii* (Pima Co., 0.8 km se. of hwy 386 along a gravel road 3.2 km s. of the jct of hwys 86 and 386, 14 Apr 1973, *Davis 348*) and chromosome counts of $2n = 28$ were obtained. Plants of *M. stebbinsii* have been grown from seed in a controlled environment under the same conditions as *M. clevelandii* (from populations in Kern, Riverside, and Ventura cos., CA). *Malacothrix stebbinsii* bolts earlier, flowers earlier, and the flowers are white rather than yellow as in *M. clevelandii*. Both species are self-compatible and highly self-pollinating even when the florets are not mechanically disturbed. Meiosis in *M. stebbinsii* is regular and stainable pollen ranges from 90 to 100 percent in field-collected and cultivated material.—W. S. DAVIS, Department of Biology, University of Louisville, Louisville, KY 40208. (Accepted 22 Jun 1979.)

WAS REDDING OF *Oxytheca reddingianum* M. E. JONES THE REDDING OF REDDING, SHASTA COUNTY?—Yes (see Gudde, Calif. Place Names, Univ. California Press, Berkeley).—ROBERT ORNDUFF, Department of Botany, University of California, Berkeley 94720. (Accepted 27 Aug 1979.)

BOOKS RECEIVED AND LITERATURE OF INTEREST

Systematic Botany Resources in America, part 2: the Cost of Services. Issued by THE ADVISORY COMMITTEE FOR SYSTEMATIC RESOURCES IN BOTANY OF THE AMERICAN SOCIETY OF PLANT TAXONOMISTS.

Contents include a discussion of the roles of herbaria in American society, the costs of herbarium services, the value of an herbarium specimen, and six appendices concerned with diverse topics. Herbaria that participated in the survey leading to the production of this report have received copies of it. A few extra copies were received in Berkeley and are available for curators of non-participant herbaria from Robert Ornduff, Department of Botany, University of California, Berkeley 94720.

Handbook of Principal Tropical Forage Grasses and their Management. By B. IRA JUDD. x + 116 pp., illus. Garland STPM Press, New York. 1979. ISBN 0-8240-7050-X. $14.50.

REVIEWS

The Agaves of Baja California. By HOWARD SCOTT GENTRY. 119 pp., frontis. + 6 pls, 62 figs., 11 tables. Occasional paper 130, Calif. Acad. Sci., San Francisco. 1978. ISSN 0068-5461. $8.00.

This is the long-awaited companion volume to Gentry's *The Agave Family in Sonora* (U.S.D.A., Agricultural Research Service, Agriculture Handbook 399, 195 pp. 1972. Washington, D.C.). Because both volumes are concerned primarily with the agaves of the Sonoran Desert, one would think that there would be considerable overlap of species, but such is not the case: only one taxon occurs in both Baja California and Sonora. This high degree of endemism among peninsular agaves may be accounted for by geological isolation—not only because of the Gulf of California trough, but also by what Gentry terms upper Tertiary and Pleistocene "seaways" on the peninsula itself.

For Sonora, Mexico, Gentry recognized 18 species of *Agave,* of which only *A. deserti* occurs in Baja California where it is found north of Lat. 30°N. The closely related *A. subsimplex* (which is included in both treatments) occurs on Isla Tiburón and adjacent coastal Sonora, but does not cross over onto the peninsula. In his Baja California monograph, Gentry treats 16 species, two of which (*A. subsimplex* and *A. mckelveyana*) do not occur within the political boundaries of Baja California, but because of their close taxonomic and geographic relationship to *A. deserti,* are included in this volume. For a discussion of Dr. Gentry's species concept in this plastic group of arid region plants one has to refer to his treatment of *Agave* in Sonora. His extensive field observations over the past thirty years form much of the basis for his taxonomic concepts. The Baja California agaves are divided into four groups: Deserticolae, Campaniflorae, Umbelliflorae, and Datyliones. The majority of the taxa fall into the Deserticolae. Four species and eight subspecies are proposed as new.

In addition to excellent habitat and habit photographs of the taxa treated, for each group there are included comparative diagrams of longitudinal sections of the flowers as well as floral ideographs depicting relative proportions of the tube to the outer tepals and the level of insertion of the filaments. Other ideographs indicate clearly the period of flowering in relation to seasonal rainfall. This is an interesting comparison because, although agaves occur the entire length of the peninsula, those in the north are more apt to be subjected to winter rains and those in the south to late summer tropical storms. Some taxa flower following winter rains and may continue blooming into June; many flower at the height of the dry season; and a few come into flower with the advent of the late summer rainy season. In some cases, this difference in flowering period is an important criterion for distinguishing taxa. The volume is further enhanced by a frontispiece and six plates in color.

For each taxon are included synonymy, detailed description, a distribution map (except for *A. datylio*), and discussion of distribution, variability, and relationships. In addition are included detailed information on economic values, e.g., saponin content of various parts of the plant, fiber yield, and even edibility—the latter relating primarily to the use of these plants by indigenous Baja Californians. The roasted *Agave cabeza* was one of their principal food resources. Following the taxonomic treatment is citation of all specimens studied. Also at the end is a two-page glossary of special terms applicable to agaves, a very useful feature for those not too familiar with these desert plants.

In his treatment of *Agave* in *Flora of the Sonoran Desert,* Ira Wiggins makes the following apology: "The treatment of the genus is dishearteningly inadequate. . . . A reasonably acceptable classification of the genus *Agave* can be presented only after extensive and painstaking study in the field, prosecuted at all seasons of the year." Such a study has been achieved by Dr. Gentry. Now we can have a much better appreciation of these plants that are such a conspicuous and important part of our desert vegetation, and, with some effort on our part, be on speaking terms with them.—ANNETTA CARTER, Herbarium, Department of Botany, University of California, Berkeley 94720.

Rare Plants of the Ozark Plateau. A Field Identification Guide. By BEVERLY J. ROEDNER, DAVID A. HAMILTON, and KEITH E. EVANS. 238 pp. North Central Forest Exp. Station, U.S. Forest Service, 1992 Folwell Ave., St. Paul, MN 55108. 1978. Free from publisher.

This pocket-sized book will interest California's botanists not so much for its subject matter as for its optimism, pertinent ideas, and purpose. "The main purpose of this guide is to stimulate you—the amateur botanist—to look for these plants and provide notes on them and their associated species, and on the habitat in which they are found. Such information will help public land managers formulate plans to ensure the preservation of these rare plants . . . . We present this book with a different message. We hope this guide will stimulate your interest in searching for, identifying, and reporting findings of those plant species that are *least* likely to be encountered on an average outing" (p. 1).

The 103 species selected are located verbally in Missouri (not mapped) and described in a perceptive way morphologically and by habitat on one page faced by an excellent line drawing. Endangered status is given. Species are arranged in groups characteristic of woodlands, glades, wet lowlands, aquatic habitats, and prairies.

The Swiss in a somewhat different vein have published a beautifully color-illustrated book on their legally protected plants (Landolt, Geschützte Pflanzen in der Schweiz. 1970. Reviewed by Major, Ecology 53:368. 1972).

Perhaps organized botanists in California could produce something similar in conjunction with the federal agencies that manage most of our lands where native plants occur—the U. S. Forest Service, National Park Service, Bureau of Land Management, Defense Dept., and with the corresponding state agencies such as the Division of Forestry, Beaches and Parks, Caltrans, and even with large private landholders such as Southern Pacific, Pacific Gas & Electric, banks, and ranchers. Or should the more or less organized botanists concentrate on the urgent and primary job of keeping a modern flora of California modern and in print?—JACK MAJOR, Botany Department, University of California, Davis 95616.

EDITOR'S REPORT FOR VOLUME 26

I have three goals in this report: to acquaint members with the pattern of manuscript flow in their journal, to encourage members to submit manuscripts for publication, and to point out recurring difficulties with submitted manuscripts.

The 31 manuscripts submitted to the previous editors that remained to be considered for inclusion in volume 26 can be placed in the following categories: rejected (6 papers, 1 note); withdrawn (2, 1); apparently withdrawn, no response having been made to reviewers' criticisms for more than a year (2, 3); being revised by authors (3, 5); awaiting publication (1, 0); and published (5, 3).

Between 1 Jul 1978 and 30 Jun 1979, 69 manuscripts were received: rejected (2, 4); withdrawn (2, 5); in review (1, 0); awaiting action by editor (2, 0); being revised by authors (11, 2); awaiting publication (3, 0); and published (14, 23).

There is no backlog of manuscripts ready to publish. More than half of the manuscripts received this reporting year were published during the volume year. Some recent issues have been delayed because of a paucity of material. This is not due to a high rejection rate (13 percent for all manuscripts considered this year, 9 percent for those received during the year) but to a low submittal rate and to delays in revising. This report, in part, is a call for more papers from the membership. I would be particularly happy to receive more papers on topics other than systematics and ecology so that coverage of West American botany can be broadened.

There are two major bottlenecks to manuscript flow. The most important is delay by authors in revising papers that have been reviewed. This applies to notes as well as papers. Second, when long papers need major revision, the editor may be delayed in reconciling complex reviews and editing copy so that all important revisions can be made at once. Manuscripts that are publishable essentially as submitted may see print within three months, an unusually short turnaround time. If major revision is required, which has been unfortunately and unnecessarily normal for long papers, delays can exceed a year if authors are not prompt with their revisions.

The three most important recurring problems are bad design or execution of figures and tables, poor organization, and imprecise, unfocused writing. The editor will be happy to discuss illustrative materials in advance of their preparation. Such consultation would save authors and the Society time, labor, and money. Colleagues with high critical standards can be extremely helpful in uncovering and overcoming organizational and writing problems prior to submittal. Most authors do not heed INFORMATION FOR CONTRIBUTORS on the inside back cover even though doing so might save months of delay.

Substantial publication delays for volume 25 (4) and volume 26 (1, 2, and 3) were the result of the editorial transition and a (finally) highly successful switch to Allen Press. Efficient working patterns with Allen Press are now established and many operating procedures for the journal have been clarified and put into writing. Publication is now effectively back on schedule and no further delays are anticipated unless submittal rate fails to increase. The editor welcomes suggestions, expressions of concern, and criticisms from members.—J. C. H.

REVIEWERS OF MANUSCRIPTS

Many people have aided in the preparation of volume 26. The Board of Editors and the Council of the Society have provided several important services and authors have been most cooperative. John L. Strother, revirescent editor (of Systematic Botany), has acted virtually as an Associate Editor for Madroño. He and Alan R. Smith have provided a needed sounding board for many editorial ideas. Special thanks also to the staff of Allen Press, whose collective guidance has made Madroño much more efficiently run. Their cooperation has been of paramount importance in returning the journal to a reasonable publication schedule. Reviewers of manuscripts during the past eight months are acknowledged gratefully below.

Robert P. Adams
Frank Almeda
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Richard J. Vogl
Walter E. Westman
Paul H. Zedler

INDEX TO VOLUME 26

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. Names of authors followed by titles of articles are listed alphabetically in Table of Contents, p. iv.

CALIFORNIA BOTANICAL SOCIETY, 1979–1980 PROGRAM

October 18:	LYMAN BENSON, Department of Botany, Pomona College. The Weather And The Deserts.
November 15:	JAMES HICKMAN, University Herbarium, University of California, Berkeley. Natural History Of Some Oregon Cascade Mountaintops.
December 6:	NANCY MORIN, Department of Botany, University of California, Berkeley. Discovering California Botanists Who Discovered *Githopsis*.
January 17:	JEAN LANGENHEIM, Department of Biology, University of California, Santa Cruz. A Botanist In The Brazilian Amazon.
February 27:	ANNUAL DINNER. HAROLD MOONEY, Carnegie Institution, Stanford University. Atacama Trails.
March 20:	ROBERT ROBICHAUX, Department of Botany, University of California, Berkeley. Adaptively Radiating In The Hawaiian Islands: In Search Of The Naupaka, Kupaoa, And Akoko.
April 17:	JAMES DOYLE, Department of Botany, University of California, Davis. Early Angiosperm Evolution.
May 15:	BRENT BERLIN, Department of Anthropology, University of California, Berkeley. Ethnobotanical Studies Among The Aguaruna/Jivaro Of Amazonas, Peru.

Membership in the California Botanical Society is open to individuals ($15 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Institutional subscriptions to MADROÑO are available ($22 per year). The membership or subscription year begins on January 1.

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Vol. 24 (1977) et seq., one volume per year, each consisting of 4 numbers: $4.00 per issue and $15.00 per volume for members; $6.00 per issue and $24.00 per volume for institutions.

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Manuscripts submitted for publication in MADROÑO should be sent to the Editor. Membership in the California Botanical Society is prerequisite to review.

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Line copy illustrations should be clean and legible, proportioned (including their captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in Figures, as should explanation of symbols. In addition, 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 board and mailed flat.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren and Keuken's list (*Index herbariorum, Part 1. The herbaria of the world.* Sixth edition. 1974. Regnum Veg. vol. 92). Abbreviations of names of journals should be those in *Botanico-Periodicum-Huntianum* (Lawrence, G. H. M. et al. 1968. Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full title of the journal should be used. Titles of books should be given in full, together with the place and date of publication, name of publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted eight pages in the journal over a two-year period. Beyond that number of pages, a required editorial fee of $40.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. 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.

Contents, continued

REVIEWS

CALIFORNIA BOTANICAL SOCIETY

STATEMENT OF OWNERSHIP, MANAGEMENT, AND CIRCULATION

(Act of Oct. 23, 1962; Section 4369, Title 39, United States Code)

Madroño, A West American Journal of Botany, is published quarterly at Berkeley, California.

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I certify that the statements made by me above are correct and complete.

November 1, 1979 JAMES C. HICKMAN, *Editor*

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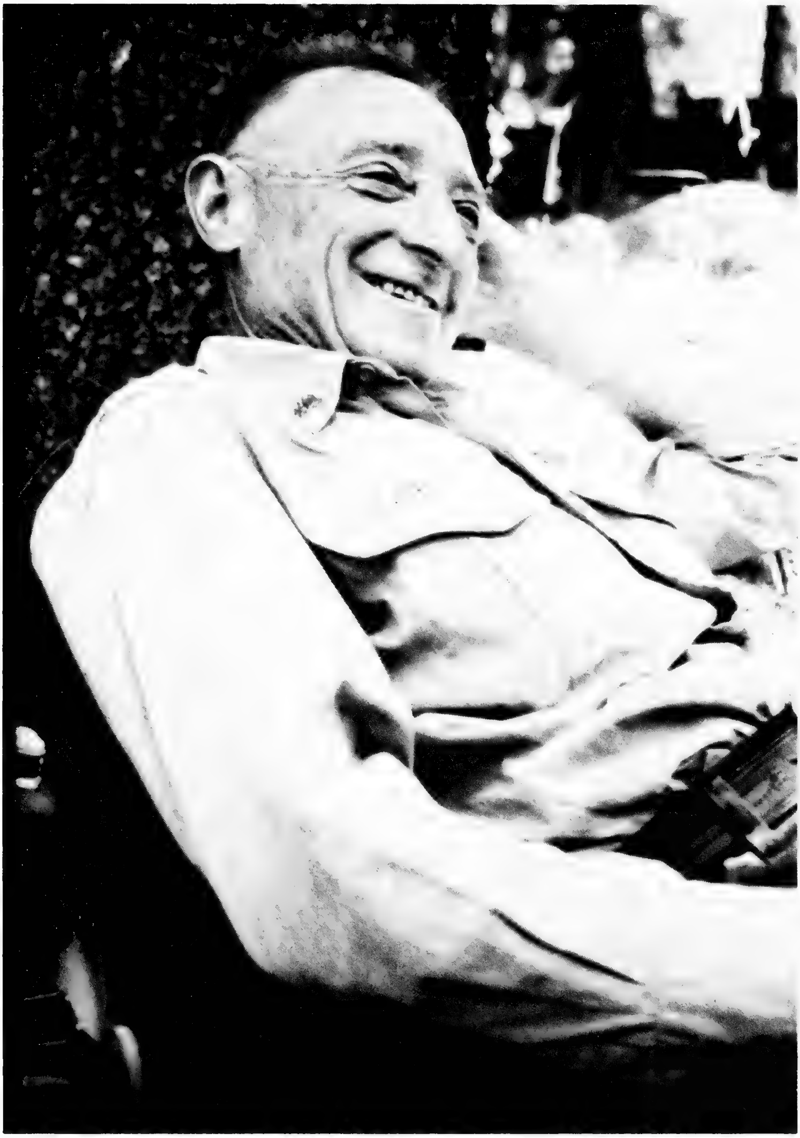

Margaret S. Kelley, Yosemite National Park, 1977

For his unsurpassed success at interpreting the Yosemite high country to countless thousands, for his long service to the teaching of botany at San Jose State University and elsewhere, and for his service to the California Botanical Society as its President in 1967, volume 27 of MADROÑO is dedicated to CARL W. SHARSMITH.

Carl is probably the best-known and best-loved ranger-naturalist in the world. For 50 years he has communicated his uncanny perceptions of natural phenomena in the high montane and alpine to Yosemite National Park visitors, instilling a sense of wonder and curiosity about native plants, animals, and their interactions, and developing an enormous following for whom he is the master interpreter of nature. Many visitors return to Yosemite specifically to walk with and listen to the "old ranger" with the Stetson hat. He has also led several highly acclaimed UCLA Extension trips to the Swiss alps and his ability to compare European and Sierra Nevadan alpine floras is unequalled. Carl's accomplishments both as academician and as naturalist were recognized in 1977 when San Jose State University dedicated the Carl W. Sharsmith Herbarium. At 77, Carl rides his bicycle to campus nearly every day, rain or shine. We continue to owe him thanks for winning so many friends for California's plants and natural habitats.

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EDITOR'S REPORT FOR VOLUME 27

Between 1 Jul 1979 and 30 Jun 1980, 76 manuscripts were received. Their current statuses are summarized as follows: rejected (3 articles, 1 note); withdrawn (3, 0); in review (12, 0); being revised by authors (10, 5); accepted and awaiting publication (5, 8); published in volume 27 (8, 21). In addition, 10 articles and 2 notes received prior to 1 Jul 1979 were published in volume 27.

Manuscript flow has improved somewhat over volume 26 but there are still several problems relative to longer papers. Most importantly, submittal rate is still low and submittals are erratic in time, creating a paucity of material for some issues and editorial overloads at other times. Variance in submittal rate is reflected in variable journal size and in occasional lengthy delays in reconciling reviews and returning copy-edited articles for revision. Also, some authors continue to delay in returning final revisions, lengthening turnover times.

For articles appearing in this volume, time from submittal to publication was 5–30 months, averaging 14 months. However, time from receipt of final versions to publication date averaged less than 5 months. This is probably an irreducible minimum, given 3½ months press time and three months between submittals to the press. Clearly, more can be done to speed review and editing and attempts to accomplish this continue. A hopeful sign is that mean turnover time decreased steadily from the first issue (19 months) to the last (8 months).

Noteworthy Collections have continued to increase in number. For the first three issues after initiation of the format, an average of four species was covered per issue. The average has increased to 13 for the last six issues (there are 26 in the current issue and will be at least 23 in the next issue). The format seems to be filling a need not met elsewhere. Because Noteworthy Collections are designed to communicate a maximum of information in a minimum of space, authors of these notes are urged to study several recent examples carefully for kinds of information required, precise sequence, and details of format.

I continue to welcome suggestions and criticisms from members.

J.C.H. 23 Sep 1980

REVIEWERS OF MANUSCRIPTS

The Editor thanks all those who have contributed to the preparation of volume 27. John L. Strother, Alan R. Smith, and John H. Thomas were especially helpful, even though all three have editorial duties of their own. James R. Griffin and Richard J. Vogl graciously and expertly accommodated unusually heavy demands as members of the Board of Editors. Special thanks to Annetta Carter, Wanna D. Pitts, Clifford L. Schmidt, and Herbert L. Mason. Reviewers of manuscripts have given uniformly thoughtful advice and have been exceedingly helpful in maintaining the quality of papers published in Madroño. They are acknowledged gratefully below.

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No. 1, pp. 1–48: 25 March 1980
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ERRATUM

vol. 27, p. 141, lines 35, 42, 47; p. 142, last line; p. 143, lines 4 and 12. For “AR” read “AZ”. The latter is the accepted abbreviation for Arizona (the former for Arkansas).

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 27, NUMBER 1 JANUARY 1980

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NOTES AND NEWS

REVIEWS

UBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

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SEED DESTRUCTION OF CALIFORNIA MORNING GLORIES (CONVOLVULACEAE: CALYSTEGIA) BY BRUCHID BEETLES

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Chico 95929

ABSTRACT

The bruchid (seed) beetle *Megacerus impiger* is usually found in populations of perennial, native morning glory (*Calystegia*) in California. Each beetle matures inside a single *Calystegia* seed, destroying the seed. Seed set of the four ovules per flower prior to predation by the beetles varies among the populations sampled from 1.6 to 3.8. Mean seed weight varies also, from 32.8 mg/seed in *C. atriplicifolia* to 11.2 mg/seed in *C. stebbinsii* but beetles can develop to adults in all. Beetles lay eggs on young seeds in May or June in most *Calystegia* populations in cismontane California. Adults emerge from mature seeds by July or August and oviposit on other mature seeds retained in open capsules. The second crop of adults produces a third ovipositing or overwintering group of beetles; there is thus a potential for extensive seed destruction in the plants. Minimum seed destruction (in *C. fulcrata*) varied from 0.005 percent to 36.3 percent, not considering predation on fallen seeds. Genus-specific seed predation by *M. impiger* among at least 13 taxa of *Calystegia* in California suggests close similarities in reproductive features of a group in which taxa have been difficult to distinguish by reproductive features alone.

Following a pollination study of *Calystegia fulcrata* (Convolvulaceae) in Los Angeles County, California, the seed collected for weighing was found to have seed beetles (Bruchidae) 3–4 mm long emerging from individual seeds, leaving each seed hollowed out and inviable. Attention has been focused for several seasons on aspects of seed production, and seed exploitation by these beetles is now known to be an important aspect of the reproductive biology of the plants. The beetles belong to a single species, *Megacerus impiger* (Horn), and occur extensively throughout the range of *Calystegia* taxa in California. Because the larval stage of this beetle is restricted to an individual seed of a morning glory, the following four questions have been asked: 1) how similar are aspects of seed production in the different *Calystegia* taxa fed upon by the beetle larvae? 2) how widespread are these seed predators? 3) how is the life cycle of the beetle synchronized with seed production in the plants? and 4) to what extent do the plants suffer seed destruction by the beetles?

Seed destruction and restriction by species of bruchid beetles in their larval foodplant utilization are well known. Different species utilize plants in about 30 families (Johnson, 1970; Center and Johnson, 1974), with the Leguminosae providing host seeds for 84 percent of the bru-

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chid species known (Johnson, 1970). Best known relationships are between bruchids and woody (especially tropical) legumes (see Janzen, 1969, 1970); bruchid use of herbaceous legumes is also becoming known (e.g., Johnson, 1970; Green and Palmbald, 1975; Baskin and Baskin, 1977). Bruchid seed predation on non-leguminous plants has also been described (see Wilson and Janzen, 1972, for Palmae; Forister and Johnson, 1971, for Rhamnaceae; Janzen, 1975, and Johnson and Kingsolver, 1971, for Sterculiaceae). Among the non-legumes used, the Convolvulaceae may provide host seeds for up to 4.5 percent of all bruchid species known (Johnson, 1970) but there are no detailed studies on use of seeds in this family. The present study on *Calystegia* seed use by *Megacerus impiger* provides information on reproductive biology for both the morning glories and the beetles.

Megacerus is the only bruchid genus in the New World tribe Megacerini (Bottimer, 1968) and all species apparently utilize seeds only of the Convolvulaceae (Johnson, 1970). The host plants listed for species of *Megacerus* by Zacher (1952), Bottimer (1961), and Center and Johnson (1976) are several species of *Ipomoea* (with the last reference specifically listing "*Ipomoea* sp." for *M. impiger*). Bridwell (1929, p. 112) referred to *Megacerus* as "extending throughout the range of Convolvulaceae on the [North American] continent and in the West Indies, and represented by many species in the American tropics." He too listed species of *Megacerus* occurring in seeds of several species of *Ipomoea*.

Fifteen taxa of *Calystegia* (formerly referred to as *Convolvulus*) have now been examined for *Megacerus* in lower elevations of cismontane California. They are all perennial plants with more or less sagittate or deltoid leaves. Plants in half the taxa studied are climbers, producing vines up to several meters long that clamber over vegetation; vines of the rest are more prostrate and shorter—up to 0.5–1 m long. All produce cream- or pink-tinged, whitish flowers that last but one day each. Many populations flower for 4–6 weeks, and vines may produce the first ripe fruits about 7–8 weeks after flowering begins (e.g., in *C. fulcrata* of Tulare Co. and *C. occidentalis* of Butte Co.; see Schlising, 1972).

METHODS

When sampling fruits and seeds of the different *Calystegia* taxa, it is usually difficult or impossible to determine the extent of an individual plant. In most cases, numerous vines arise from a vigorous underground network of rhizomes. When possible, capsules or seeds were collected from vines at least several meters apart to maximize chances of sampling different plants. In cases where individual plants could be determined, a maximum of five capsules per plant was collected if the total sample was to be 100 or more capsules.

All *Calystegia* taxa discussed below have four ovules per flower. There is variation, however, in the extent that ripened capsules dehisce—some by only a crack at the top, others by the capsule valves spreading widely, leaving the seeds exposed and likely to be shaken or blown to the ground. Number of seeds per capsule was recorded only if reasonable certainty existed that no seeds were lost from the capsules. This selection could bias the counts slightly. All counts reported are of dark, hard, mature seeds. In cases where capsules sampled were normal and dry (mature) but all seeds inside were aborted or shrivelled, these were counted as having no mature seeds. Fresh seed weights were made on random samples of usually 200 seeds that represented mixtures of seeds from at least 100 capsules. Seeds were weighed in lots of 20 on a Mettler Type 5 balance 8–14 weeks after collection. None of the seeds weighed was from lots infested with beetles.

Morning glory seed infestation and destruction by seed beetles were assayed in two major ways in the laboratory, using techniques listed by Bottimer (1961). Beetle emergence was determined by observing samples of seeds and capsules put into closed glass jars or petri dishes, and samples in which capsules were put singly into closed gelatin capsules (E. Lilly & Co., size 000). Frequent examination of the gel caps provided information on dates of emergence and on numbers of beetles emerging in a population sample. A bruchid larva may die in the seed, and possibly cause a seed that appears "sound" to be inviable. Therefore, apparently undamaged seeds from two infested lots were examined using a Model 2042 Picker Therapeutic X-ray machine at 80 kV and 5 mA, AlCu filter, and "no screen X-ray film". Emerged adult beetles were mounted, labelled, and identified. Voucher specimens from all beetle populations are on deposit at the U.S. National Museum. Herbarium vouchers for the *Calystegia* populations are at CHSU. Names follow Munz (1968).

RESULTS AND DISCUSSION

Seed production

Seed number per capsule. Despite the potential of four seeds per capsule in all California *Calystegia,* there is considerable variation in mean number of seeds that mature in the 14 taxa studied (Table 1). The southern *C. macrostegia* subsp. *cyclostegia* showed the highest mean ($\bar{x}$ of $\bar{x}$'s = 3.6, n = 464; for one population $\bar{x}$ = 3.8, n = 110), and the northern *C. atriplicifolia* showed the lowest ($\bar{x}$ = 1.6, n = 187). In the two species most thoroughly sampled (*C. fulcrata* and *C. occidentalis*), population means ranged roughly from 2 to 3.4, suggesting only about 50–85 percent realization of the potential seed crop in these populations. All counts in Table 1 do include mature seeds hollowed out by the seed beetles; these will be described in more detail.

TABLE 1. NUMBER OF MATURE SEEDS PER CAPSULE AND FRESH SEED WEIGHT IN CALIFORNIA *Calystegia* POPULATIONS. Sample numbers following taxa are: (total populations sampled: samples counted, samples weighed). Seed number includes those from which adult beetles emerged. Numbers are grand means of seeds per capsule ± s.e. (number of capsules examined) and grand means of seed weights in mg (number of seeds weighed).

Species (number and distribution of samples)	Seeds per capsule	Seed weight
Calystegia atriplicifolia (2: 2, 1 Butte Co.)	1.6 ± 0 (187)	32.8 (160)
C. fulcrata (10: 10, 1 Fresno, Los Angeles, Madera, and Tulare Cos.)	2.7 ± 0.14 (1213)	25.4 (200)
C. longipes (3: 2, 1 Kern, San Luis Obispo, and Tulare Cos.)	2.8 ± 0.70 (137)	13.4 (200)
C. macrostegia ssp. *cyclostegia* (6: 5, 3 Los Angeles, San Luis Obispo, Santa Barbara, and Ventura Cos.)	3.6 ± 0.07 (464)	17.5 ± 0.69 (600)
C. macrostegia ssp. *macrostegia* (1 Santa Barbara Co.)	3.6 (100)	22.6 (200)
C. malacophylla var. *deltoidea* (2 Kern and Ventura Cos.)	3.4 ± 0 (174)	—
C. malacophylla ssp. *malacophylla* (1 Tulare Co.)	3.5 (100)	—
C. malacophylla ssp. *pedicellata* (1 San Luis Obispo CO.)	—	15.9 (94)
C. occidentalis (14: 12, 8 Butte, Nevada, Placer, and Yuba Cos.)	2.9 ± 0.14 (2550)	26.3 ± 1.0 (1870)
C. peirsonii (1 Los Angeles Co.)	2.2 (39)	—
C. polymorpha (2: 1, 2 Tehama Co.)	1.8 (52)	23.1 ± 2.5 (360)
C. purpurata (2 Los Angeles and Mendocino Cos.)	3.3 ± 0.05 (233)	—
C. soldanella (1 Ventura Co.)	2.9 (88)	—
C. stebbinsii (1 El Dorado Co.)	—	11.2 (200)

Not included in these counts were minute aborted ovules and partially developed seeds; it is possible that both are due to presence of beetle larvae that died (see below). Another feature may account for less-than-total seed set. *Calystegia fulcrata* and *C. occidentalis* are self-incompatible, as are probably most taxa of this genus in California (Schlising, 1972, unpubl. data). Thus the number of different individual plants making up a population can probably influence seed set. Several small and isolated populations of *C. fulcrata* are known in Los Angeles County that flower vigorously and are visited by insects, but set no seed; these are probably clones of single or few individuals. Calystegias in California do have a rich and varied pollinator fauna, including an oligolectic bee (Schlising, 1972, unpubl. data), so one might expect abundant pollen transfer and maturation of all four seeds per ovary.

Seed weight. Seeds of California morning glories are varied in surface features, size, and weight. Some seed coat features, as well as length and width measurements, are given for several taxa in Munz (1959, 1968), Abrams (1951), Brummitt (1975), and Lochhead (1974). Mean seed weights for population samples of nine California taxa are shown in Table 1, and indicate a low of 11.2 mg per seed in *C. stebbinsii* and a high of 32.8 mg per seed in *C. atriplicifolia.* Seeds of most species average 15–25 mg each.

Geography of beetle infestation

Megacerus impiger larvae utilize seeds of 13 taxa of California *Calystegia,* although the degree of population infestation and seed destruction vary considerably. Orange and San Diego Counties have not been studied; the beetle probably occurs here in several additional taxa of *Calystegia.* Capsule and seed samples of vastly different sizes have been collected, and in some cases the emergence of a single beetle is the only record for a population (e.g., in *C. macrostegia* subsp. *arida* and in *C. malacophylla* subsp. *deltoidea*). Figure 1 shows the California range of *Megacerus impiger,* based solely on collections from the taxa of *Calystegia* sampled in this study. Each locality represents beetle emergence from seed. Throughout this area the beetle can be expected, at least in low densities, in almost all large, seed-producing populations of *Calystegia.*

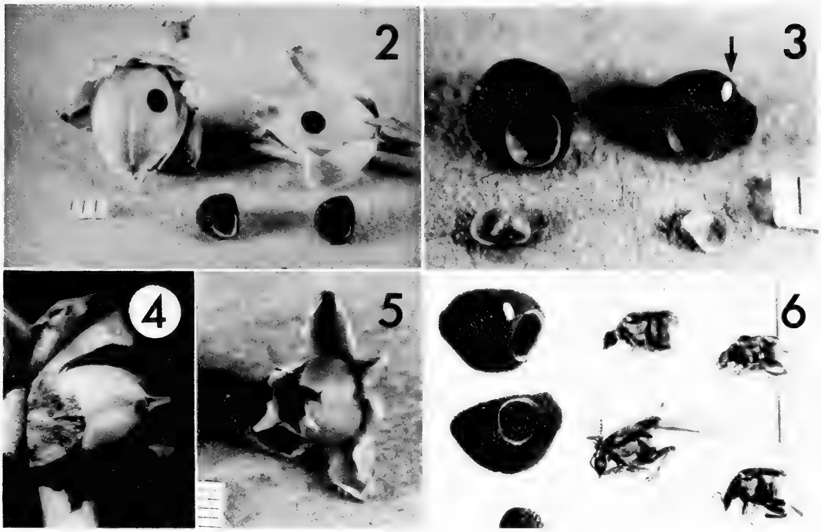
This beetle may also occur more extensively in the Coast Ranges, both north and south of the Golden Gate. Sampling has been less extensive in northern California and at the higher elevations of occurrence of the morning glories, but it appears the beetles are generally restricted to the lower elevations with summer-dry (Mediterranean) climate. Large seed samples from the following localities (shown as plain dots in Fig. 1) did not contain beetles: Westport, Mendocino Co. (*C. purpurata*); near jct hwy 32 and hwy 36 s.e. of Lassen Park, Tehama Co. (*C. polymorpha*); De Sabla, Butte Co. (*C. atriplicifolia*); and Montana de Oro State Park, San Luis Obispo Co. (*C. macrostegia* subsp. *cyclostegia*). The northern localities may be near northern limits in the range of the beetle. In addition, within this overall range,

FIG. 1. Natural range of the seed beetle *Megacerus impiger* (Horn), based on emergence from seed samples in populations of 13 *Calystegia* taxa studied in California. Letter at each locality indicates taxon of morning glory the beetle emerged from as follows: A = *C. macrostegia* subsp. *arida,* C = *C. macrostegia* subsp. *cyclostegia,* D = *C. malacophylla* var. *deltoidea,* E = *C. malacophylla* subsp. *pedicellata,* F = *C. fulcrata,* L = *C. longipes,* M = *C. malacophylla* subsp. *malacophylla,* O = *C. occidentalis,* P = *C. purpurata,* R = *C. macrostegia* subsp. *macrostegia,* S = *C. soldanella,* T = *C. stebbinsii,* X = *C. peirsonii.* Beetles were lacking in large samples of *Calystegia* seeds from locations marked with dots (see text).

M. impiger has not been found in small, disjunct, poorly-seeding populations that probably represent clones of few *Calystegia* individuals.

Life cycle synchronization

Information on the life cycle of *Megacerus impiger* is based on observations on beetles in the field and on those reared indoors from



FIGS. 2–6. Scale units in mm. 2–5. *Calystegia occidentalis*. 2. Capsules with *Megacerus* emergence holes. 3. Empty seeds, showing bruchid emergence holes. Note *Megacerus* egg chorion on seed (arrow). 4. Indehisced capsule. 5. Capsule with wide natural dehiscence that has permitted bruchid exit. 6. Pinned (and "pointed") *C. fulcrata* seeds and four individuals of *M. impiger*. The single female, with smaller antennae, is at lower right.

enclosed *Calystegia* seeds. Because laboratory conditions such as temperature and relative humidity did not reflect conditions in nature, some of the information given below may not match the biology of the beetles in nature.

Emergence and selection of host. A bruchid larva hatching from an egg laid on the outside of a seed must bore into the seed, where (for many but not all bruchid species) larval instars as well as pupation then occur. In *Megacerus impiger,* each larva develops within a single seed and the adult emerges via a round exit hole cut through the hard seed coat (Figs. 3, 6). The beetle then emerges from the capsular fruit containing the seed by cutting a similar circular exit in the capsule wall (Fig. 2), unless the capsule permits exit via natural dehiscence at the top (Fig. 5). Occasionally a bruchid must cut a third exit hole through a sepal or bract if it is tightly appressed to the capsule.

Mating of adult beetles was not observed, but probably occurs at night (Wilson and Janzen, 1972). If virgin females, even as soon as 24 hours after emergence from seeds, are kept overnight with young males, they then immediately proceed with egglaying when *Calystegia* seeds are placed in containers with them. A female examines a seed with face and antennae from 1 to more than 10 minutes before laying an egg on it. Usually a seed is grasped and pulled to the body before the telescopic ovipositor is extruded beneath the seed. An egg leaves the ovipositor with a viscous fluid that dries quickly, gluing the egg to the seed; it may be placed anywhere on the surface of the seed. In these instances with captive beetles, the females immediately left the seed after laying a single egg upon (under) it, and proceeded to examine other seeds; in two instances, five eggs were laid on five seeds in about 80 minutes. Without having access to green vegetation or free water, seven individual females in separate petri dishes laid 19 ± 2 (s.e.: n = 7) eggs (1 per seed). Johnson (1970) cited work noting that some species of bruchids may lay more eggs if the adults feed. It has not been established if this species feeds as an adult, but on five occasions a female of *Megacerus impiger* was collected in the field on a flower of *Calystegia*. In two of these cases, she was palpating and probably feeding on nectar and pollen. Without food or water, females usually live up to three weeks in glass containers indoors, but they apparently lay eggs only the first day or so, even if new males and additional seeds are provided.

There is probably a chemical or textural cue that stimulates or restricts egglaying, because eggs are rarely laid adjacent to seeds or on other materials, but rather directly on morning glory seeds. This species of bruchid is restricted to *Calystegia* seeds, but beetles emerging from seeds of one species of *Calystegia* can produce more beetles by ovipositing on seeds of different species of *Calystegia* (e.g., beetles emerging from Tulare Co. *C. longipes* produced adults by ovipositing on Fresno Co. *C. fulcrata* seeds).

These beetles prefer *Calystegia* seeds if they are offered along with seeds of other large-seeded species. For example, several females ready to oviposit that were presented with *Paeonia californica* or *Cercis occidentalis* seeds along with *Calystegia* laid eggs only on the latter. Yet, the introduced *Convolvulus arvensis*—frequently occurring near various species of native *Calystegia*—may occasionally be used (e.g., females from *Calystegia fulcrata* and *C. occidentalis* produced small adults by laying eggs on *Convolvulus*). Use of *Convolvulus* is apparently very rare in nature (e.g., at Forest Ranch, Butte County, where *Convolvulus* was growing adjacent to very heavily infested *Calystegia occidentalis*). There are no host plants other than *Calystegia* on record at the U.S. National Museum (J. Kingsolver, pers. comm., 1976), and the only other host plant reported in the literature is "*Ipomoea* sp." from Arizona (Center and Johnson, 1976).

Waves of egglaying and seed destruction. It is not known whether immature individuals in morning glory seeds or emerged adults are the overwintering stage. Nor is it known when or how the adults present in the spring lay the first eggs on new *Calystegia* seeds, but this is doubtless into or on *immature* ovaries that may have reached full size but are not yet totally hardened with mature tissues. It is not clear at what point the larva bores into the ovule or how the presence of a developing larva could affect the final maturation of a seed. In several instances, *Calystegia* capsules were collected and placed in gel caps when at full size but before they were brown and dried. These capsules (e.g., *C. malacophylla* from Tulare Co.) produced normal adults, so the first summer emergence of adult beetles does result from eggs laid before the seeds and fruits are mature. (Johnson, 1967, and Center and Johnson, 1974, describe other species of bruchids that oviposit on immature fruits.) Beetles that emerge from seeds during the summer must oviposit on hard, mature seeds to give rise to yet another generation that emerges in later summer or fall, because they lay their eggs when there are no longer flowers or immature fruits available on the plants.

In laying eggs on mature seeds (still located in capsules on the plants) females may utilize existing exit holes to regain entrance to the capsules (Fig. 2). Or, more commonly, they enter a dehisced fruit through its open valves (Fig. 5); they do not enter undehisced capsules (Fig. 4) by chewing their way in. As a rule, one egg is laid per seed in recently opened capsules. In a detailed study of oviposition strategy for another species of bruchid, Mitchell (1975) stated that females tend to avoid adding second eggs as long as there are unused seeds available; a single egg per seed is reported for many other species of bruchid. In *C. occidentalis* in Butte County, when open capsules on the vines contain 3 or 4 seeds, a very common situation is one egg on each of three seeds. But when morning glory seeds remain in the open capsules until late in the summer, there may be 1–4 (10) eggs per seed, even in open capsules on vines that have numerous other seeds available only a few centimeters distant. Only one adult develops in each seed, however, no matter how many eggs hatch into larvae that bore into the seed. Mitchell (1975) noted that for the bruchids he studied on *Phaseolus aureus* seeds, the presence (and interaction) of two or more larvae in one seed slows the development of the single adult that in most cases emerges. Size of the single adult *M. impiger* that emerges from a seed varies with the size of the seed, the smaller *C. longipes* and *C. stebbinsii* seeds (Table 1) producing the smallest adults. This phenomenon has been noted for various other bruchids (e.g., Johnson, 1970; Center and Johnson, 1974).

Table 2 gives the dates of first emergence of the first summer-generation adults—all determined with samples of capsules isolated in gel caps. The July to August emergence period usually begins several weeks after the morning glory seeds are hard and mature. Total length of emergence period varies (Schlising, unpubl. data), but typically it lasts 4–6 (8) weeks. Some late emergents of this first generation may reflect differences in individual development time (including, very possibly, larvae in competition), or the fact that several females had ovi-

TABLE 2. *Calystegia* POPULATION SAMPLES, SHOWING PERCENT CAPSULE INFESTATION, SEED DESTRUCTION, AND SEED INFESTATION (SEEDS DESTROYED OR BEARING BEETLE EGGS) DUE TO *Megacerus impiger*. Data reflect activity of the beetles only in the field, up to the date of collection. N = number examined; % D = percent dehiscence in the field; % I = percent infested; 1st E = first emergence in lab; % K = percent killed.

Species, locality, and date collected		Capsules				Seeds		
		N	% D	% I	1st E	N	% K	% I
Calystegia fulcrata								
Fresno Co.:								
Alder Spgs.	13 Jul 72	125	10	24.8	16 Jul	304	13.5	13.8
Auberry	13 Jul 72	75	10–50	21.3	17 Jul	173	8.7	9.8
Miramonte	16 Jul 72	99	10	7.1	01 Aug	314	2.2	3.2
Miramonte	15 Sep 72	69	90	46.4	—	168	15.5	29.8
Los Angeles Co.:								
Wrightwood	27 Jul 72	121	10–50	47.1	31 Aug	317	36.3	38.2
Wrightwood	14 Jul 73	211	0	0.9	20 Aug	671	<0.1	<0.1
Madera Co.:								
Northfork	13 Jul 72	103	10–50	14.6	16 Jul	324	2.8	4.6
Oakhurst	13 Jul 72	71	10	16.9	18 Jul	202	9.9	9.9
Tulare Co.:								
Badger	16 Jul 72	175	10–50	1.7	20 Jul	517	0.6	0.6
C. longipes								
Tulare Co.:								
Badger	15 Sep 72	48	90	66.7	—	99	14.1	32.3
C. macrostegia ssp. *cyclostegia*								
Santa Barbara Co.:								
SW Lompoc	03 Jul 73	122	10	8.2	22 Aug	450	2.2	2.4
S. Lompoc	03 Jul 73	74	10	6.8	20 Aug	253	1.6	2.4
C. malacophylla var. *deltoidea*								
Kern Co.:								
San Emigdio	07 Jul 73	110	0	0.9	—	371	0.3	0.3
Ventura Co.:								
Mt. Abel	07 Jul 73	64	0	1.6	29 Aug	220	0.5	0.5
C. malacophylla ssp. *malacophylla*								
Tulare Co.:								
Wishon	17 Jun 72	100	0	27.0	17 Jul	352	9.9	10.2
C. occidentalis								
Butte Co.:								
Cohasset	28 Jul 74	103	10	11.6	30 Aug	295	3.7	5.1
Cohasset	02 Sep 74	104	90	40.4	—	298	5.4	22.8
Cohasset	12 Nov 74	103	100	35.0	—	279	7.5	19.0
Cohasset	28 Aug 75	168	100	59.5	15 Sep	475	8.2	36.8
Forest Ranch	02 Aug 74	541	10	11.3	30 Aug	1712	1.6	4.0

TABLE 2. Continued.

Species, locality, and date collected		Capsules				Seeds		
		N	% D	% I	1st E	N	% K	% I
Single plant of same	20 Oct 74	246	100	30.5	—	533	11.8	21.4
Forest Ranch	28 Jul 75	100	50–90	38.0	28 Aug	347	9.2	15.8
Forest Ranch	03 Sep 75	119	100	44.5	—	412	2.4	21.6
Nevada Co.:								
Nevada City	08 Sep 73	309	50–90	25.2	—	993	9.0	13.0
C. peirsonii								
Los Angeles Co.:								
Bouquet Res	02 Jul 72	39	50–90	12.8	23 Jul	85	7.1	8.2
C. purpurata								
Los Angeles Co.:								
L. Eleanor	24 Jun 72	164	10–50	7.3	25 Jun	520	2.1	2.9

posited in the same population at slightly different times. Adults emerging mostly in July and/or August lay eggs that develop into adults the same summer, emerging from September to November. This second summer generation is responsible for producing a third and possibly overwintering generation, although some of the eggs laid by earlier generations could possibly provide overwintering stages too.

To determine the length of time for the development of *Megacerus impiger* adults from eggs, beetles reared from *Calystegia* seed collected in the field were placed in petri dishes, with various combinations of beetles and seed from different localities. Most combinations gave rise to at least some adult beetles. Developmental periods varied considerably, with the first summer generation having a shorter minimal larval and pupal period than the second summer generation. Examples of minimal periods from egg to adult are 49 days and 58 days in seed samples of *C. longipes* (the smallest among seeds studied), 75 days in lots of both *C. fulcrata* and *C. macrostegia* subsp. *cyclostegia,* ca. 82 days in *C. m.* subsp. *macrostegia,* and 86 days in *C. occidentalis.* Longer developmental periods in the same species are hard to interpret or categorize because they were determined in the relatively unnatural conditions of the laboratory.

In nature it is likely that the first adults to emerge in the summer usually had a 45–60 day developmental period; this roughly corresponds with time from flowering of the plants to emergence of beetles from mature seeds and with minimal developmental periods for other species of bruchids (Johnson and Kingsolver, 1971; Johnson, 1967, 1970; Forister and Johnson, 1971). In any case, developmental time for *Megacerus impiger* in the field is short enough for two or three generations of beetles to exploit each crop of seed. This sequence, involving several generations per year, may be very similar to the one described and diagrammed (Forister and Johnson, 1971, p. 230) for a species of bruchid infesting seeds of *Ziziphus* (Rhamnaceae). This yearly sequence of three successive "waves" of seed exploitation is important to the life cycle of *Calystegia*.

Extent of seed destruction

Percent capsule infestation and seed destruction by *Megacerus impiger* are shown in Table 2 for major *Calystegia* populations studied. The extent of capsule dehiscence per sample was quantified roughly following each collection date; these estimates are of use in interpreting data in the table, because there is a decided relationship between date of collection, extent of capsule dehiscence, and the degree of exposure of the seeds to continuous oviposition by female bruchids. In addition to percent of seeds destroyed per population (seeds actually hollowed out by beetle larvae before the adults emerged), a number is given for "percent seed infested" in each sample that includes the sum of seeds destroyed plus seeds bearing beetle eggs. Each *Calystegia* seed with an egg on it may not give rise to an adult beetle, but the percentage in this category in the table do suggest a reasonable minimum *potential* destruction for the seed crop present at the date of collection. Aborted or "half grown" seeds are often found in *Calystegia* capsules along with mature seeds but have not been included in any tabulations of Table 2; it is possible that the presence of bruchid larvae that later died had caused breakdown in development of these seeds. This has been suggested for other species by Wilson and Janzen (1972), and Janzen (1969). On the other hand, apparently intact seeds could in some cases contain bruchids that died before emergence. Hand cutting of 300 "intact" seeds of a Butte County population of *C. occidentalis* and X-ray examination of 75 "intact" seeds of a Madera County population of *C. fulcrata* showed no signs of internal damage, and no signs of immature bruchids. It is still possible that larvae died at a very early instar in some seeds and were not discernible, but figures in the table on seed infestations have not been adjusted for such cases, as is sometimes necessary (D. Janzen, pers. comm., 1978).

Even if all eggs present on the outside of seeds were to develop into destructive larvae, figures given in Table 2 for "percent seeds infested" would still be lower than those occurring in nature for these populations. Some beetle eggs may fall, or be rubbed off seeds during sample handling, but such loss is considered minimal. More importantly, none of the samples in Table 2 can show complete tabulations of seed destruction because continued egg laying doubtless occurs in a population after a sample is taken.

The fairly low percent seed losses listed in Table 2 deal only with seeds in capsules on the plants, and it is not known to what extent these bruchids also oviposit on seeds that have fallen to the ground (nor is it known to what extent seeds are dispersed away from the plants producing them). Many species of the Bruchidae are host-specific and succeeding generations in some species may quite thoroughly destroy nondispersed seeds lying under parent trees (Janzen, 1969, 1970; Solbrig and Cantino, 1975). Seed destruction may be higher than estimated in Table 2, due to additional exploitation of seeds on the ground.

Seed destruction by the first summer generation of bruchids does vary from sample to sample (e.g., from 0.005 percent seeds destroyed in *C. fulcrata* to 9.9 percent in *C. malacophylla* with no dehiscence of capsules, Table 2). It is clear that this is due to eggs laid before capsules dehisced, by the adults that had overwintered. Samples taken later usually show slightly higher percentages of seed destruction—doubtless due to the new opportunity for oviposition on seeds exposed now in dehisced capsules (and done by late emergents of the first adults as well as by later generations of adults). For example, *C. fulcrata* sampled at Miramonte (Fresno Co.) 16 July 1972 showed 2.2 percent seed destruction, and a second sample from the same population on 15 September showed 15.5 percent.

Data for *C. occidentalis* at Cohasset (Butte Co.) similarly show an increase in percent seed destruction with advance of the season. Data for this species also illustrate several other features of seed destruction. Data from *Calystegia occidentalis* from both Cohasset and nearby Forest Ranch suggest that seed destruction varies somewhat in local populations over two succeeding years: Cohasset had 5.4 percent destruction by early September, 1974, but 8.2 percent by late August of the next year; Forest Ranch showed a similar trend, with 1.6 percent by early August, 1974 and 9.2 percent already by late July the next year. Other variation can be noted in *C. occidentalis* samples made at Forest Ranch. One made in 1975 had 9.2 percent destruction (hollow seeds), and had about 6.6 percent additional infestation (seeds bearing beetle eggs); another sample here that year showed only 2.4 percent hollow seeds but a higher percentage (almost 20 percent) of the seeds bearing eggs—and potential destruction. Finally, a single plant of *C. occidentalis* was sampled from a population there in late October, 1974 (probably close to the end of the season during which beetles continue to oviposit); 11.8 percent of the seeds remaining on this plant had been destroyed, and an additional 10 percent of the seeds had attached eggs. This particular plant was atypical in being isolated from others in the population and in growing prostrate on the ground rather than climbing on chaparral shrubs. Such variations within one species or at one locality, even in plant spacing or habit, suggest numerous complexities in this plant—animal interface that can possibly influence the behavior of both ovipositing beetles and their seed-destroying larvae.

Evolution of the interaction

Megacerus impiger is associated with taxa of *Calystegia* in cismontane California. The beetle seems most closely associated with the inland, smaller-seeded species, but has also been found on the widespread coastal strand morning glory *C. soldanella* (Fig. 1, Ventura Co.). In this large-seeded species, the beetles occur in low densities and the larvae use only a portion of the food-stores during their development, a situation totally unlike that occurring in other *Calystegia* taxa where each larva consumes the entire seed contents before pupating in the seed. It seems likely that *Megacerus impiger* has evolved its larval foodplant "preference" through time in association with the non-strand species of *Calystegia.*

There is no information on the phytogeographical affinities of the present-day xerophytic *Calystegia* species in California, but it is likely that this group of plants spread throughout the lowland areas in response to Quaternary events, as postulated for the herbaceous flora of California in general by Axelrod (1973). Southern origin or source is likely for both these plants and their seed predators, as most members of both Convolvulaceae and *Megacerus* tend to be southern in distribution. The present range of the beetle on these plants (Fig. 1) even suggests potential continued northward expansion by the predator. Several of the more northern populations of *Calystegia* have not contained *Megacerus* in the seed samples. Yet laboratory tests with Butte Co. *C. atriplicifolia,* a species that ranges north to Washington, show that vigorous adult beetles can be grown when females from farther south in California (e.g., from Yuba Co. *C. occidentalis* seeds) are given northern California *C. atriplicifolia* seeds on which to oviposit.

The seed exploitation described could represent a fairly ancient association of plant and insect. Most populations studied in nearly all taxa of lowland calystegias in this large geographic area of California are presently exploited by a *single* successful species of bruchid. Furthermore, the bruchids are now apparently entirely dependent on *Calystegia* seed for their existence, suggesting a well-established association.

A single species of bruchid is known in some cases like this to exploit related species of plants, and according to Johnson (1970), it may even be possible for the botanist to use such a bruchid as a "taxonomic tool". This idea seems applicable to calystegias. California taxa in this genus (and in *Convolvulus*) have had a complex history of treatment with specific and subspecific entities alternately and variously being merged and split (see especially Abrams, 1951, for synonymies; Munz, 1959, 1968; Brummitt, 1965, 1975). Extensive field studies have shown this group of plants to be poorly differentiated in many aspects of their reproductive structures and behaviors. Instead, *Calystegia* taxa are quite clearly defined (e.g., Munz, 1968) on nonreproductive features relating to inflorescence bracts, leaf shape and size, and plant pubescence, habit, and habitat. The present study on widespread seed exploitation by a single species of bruchid beetle further documents close similarities in reproductive aspects of California calystegias.

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REVIEW

Botanists of the Eucalypts. By NORMAN HALL. v + 160 pp. CSIRO, Melbourne (US distributor: ISBS, Forest Grove, OR). 1978. $10.00.

Botanical biographies have been collected mostly according to nationality (e.g., Desmond's *Dictionary of British and Irish Botanists*), floristic region (Van Stennis-Kruseman's *Cyclopaedia of Collectors* in *Flora Malesiana*), or collection (Dandy's *Sloane Herbarium*). Subtitled "short biographies of people who have named eucalypts, whose names have been given to species or who have collected type material", this book is of a rarer species—a compilation of biographies of people concerned with a particular plant taxon. The biographical sketches are not limited to each person's involvement with eucalypts, and most of the approximately 400 accounts are general reviews of botanical careers. However, *Eucalyptus* specialists will find interesting details of bibliography and collecting localities in some of the accounts. Much of the information on persons still living was acquired directly from those individuals. Appended is a long list of *Eucalyptus* species with cross-references to those persons in whose biographies the plants are mentioned.

Cultivated in California in the 19th century as a source of wood for railroad ties and to dry out swampy areas, fast-growing and thirsty gums and ironbarks are now planted mostly for ornament. Other taxonomically oriented collective biographies of interest to botanists and horticulturists remain to be written.—DALE E. JOHNSON, 12283 Ranch House Road, San Diego, CA 92128.

CARBON DIOXIDE EXCHANGE IN PINUS FLEXILIS AND P. STROBIFORMIS (PINACEAE)

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ABSTRACT

Seedlings of *Pinus strobiformis* Engelm. from central Arizona demonstrated significantly higher rates of photosynthesis at 25°C than seedlings of *Pinus flexilis* James from any of five populations from California, Wyoming, or Nevada. The reduction in the rate of carbon fixation in dry soils was significantly less at four temperatures in a Wyoming population of *P. flexilis* than in a *P. strobiformis* population from Arizona. These results are interpreted as responses to the relatively warm and mesic climate of the site where the Arizona seedlings were collected.

Pinus strobiformis (southwestern white pine) and *Pinus flexilis* (limber pine) are closely related white pines of the western United States and Canada (members of the subgenus *Strobus* Lemm. sect. *Strobus* subsect. *Strobi* Loud.: Critchfield and Little, 1966). *Pinus flexilis,* the more northern species, was named in 1823 by James. Engelmann (1848) described *P. strobiformis,* but later (1878) he considered it to be only a variety of *P. flexilis*. Overlapping ranges, morphological similarity, and hybridization have long confused the taxonomy within what has been called the "*Pinus flexilis* complex". Steinhoff (1964) has summarized the nomenclatural and taxonomic history within this group.

The range of *Pinus flexilis* extends from British Columbia to northern New Mexico. *Pinus strobiformis* occurs in New Mexico as well, but its range extends southward into Mexico, as reflected by one of its common names, "Mexican border pine" (Steinhoff, 1964). The distributional patterns of *P. flexilis* and *P. strobiformis* are shown in Fig. 1 [redrawn from Little (1971)], which shows most of the extensive latitudinal ranges of these two species, encompassing more than 17°. One might speculate that differences in latitude as well as other factors would result in distinct *P. flexilis* and *P. strobiformis* habitats. Individuals of these two species might consequently differ in adaptive physiological characteristics. In order to investigate this, gas exchange was studied in seedlings of both species at various temperatures. CO_2 fixation was also investigated in seedlings after the potting soils were allowed to become quite dry.

METHODS

Experimental seedlings of *Pinus flexilis* and *Pinus strobiformis* were grown from seeds collected in natural stands in the western

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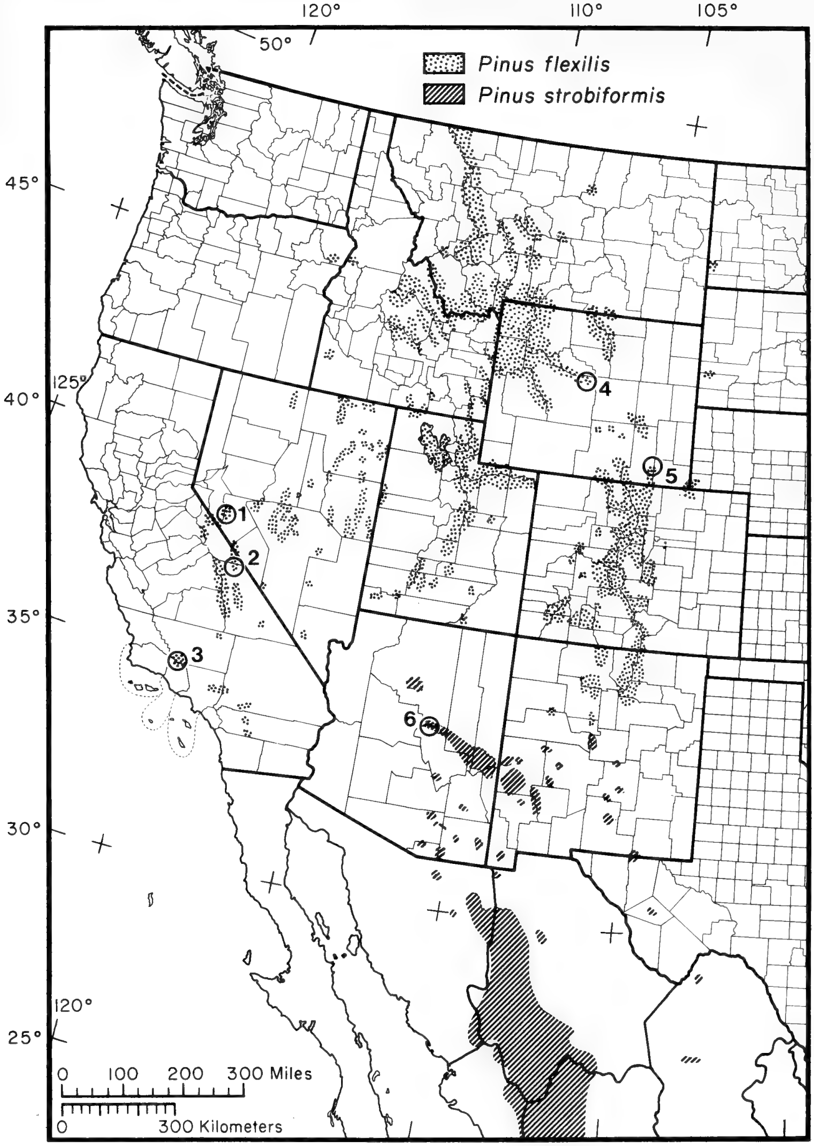


FIG. 1. Distribution of *Pinus flexilis* and *Pinus strobiformis*, taken from Little (1971). Seedling sources: 1. Mt. Grant; 2. White Mountains; 3. Mt. Pinos; 4. Wind River Indian Reservation; 5. Lincoln Monument; 6. Mogollon Rim.

TABLE 1. HABITAT INFORMATION ON SEED SOURCES FOR EXPERIMENTAL SEEDLINGS. Site numbers refer to text and Fig. 1. Precipitation and temperature data are annual means. D = number of trees of all species per hectare; (f) = *Pinus flexilis*; (s) = *Pinus strobiformis*. Precipitation and temperature data given for Mogollon Rim are from Snowbowl, AZ, 100 km north.

	Site and species	Elev. (m)	Precip. (mm)	Temp. (°C)	Lat. N	Parent rock	D
1	Mt. Grant, NV (f)	3273	175	—	38°34′	Keratophyre	4
2	White Mtn., CA (f)	3075	325	0.9	37°31′	Granite	150
3	Mt. Pinos, CA (f)	2676	—	—	34°45′	Gneiss	140
4	Wind River, WY (f)	2152	200	—	43°35′	Sandstone	70
5	Lincoln Mon., WY (f)	2618	320	—	41°14′	Granite	100
6	Mogollon Rim, AZ (s)	2195	557	6.1	34°25′	Limestone	2300

United States (Fig. 1 and Table 1). Species designations of the sampled populations agree with those of Steinhoff (1964), Critchfield and Little (1966), and Little (1971).

Seedlings were grown under uniform conditions in a soil of sand and peat moss. It was necessary to maintain seedlings at relatively cool temperatures and satisfactory conditions for the growth of seedlings were achieved in a growth chamber at 20°C light and 10°C dark with a 15-hour light period. All seedlings were treated during the first year of their growth with one 3-month period of "winter" conditions (7°C and an 8-hour light period). At the time of testing seedlings were about 1.5 years old and were 7.5–15 cm tall.

CO_2 exchange by seedlings was measured with an infrared gas analyzer using a closed system of air flow, as outlined by Wright (1970, 1974). During all tests the wind speed inside the chamber was 61 meters per minute horizontally at plant height. Light intensity was 75,350 lux. Runs were made at CO_2 levels between 300 and 304 ppm. Each individual plant was tested repeatedly once the chamber attained the proper temperature. Results were not recorded until the plant was acclimated and the rate of CO_2 fixation had stabilized.

Rate of CO_2 fixation in the light was considered to be a measure of net photosynthesis. CO_2 losses due to "dark" respiration as well as to photorespiration are incorporated in this value. Fixation rates have been expressed on the basis of the dry weight of photosynthetic tissue.

Periodic measurements of gas exchange were made in unwatered seedlings as the potting soils progressively dried. The entire pot was weighed each time a plant was tested. Later, when the plant was sacrificed, the potting soil was dried and weighed separately. The oven dried weight was then subtracted from the weight of the soil at the time the plant was tested, and soil moisture percentages could be determined for each test. Tests conducted at a soil moisture of 5.8 percent were chosen for comparative purposes, because at lower levels the *P. strobiformis* seedlings began to die.

Net photosynthesis and dark respiration were measured at 10, 15, 25, and 35°C in seedlings from each of six populations. Table 1 gives information concerning the sites of origin of experimental seedlings. Gas exchange was measured in four seedlings from each population at each temperature.

Thornthwaite water balance diagrams were used to compare the climates of representative *P. flexilis* and *P. strobiformis* sites. Fig. 2A summarizes the yearly precipitation, temperature, and evaporation adjacent to *P. flexilis* stand 2 in the White Mountains of California. A seven-year temperature and a five-year precipitation record from this weather station (at Crooked Creek Laboratory of the University of California) were averaged in the construction of Fig. 2A (U.S. National Oceanic and Atmospheric Administration, 1972). In comparison, Fig. 2B summarizes this same information for possibly the only long-term weather station with year-round data relevant to *P. strobiformis*. This is the Snowbowl weather station north of Flagstaff, Arizona, less than 1 km from a *P. strobiformis* stand. This station is 104 km north of the Mogollon Rim seedling source (site 6). A 12-year record of temperature and precipitation was available from this station for the construction of Fig. 2B (U.S. National Oceanic and Atmospheric Administration, 1972).

RESULTS

Temperature curves for the average net rate of carbon fixation in four seedlings from each of six populations are shown in Fig. 3. The optimum temperature for net photosynthesis in seedlings from each of the *P. flexilis* populations appeared to be near 15°C. Data for 20°C were obtained from only one *Pinus flexilis* population but in this case photosynthetic activity fell off rapidly above 15°C indicating that the optimum temperature is perhaps nearer to 15°C than to 20°C in *P. flexilis*. The optimum temperature for carbon fixation by *P. strobiformis* from site 6, on the other hand, appeared to be nearer 25°C (Fig. 3).

Analysis of variance showed that the difference between one population of *P. strobiformis* and five populations of *P. flexilis* in net rate of photosynthesis was statistically significant ($F(1,4) = 8.20$, $p < 0.05$) at a temperature of 25°C.

The Thornthwaite water balance diagram of Fig. 2A shows the development of an average net water deficit of 66 mm during the year in the White Mountains. Snowbowl, Arizona, is a more mesic site, developing an average yearly water *surplus* of 27 mm (Fig. 2B). Although the potential and actual evaporation of the Snowbowl site is high due to relatively high summer temperatures, summer precipitation is also relatively high.

Figure 4 demonstrates the decrease in rate of carbon fixation that

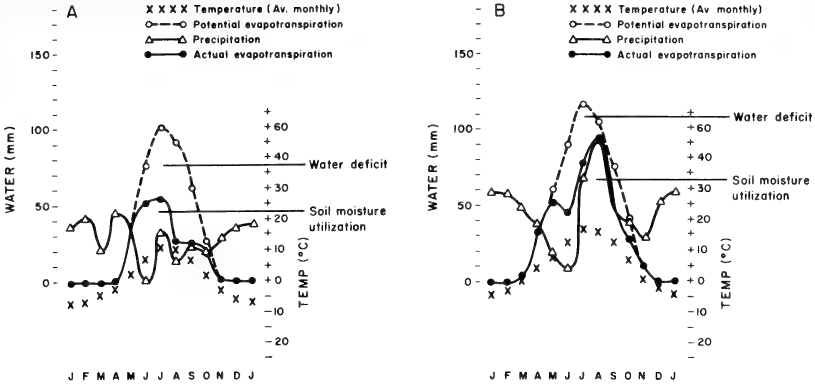


FIG. 2. Thornthwaite yearly water balance diagrams for *Pinus flexilis* and *Pinus strobiformis* sites. A. White Mountains, CA (Crooked Creek Field Station), source of *P. flexilis* seedlings. B. Snowbowl, north of Flagstaff, AZ, a *Pinus strobiformis* site.

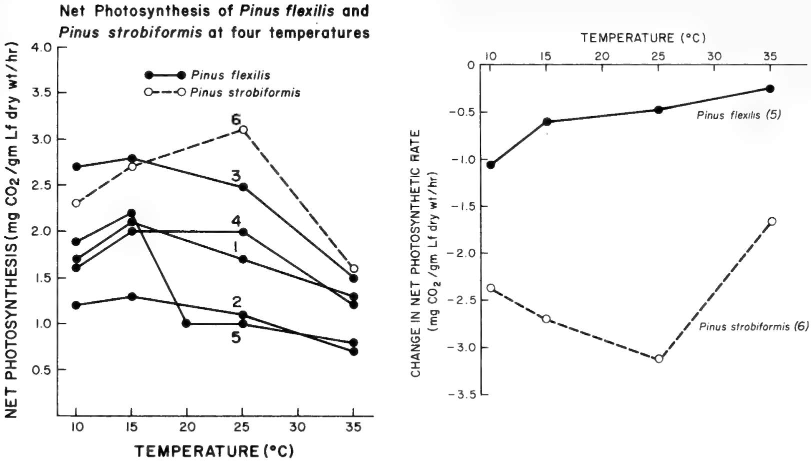
occurred in these two taxa after a decrease in soil moisture from a saturated state to a water potential of −20 bars. Four *Pinus strobiformis* seedlings from Mogollon Rim showed a much greater average depression in photosynthetic rate than did four *Pinus flexilis* seedlings from site 5.

Univariate F tests demonstrated statistical significance in this photosynthetic depression at the 5 percent level at each temperature used. At 10°C, $F = 12.7$ ($p < 0.02$); at 15°C, $F = 19.6$ ($p < 0.005$); at 25°C, $F = 29.4$ ($p < 0.002$); and at 35°C, $F = 16.4$ ($p < 0.01$). The Bonferroni approach (Harris, 1975) was used here to correct for the inflation of the probability of making a type-one error when multiple tests are involved.

DISCUSSION

The optimum temperature for carbon fixation is higher in at least one *P. strobiformis* population than it is in four *Pinus flexilis* populations, and depression of carbon fixation by low soil moisture was less in one population of *P. flexilis* at four temperatures. Do these observations support separation of *P. flexilis* and *P. strobiformis*? Are they correlated with variations in the habitat?

Steinhoff (1964) concluded that his data on growth rates and morphological characteristics of seedlings, and the characteristics of mature trees and cones, warranted differentiation of *P. flexilis* and *P. strobiformis* at the species level. The data presented here support the existence of two taxa or ecotypes. It may be relevant that Steinhoff found less morphological separation between the two taxa as the



FIGS. 3–4. FIG. 3 (left). Net photosynthesis of *Pinus flexilis* and *P. strobiformis*. Average of four individuals from each of six populations: 1. Mt. Grant; 2. White Mountains; 3. Mt. Pinos; 4. Wind River Indian Reservation; 5. Lincoln Monument; 6. Mogollon Rim. FIG. 4 (right). Depression in rate of net photosynthesis when soil moisture decreased from saturation to −20 bars. Four *P. flexilis* seedlings from Lincoln Monument (site 5) are compared with four *P. strobiformis* seedlings from Mogollon Rim (site 6).

northern boundary of the range of *P. strobiformis* was approached. This he attributed to hybridization and environmental plasticity.

The *P. strobiformis* seedlings that were the subject of the gas exchange studies described here were from near the northern edge of the species range. Opportunities for hybridization of the parent population with *P. flexilis* and latitudinal effects on the habitat may have been maximal, but these northern *P. strobiformis* seedlings were still found to be distinct from *P. flexilis* in adaptive aspects of the process of gas exchange. This occurred in spite of the maintenance of seedlings of both species under uniform environmental conditions.

Evidence such as this supports the coherence of each taxon as a genetic unit despite the possibility of hybridization. The intergradation that Steinhoff (1964) measured in the characteristics of northern *P. strobiformis* and southern *P. flexilis* stands may have been, as he mentions, a plastic response to similar environments, especially as it was most noticeable in mature trees.

Correlations of physiological variations with habitat in these two species are difficult to make. This is due partly to the limited availability of habitat data for *P. strobiformis* and the sampling here of only one population of this species.

Latitude and altitude are determinants of the environment of both species, but their effects may interact. "A decrease in latitude appears to compensate for increasing altitude of origin for more southern *P. flexilis* collections" (Steinhoff, 1964, p. 65). So elevation may not be directly correlated with seedling characteristics. In addition, *P. flexilis* is a pioneer species and seems not to be restricted by elevation as long as competitors are absent (Lepper, 1974). Preston (1947) lists *P. flexilis* as "socially intolerant", with an elevational range of 1372–3505 m. Britton (1908) describes a range of 1500–3600 meters above sea level. *Pinus strobiformis* seems also to be variable in its elevational occurrence, although information is difficult to find. Kearney and Peebles (1951) give its elevational range as 1980–3048 m. *Pinus strobiformis* may, as suggested in Table 1, grow at lower average elevations than *P. flexilis* (Steinhoff, 1964) but its habitat is probably warmer, if due only to its more southern distribution. Table 1 and Fig. 1 show that *P. strobiformis* populations are found at lower elevations and latitudes than most *P. flexilis* populations. Table 1 also shows that the Snowbowl Weather Station, near a *P. strobiformis* stand, records a higher average annual temperature and precipitation than the *P. flexilis* sites for which data were available. The Mogollon Rim, which has no relevant weather station, is at least superficially a very wet area, with frequent summer fog.

Therefore, *Pinus strobiformis* populations may well have a warm and wet habitat relative to *Pinus flexilis* due partly to elevation and latitude. This may explain the higher optimum photosynthetic temperatures and reduced drought tolerance in *P. strobiformis* relative to *P. flexilis*. Other populations of *P. strobiformis* must be sampled, however, before generalizations are made.

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I acknowledge the help of Dr. Robert Wright, whose laboratory, equipment, and expertise I relied upon in the planning and completion of this research. I also thank Dr. David Randall, who wrote the computer program used to generate the Thornthwaite water-balance diagrams, and Dr. Robert Kowal, who provided statistical advice.

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A Flora of California. By WILLIS L. JEPSON. Vol. 4 (2), *Rubiaceae*. By LAURAMAY T. DEMPSTER. 47 pp., 29 figs., paper. Jepson Herbarium, Berkeley. 1979. $3.00. A reactivation of the *Flora,* which was published through Vol. 3, part 2, before Jepson's death in 1946. Vol. 3(3) and Vol. 4(1) have not yet been published. Vol. 4(2) is available with advance payment (checks payable to Regents, University of California) from the Jepson Herbarium, Botany Dept., University of California, Berkeley 94720. An index of the families treated in the *Flora* to date will be included with each order. Previous volumes (1–3) of the *Flora* are also available.

ANNOUNCEMENT

SYMPOSIUM ON AIR POLLUTION AND FORESTS

An international symposium on "Effects of Air Pollutants on Mediterranean and Temperate Forest Ecosystems" will be held June 22–28, 1980, in Riverside, CA. The conference will focus on major areas of research in forest air pollution, including the effects of air pollutants on tree growth, on species composition of forest stands, and on forest wildlife, insect pests, and tree diseases. The effects of acid precipitation and heavy metals on forests, and the emission of nitrogen oxides, hydrocarbons, and other natural pollutants from forests will also be discussed. One of the major purposes of the conference is to examine progress in integrating data from diverse, specialized studies into ecosystem-level analyses.

Further information is available from Dr. Paul R. Miller at the Pacific Southwest Forest and Range Experiment Station, 4955 Canyon Crest Drive, Riverside, CA 92507. Pre-registration is advised.

ALPINE FLORA OF THE WASSUK RANGE, MINERAL COUNTY, NEVADA

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ABSTRACT

The peak of Mt. Grant, 3426 m elevation, in the Wassuk Range of Nevada is one of a number of small alpine islands in the Great Basin. In this study, the alpine zone was defined to be the zone above the highest areas dominated by shrubby *Artemisia* species. Its total area on Mt. Grant was about 2.6 km^2. The alpine flora consisted of 70 species. Of these, 12 species are found in the Sierra Nevada, 13 in the Sierra Nevada and Great Basin, two in the Great Basin only, one in the Great Basin and Rocky Mountains, 30 are widespread in western North America, and 12 are widespread arctic-alpine species. There were no endemic species. Most species are not restricted to alpine habitats.

The alpine areas of Great Basin ranges consist of a number of small islands that have probably never formed continuous habitat. Their isolation raises questions about the source of their floras. Billings (1978) suggested that migration into Great Basin alpine zones was generally from north to south. He also has described endemics as contributing significantly to alpine floras only in the southwestern portion of the interior drainage area.

Data for testing these ideas can currently be derived from descriptions of relatively few alpine floras. Extensive species lists are available for the White Mountains of California (Lloyd and Mitchell, 1973), the Ruby and East Humboldt Ranges in Elko Co., Nevada (Loope, 1969; Lewis, 1971), and the Deep Creek Range of Utah (McMillan, 1948). Less complete lists exist for the Toiyabe and Snake Ranges of Nevada (Linsdale et al., 1952; Lewis, 1973), the Raft River Range in Utah (Preece, 1950), and the Sweetwater Mountains of California (Major and Taylor, 1977). These ranges make up most of the larger alpine areas in the Great Basin. Billings (1978) points out that almost no information is available on the floristics of small alpine areas. Yet these small areas, which may be expected to have the most depauperate floras, are likely to yield useful information for understanding the differential abilities of alpine species to migrate and survive.

As part of a study comparing the floras of Great Basin alpine areas, we here report the composition of the alpine flora of one small island, the Wassuk Range in Mineral County, Nevada. The alpine zones

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nearest the Wassuks are in the Sweetwater Range 48 km to the west, the White Mountains 88 km to the south, the Toiyabe Range 125 km to the east, and the Carson Range (Mt. Rose) 125 km to the northwest. The alpine zone of the Wassuk Range is restricted to Mt. Grant, 3426 m elevation.

The physical environment of the upper reaches of the Wassuk Range is poorly known. The range lies in the rain shadow of the Sierra Nevada and Sweetwater Mountains. A storage rain gauge installed at 2740 m on Mt. Grant from March, 1952, to May, 1954, measured 48.3 cm of precipitation over that period; summer precipitation slightly exceeded that of winter (U.S. Weather Bureau, 1958). On Mt. Grant, no surface snowdrifts persisted past early July in 1976 and 1977, although snow and ice buried among boulders high on the eastern slope continued to melt after 15 July 1977. No information on alpine temperatures is available.

The Wassuk Range is composed of pre-Tertiary intrusives, primarily granites of the Sierra batholith (Ferguson and Muller, 1949). Soils are poorly developed in the alpine zone, with no organic horizons except under scattered grass tussocks. Slopes are predominantly talus or scree, much of which is unstable. Flat ridges and shallow depressions are gravelly. There is no evidence of frost features such as sorted polygons, sorted stripes, or stone-banked terraces.

Access to Mt. Grant has been restricted since about 1938, and grazing on the mountain has been minimal for about 40 years.

A Definition of the Alpine Zone

Because we wish ultimately to compare alpine floras across the Great Basin, a definition of the lower limit of the alpine zone on Mt. Grant should be widely applicable throughout the region. Many authors have commented on the difficulty of defining an alpine zone in the absence of continuous subalpine forests (Loope, 1969; Mooney, 1973; Höllermann, 1973; Major and Taylor, 1977; Billings, 1978).

Examination of high elevation vegetation on Mt. Grant showed several zones, in many places separated by indistinct boundaries. In order of increasing elevation these were: (1) A community dominated by *Artemisia tridentata* generally occurred up to 3050 m and in relatively protected sites up to 3325 m. This community was clearly subalpine following definitions of Billings (1951) and Mooney (1973). (2) Above the *A. tridentata,* up to about 3375 m, and on south slopes and exposed ridges as low as 2850 m, were *A. arbuscula* communities with the physiognomy of an alpine fellfield. Many species that were abundant in this fellfield also grew at higher elevations as well, including *Koeleria cristata, Sedum lanceolatum, Astragalus calycosus, A. whitneyi, Leptodactylon pungens, Erigeron clokeyi,* and *Hymenoxys cooperi.* (3) Above the *A. arbuscula* communities lay a narrow zone lacking woody *Artemisia* species and characterized by the dominance of several subshrub species, including *Ribes cereum, Leptodactylon pungens, Chrysothamnus viscidiflorus,* and *Haplopappus macronema.* Some herbaceous species (e.g. *Poa fendleriana, Stipa pinetorum,* and *Lewisia rediviva*) reached their upper limits in this zone; most, however, were also found above the subshrubs. (4) At the highest elevations (above about 3350 m) and at somewhat lower elevations on steep north slopes, vegetation was dominated by herbaceous forms. On gravelly ridges, prostrate or cushion forms were most common, including *Arenaria kingii, Draba densifolia, Astragalus calycosus,* and *Erigeron clokeyi.* Scree slopes were dominated by grasses. *Cystopteris fragilis, Festuca brachyphylla, Oxyria digyna,* and *Arabis lemmonii* were the most common plants on steep rocky north slopes. Total vascular plant cover in this zone was rarely above 25 percent.

The lower boundary of the alpine zone on Mt. Grant could be drawn in at least four different positions: (a) above some elevational limit (after Billings, 1978), (b) at the upper edge of *Artemisia tridentata* (after Billings, 1951; and possibly Mooney, 1973), (c) at the boundary between the *A. arbuscula* and subshrub communities, or (d) at the upper limit of woody plant dominance.

Elevation alone, while easily and repeatably determined, has relatively little biological significance. Where trees are present in other ranges, wind exposure, aspect, latitude, and snow cover greatly influence the position of a krummholz treeline. Distribution of high elevation shrubs and herbs is often similarly affected.

The absence of *Artemisia tridentata* appears to be the most widely used definition of Great Basin alpine. But use of this boundary would include the relatively low elevation *A. arbuscula* fellfields in the alpine zone. These are clearly not alpine because they extend as much as 475 m below the upper limits of *A. tridentata* on south-facing slopes. In addition, we have seen similar communities on ridges in pinyon-juniper forests in the Sweetwater Range of California.

The exclusion of all woody vegetation from the alpine zone is probably too stringent a definition in that alpine floras of the Sierra Nevada and Rocky Mountains contain such woody genera as *Salix, Kalmia, Ribes,* and *Dryas* (Marr, 1967; Major and Taylor, 1977).

We have, therefore, chosen to include high elevation subshrub communities in the alpine zone of Mt. Grant and to classify *A. arbuscula* fellfields as subalpine. Following this definition, about 2.6 km^2 of the Wassuk Range is alpine.

To ensure that the definition of the alpine zone on Mt. Grant can be used widely in the Great Basin, we have made preliminary observations in nine other ranges: the Sweetwater Mountains (Mono Co., California), the Toiyabe Range (Nye and Lander Cos., Nevada), the Humboldt Range (Pershing Co., Nevada), the Santa Rosa Range (Humboldt Co., Nevada), the Independence and Jarbidge Ranges

(Elko Co., Nevada), the Schell Creek and Snake Ranges (White Pine Co., Nevada), and the Raft River Range (Box Elder Co., Utah). The definition of alpine used on Mt. Grant appears applicable to these ranges as well. Where a krummholz treeline is present, the upper limit of trees generally coincides with the upper limit of shrubby *Artemisia*.

Collections were made on Mt. Grant on the following dates: 26–30 June and 4–6 August 1976, 11–15 July 1977, and 15–16 August 1979. Nomenclature and descriptions follow Munz (1959) except where authorities are listed. Voucher specimens are deposited in UNLV and WS.

ALPINE PLANTS OF THE WASSUK RANGE

Geographical distributions are summarized as follows: SN—Sierra Nevada, including the White and Sweetwater Mountains of California (Lloyd and Mitchell, 1973; Major and Taylor, 1977; Munz 1959; Sharsmith, 1940); GB—Great Basin, excluding the White and Sweetwater Mountains (Bell and Johnson, unpubl. data; Cronquist et al., 1972, 1977; Lewis, 1971, 1973; Linsdale et al., 1952; Loope, 1969; McMillan, 1948; Preece, 1950); Ro—Rocky Mountains (Harrington, 1964; Weber, 1976); Ar—Arctic (Polunin, 1959).

LEPIDOPHYTA

Selaginellaceae

Selaginella watsonii. Common among rocks in snow accumulation areas. SN, GB

PTEROPHYTA

Aspidiaceae

Cystopteris fragilis. Locally abundant on north-facing slopes, especially among rocks. SN, GB, Ro, Ar.

Pteridaceae

Pellaea breweri. Locally abundant on north-facing cliffs and stable talus. SN, GB, Ro.

ANTHOPHYTA—MONOCOTYLEDONEAE

Amaryllidaceae

Allium parvum. Uncommon on flat ridges or gentle south slopes in fine, stable scree. SN.

Cyperaceae

Carex phaeocephala. Common in snow accumulation areas. SN, GB, Ro.

Carex rossii. Locally abundant only in fine-textured soils of some snow accumulation areas. SN, GB, Ro.

Gramineae

Calamagrostis purpurascens. Abundant and dominant on rocky, north-facing slopes; uncommon elsewhere. SN, GB, Ro, Ar.

Festuca brachyphylla. Common on north-facing slopes; uncommon in all other alpine habitats. SN, GB, Ro, Ar.

Koeleria cristata. Abundant to common on north- and east-facing slopes except talus. SN, GB, Ro.

Leucopoa kingii (S. Wats.) Weber. Uncommon on rocky, east-facing slopes in subshrub communities. SN, GB, Ro.

Muhlenbergia richardsonis. Locally abundant and dominant only in fine-textured soils in snow accumulation areas. Generally non-flowering. SN, GB, Ro.

Poa epilis. Abundant in all habitats except snow accumulation areas and north-facing slopes. SN, GB, Ro.

Poa fendleriana. Uncommon in flat, grassy meadows. SN, GB, Ro.

Poa rupicola. Very common in all habitats except cliffs. SN, GB, Ro.

Sitanion hystrix. Abundant and dominant on south-facing slopes and in some disturbed areas. SN, GB, Ro.

Stipa pinetorum. Rare, in shrubby meadows. SN, GB, Ro.

Trisetum spicatum. Uncommon, on east- and north-facing slopes; probably under winter snow. SN, GB, Ro, Ar.

ANTHOPHYTA—DICOTYLEDONEAE

Boraginaceae

Cryptantha humilis. Common on ridgetops, uncommon to rare elsewhere. GB.

Caryophyllaceae

Arenaria kingii var. *glabrescens*. Common on ridgetops and in subshrub communities. SN, GB.

Arenaria nuttallii subsp. *gracilis*. Rare on ridgetops and in loose, east-facing talus. SN, GB.

Chenopodiaceae

Monolepis nuttalliana. Uncommon, restricted to disturbed areas along roads. SN, GB, Ro, Ar.

Compositae

Antennaria corymbosa. Rare, in snow accumulation areas. SN, GB, Ro.

Antennaria rosea. Uncommon on rocky slopes, mostly in probable snow accumulation areas. SN, GB, Ro.

Antennaria umbrinella. Uncommon in snow accumulation areas and on north-facing slopes. SN, GB, Ro.

Artemisia ludoviciana subsp. *incompta.* Locally forming dense stands in rocky drainage areas near the lower edge of the alpine zone. SN, GB, Ro.

Chrysothamnus viscidiflorus subsp. *pumilus.* Common to uncommon in subshrub communities on slopes of all aspects. SN, GB, Ro.

Crepis nana. Rare, on scree slopes. SN, GB, Ro, Ar.

Erigeron clokeyi. Common in subshrub communities and on gravelly ridges. SN.

Erigeron compositus. Abundant and ubiquitous. SN, GB, Ro, Ar.

Eriophyllum lanatum var. *monoense.* Uncommon, in snowbeds. SN.

Haplopappus macronema. Uncommon on rocky slopes. SN, GB, Ro.

Hymenoxys cooperi var. *canescens.* Common on gravelly south-facing slopes; rare elsewhere except absent from snowbeds. SN, GB.

Senecio canus. Uncommon on gravelly slopes. SN, GB, Ro.

Senecio multilobatus. Uncommon in subshrub communities. SN, GB, Ro.

Senecio pattersonensis Hoover. Rare on north-facing talus slopes. SN.

Taraxacum officinale. Rare, in roadbeds. SN, GB, Ro, Ar.

Crassulaceae

Sedum lanceolatum. Rare, in snow accumulation areas. SN, GB, Ro.

Cruciferae

Arabis holboellii var. *pendulocarpa.* Rare, on a rocky south-facing slope at the upper edge of a snow accumulation area. SN, GB, Ro.

Arabis lemmonii var. *depauperata.* Abundant and ubiquitous. SN, GB, Ro.

Draba crassifolia. Uncommon, on rocky north-facing slopes. SN, GB, Ro, Ar.

Draba densifolia. Moderately common in all habitats except unstable slopes. SN, GB, Ro, Ar.

Erysimum perenne. Locally common on north-facing slopes or gravelly ridges, and in subshrub communities. SN, GB.

Lesquerella kingii var. *cordiformis.* Uncommon in snow accumulation areas. SN, GB.

Hydrophyllaceae

Phacelia hastata var. *compacta.* Uncommon to rare on slopes of all aspects; most abundant on disturbed soils and loose talus. GB.

Leguminosae

Astragalus calycosus. Locally abundant on gravelly ridgetops especially near the lower edge of the alpine zone. GB, Ro.

Astragalus purshii var. *lectulus*. Uncommon on gravelly ridgetops. SN.

Astragalus whitneyi. Uncommon in flat meadows. SN.

Lupinus alpestris. Locally abundant on gravelly soils in snow accumulation areas. SN.

Linaceae

Linum lewisii Pursh. Uncommon on both north and south slopes in gravel. SN, GB, Ro, Ar.

Onagraceae

Gayophytum racemosum. Uncommon on both north and south slopes in gravel. SN, GB, Ro.

Polemoniaceae

Ipomopsis congesta subsp. *montana*. Locally abundant on flat ridges and in loose gravel. SN.

Leptodactylon pungens subsp. *hallii*. Abundant on shrubby slopes and meadows. SN.

Phlox stansburyi var. *brevifolia*. Locally abundant on shrubby slopes near the lower edge of the alpine zone. SN, GB.

Polygonaceae

Eriogonum caespitosum. Rare, in gravel on flat ridges. SN, GB.

Eriogonum ovalifolium var. *nivale*. Uncommon, on north-facing rocky slopes and in gravel on flat ridges. SN, GB, Ro.

Oxyria digyna. Locally abundant on north-facing talus or boulder slopes; uncommon in fine-textured soils in snow accumulation areas. SN, GB, Ro, Ar.

Rumex utahensis. Rare in fine-textured mineral soil in a snow accumulation area. SN, GB, Ro.

Portulacaceae

Calyptridium umbellatum var. *caudiciferum*. Uncommon in disturbed soils, snowbeds, flat ridges, and rocky slopes. SN, GB.

Lewisia pygmaea. Uncommon, on rocky, north-facing slopes. SN, GB, Ro.

Lewisia rediviva var. *minor*. Uncommon, on gentle, south-facing slopes. SN, GB?

Primulaceae

Androsace septentrionalis subsp. *subumbellata*. Moderately abundant on gravelly or rocky north-facing slopes and in disturbed sites. SN, GB, Ro.

Rosaceae

Holodiscus sp., probably *H. microphyllus*. Very rare on east-facing rock slopes. Very reduced, non-flowering plants. SN, Ro.

Rubiaceae

Galium hypotrichium subsp. *hypotrichium*. Locally common among loose rocks, primarily on north- and east-facing slopes. SN.

Saxifragaceae

Heuchera duranii. Moderately common, on north- and east-facing rocky slopes. White, Sweetwater, Wassuk ranges only.

Ribes cereum. Common on rock outcrops and locally common on rocky slopes. SN, GB, Ro.

Scrophulariaceae

Castilleja nana. Locally common on gravelly ridgetops; rare elsewhere. SN, GB.

Mimulus coccineus. Locally common especially on south-facing slopes and ridges. SN, GB.

Mimulus suksdorfii. Locally common in fine-textured mineral soil. SN, GB, Ro.

Penstemon speciosus. Rare, on rocky slopes. SN, GB.

Umbelliferae

Cymopterus cinerarius. Uncommon in loose scree mostly on north-facing slopes SN.

DISCUSSION

The alpine flora of the Wassuk Range was made up of 70 species of vascular plants. Harper et al. (1978) have developed a species-area curve for vascular plants on montane islands in the Great Basin. Their curve predicts that a montane island the size of the alpine zone on Mt. Grant (2.6 km^2) will contain 65 species, a number very close to that observed. The small number of species may be related to the lack of habitat diversity in the Wassuk Range alpine zone. Mt. Grant has no permanent snowdrifts; in 1976 and 1977, the largest snowbank had completely melted before 10 July. The lack of large, late-lying snowdrifts, persistent streams and moist soils results in the absence of important alpine habitats.

The flora of the Wassuk alpine zone is a combination of widespread alpine elements and Sierran and Great Basin taxa. Sierra Nevada and Great Basin species make up 36 percent of the flora. The Sierran element contributes considerably less to the Wassuk flora (17 percent) than to the White Mountain flora (51 percent: Lloyd and Mitchell, 1973). One species, *Heuchera duranii,* is found only in the White, Sweetwater, and Wassuk Ranges. Widespread species, occurring in both the Sierra Nevada and Rocky Mountains, form the largest single floristic group (60 percent). Of this group, 12 species are also found in the Arctic. There are no endemics.

The composition of the Wassuk Range flora supports two of Billing's (1978) generalizations about Great Basin alpine plant distributions. First, distinctly Sierran taxa have had relatively poor success in becoming established in ranges to the east. In this respect, alpine species act much like montane plants (Harper et al., 1978). Secondly, the Wassuk Range appears to represent a transition zone between the Sierra Nevada and Great Basin floras. Exact definition of the western boundary of Great Basin alpine floras will require more complete alpine species lists from the Sweetwater Range to the west and the Toiyabe Range to the east.

The lack of endemic taxa in the Wassuk alpine zone is unusual among ranges on the western perimeter of the Great Basin. Lloyd and Mitchell (1973) list six alpine endemics in the White Mountains, although *Heuchera duranii* and *Trifolium monoense* should not be considered endemic there (Munz, 1959); Major and Taylor (1977) cite two endemics in a partial alpine flora of 43 species in the Sweetwaters; and Billings (1978) notes four endemic species in an alpine flora of 39 species in the calcareous Spring Mountains. The absence of endemics in the Wassuk Range may be related to a reduced probability of their evolution in a very small area with little habitat diversity.

Harper et al. (1978) suggest that a low degree of plant endemism at mid-elevations in the Great Basin may result from a low degree of isolation of these areas. This explanation may also apply to Wassuk alpine plants because a large fraction of species in the range are not restricted to the alpine zone. Based on descriptions in Munz (1959), 65 percent of the taxa are presently found below 2440 m elevation in California, and only one species (*Poa rupicola*) is not reported below 3350 m. In the Wassuk Range, there is a relatively small group of species that appears restricted to the alpine zone, including *P. rupicola, Trisetum spicatum, Oxyria digyna,* and *Draba crassifolia*. Most species extend into the subalpine zone or lower. A migration path at 1950 m elevation is possible between the Wassuk Range and the nearest alpine area in the Sweetwaters. Under present climatic conditions, 36 percent of Wassuk alpine species could move freely between alpine areas in the two ranges. For an area about 100 km to the south, Wells and Berger (1967) have estimated that vegetation zones were depressed by 600 to 1000 m during Wisconsin glaciation. If a 600 m depression occurred along the East Walker River drainage, 74 percent of the Wassuk Range alpine flora could have migrated overland from the Sweetwater Range; with a 1000 m depression, all but four species could have moved across this route.

Wassuk Range plants that are generally restricted to very high elevations are all widely distributed arctic-alpine species. Thus, their identity can provide no clue as to the route by which they moved into the Wassuk Range.

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ANNOUNCEMENTS

HUNT FELLOWSHIP

The Hunt Institute invites applications for 1980–1981 research fellowships for those with a recent Ph.D. or other appropriate terminal graduate study. Tenure normally is limited to one year in the areas of history of botany, botanical biography and iconography, botanical bibliography, or history of botanical art and illustration. Fellows undertake research projects of their own choice, working closely with senior Institute faculty.

The fellowship will be awarded for the academic year with a stipend of $10,000. Applicants should submit a curriculum vitae, names of three references, copies of any published work, and a brief description of the proposed research project. Application deadline is 1 April 1980, with selection by 1 May 1980. Direct inquiries about possible projects and all application material to Dr. Robert W. Kiger, Director, Hunt Institute, Carnegie-Mellon University, Pittsburgh, PA 15213.

NOMINATIONS FOR LAWRENCE MEMORIAL AWARD

The Award Committee of the George H. M. Lawrence Memorial Fund solicits nominations for the 1980 Lawrence Memorial Award. The purpose of the award is to support *travel for doctoral dissertation research* in systematic botany or horticulture or in their history. It is expected that the 1980 award will amount to $1000 for travel during the two-year period from date of award.

Major professors and other faculty are urged to submit letters of nomination for outstanding doctoral students who have achieved official candidacy for their degrees. A nomination may take the form of a letter that covers supporting materials prepared by the candidate. Submitted materials should describe briefly but clearly the candidate's program of research and how the travel enabled by the award would contribute significantly to its quality. They should be received no later than 1 April 1980. The awardee will be selected by 1 May 1980. All communications regarding the Fund and Award should be directed to Dr. Robert W. Kiger, Director, Hunt Institute, Carnegie-Mellon University, Pittsburgh, PA 15213.

VARIATION IN BROMUS TECTORUM (POACEAE) IN EASTERN WASHINGTON

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ABSTRACT

Four local populations of *Bromus tectorum* L. in eastern Washington display significant phenotypic differences for 71 characters as evaluated with the mean and standard deviation of the dissimilarity matrix. Analysis of change in sample size showed that ten individuals per population is sufficient to produce replicable results. Within-population variation in vegetative characters may correlate with habitat heterogeneity. Two contiguous populations differ in inflorescence characters that are not as readily altered by habitat heterogeneity. This differentiation may be the result of breeding system flexibility in *Bromus tectorum*.

Bromus tectorum L., cheatgrass or downy brome, has become a dominant member of many disturbed steppe communities in eastern Washington (Daubenmire, 1970) and Oregon (Franklin and Dyrness, 1973) since introduction from Eurasia in about 1890 (Stewart and Hull, 1949). This autumn-germinating annual is reputed to exhibit only a small degree of morphological variation. Hitchcock (1950) found variation in characters such as lengths of panicle, spikelet, glume, lemma, and awn. Hurlbert (1955) claimed variation only in plant height, lemma pubescence, and palea pubescence.

Several attempts have been made to quantify variation of grasses. Morishima and Oka (1960) used factor analysis and Sokal's weighted-group method with 42 characters to produce phenograms for species of *Oryza*. A probabilistic index with 38 characters was used to produce phenograms of populations of *Sorghum bicolor* (Clifford, 1964, 1965; Clifford et al., 1969; Clifford and Goodall, 1976). Baum (1977) used numerical techniques to circumscribe the tribe Triticeae. Neighbors (1977) sampled populations of three species of *Agrostis* to circumscribe the taxa. Using the same character list and analyses Dobrowolski (1979) sampled 50 sites with 12 plants each of *Agropyron spicatum* (Pursh) Scribn. in a study of intraspecific variability.

Using individual plants as OTUs, morphological dissimilarities within populations can be summarized by the mean and standard deviation of the values in the dissimilarity or distance matrix (Gilmartin, 1969, 1974, 1976, 1977; Adams, 1977). Heretofore, this method has not been applied from an ecological perspective to compare variation of conspecific populations in different habitats. This investigation addresses two main questions. How does sample size affect the estimate of overall variation within populations? Do differences

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in habitat between local populations alter the phenotypic mean or variance of the population?

METHODS

Plants from four eastern Washington populations of *Bromus tectorum* were analyzed. Two populations, P1 and P2, are from Pullman, Whitman Co. (S32, T15N, R45E), a third (A) is from Albion, Whitman Co. (S35, T16N, R44E), and a fourth (H) is from Hooper, Adams Co. (S25, T15N, R37E). P1 was at the crest of a NE-facing slope and covered 10 m^2. P2 was 200 m downslope from P1 adjacent to an abandoned roadway and covered 50 m^2. The soil at both sites is a silt loam. The Albion population covered 250 m^2 at the base of a hill in a large abandoned wheat field with a silt-loam soil. All three sites are within the *Festuca idahoensis–Symphoricarpos albus* zone (Daubenmire, 1970), are located on severely disturbed soils, and are dominated by *Bromus tectorum*. The Hooper site (*Agropyron spicatum–Festuca idahoensis* habitat type and zone) is also dominated by *Bromus tectorum*. It is 75 km west of Pullman along a highway roadbank and covers 100 m^2. The soil is a shallow loam with pebble-sized basalt included. Annual precipitation at Hooper is 30 cm or about 20 cm less than Pullman or Albion.

Prior to panicle shattering in June, 1977, approximately 2500 plants at each of the four sites were clipped at the soil surface and bagged in bulk. In the lab plants were separated and bagged individually. Most plants remained intact, but 12 with noticeable panicle or tiller damage were discarded. Each population was then subsampled by choosing every hundredth plant from the separated material, yielding a sample size of 24.

A set of characters was selected with a number of putatively independent, informative, and easily determined character states. The character list used was constructed specifically for the family Poaceae and included inflorescence (49), vegetative (18), and ecological (4) characters (the list is available upon request). Vegetative traits were 42 percent quantitative, requiring measurement, and inflorescence traits were 37 percent quantitative. Data were analyzed using the computer program DISTA (Gilmartin, 1974), which calculates the phenetic distance or dissimilarity between members of all pairs of OTUs. This value is unitless and is equal to $-\log_2$ of the similarity index (Rogers and Fleming, 1964). The similarity index is the sum of the number of matched characters divided by the sum of the character states that are compared. The mean phenetic distance, MPD, indicates the dissimilarity among OTUs while the standard deviation, SD, represents the amount of heterogeneity about this mean. In order to compare phenetic results for taxa, it is necessary to standardize the statistic used for the comparison. For this purpose, I employed the coefficient of phenetic variation, CV, which is the simple unitless ratio (SD/MPD) × 100.

By using two subsets of characters, inflorescence traits and vegetative traits, that contrast in their proportion of phenotypically plastic traits (Dobrowolski, 1979), it is possible to determine whether the apparent differences between two populations are more a function of plastic or genetic traits. It is assumed that vegetative characters respond most readily to habitat differences because characteristics resulting from extended periods of meristematic activity (e.g., size) are more subject to direct effects of the environment and are more flexible than are characteristics which form more rapidly (e.g., reproductive traits: Stebbins, 1950; Bradshaw, 1965).

Each population has unique MPD, SD, and CV. When populations are pooled these statistics change. Only if the statistics differ substantially are the two populations considered distinct. The percent change from individual population samples to pooled samples is used as a measure of heterogeneity.

Adequate sample size for each population was determined by generating the summary statistics with eight different subsets of plants each containing a different number of plants chosen randomly by the DISTA program. There was no interpopulation variation in the four sample size curves. Both MPD and SD peaked at a sample size of ten plants and remained essentially stable with larger samples, indicating that ten plants represent well the variation in these populations. Accordingly, summary statistics were generated using ten OTUs per population.

It is difficult to attach a biological significance to differences in MPD values. In this case, as the number of OTUs increases, the values for MPD approach an asymptote. Variability in MPD beyond a sample size of ten is within 3.2 percent of the maximum. Similarly, values for SD vary within 3.1 percent of the maximum. In determining the minimum sample size for intragroup determinations, any difference in MPD exceeding these limits is considered here to be biologically significant.

RESULTS

Table 1 shows the summary statistics MPD, SD, and CV for populations separately and pooled using the full set of characters and the subsets of inflorescence and vegetative characters. Populations exhibited varying degrees of dissimilarity as measured by all 71 characters. Comparisons of within-population variation of P1, P2, and H and comparisons of A, H, and P1 yielded no biologically significant differences in MPD. Populations A and P2 exhibit the greatest difference in populational phenotypic variation.

Albion and Hooper are the largest populations and have the lowest

TABLE 1. SUMMARY STATISTICS GENERATED BY DISTA PROGRAM FOR TEN PLANTS PER POPULATION OF *Bromus tectorum*. Stat = summary statistic; ALL = all 71 characters; % = mean percent difference between members of pairs of populations and the equivalent pooled population; INFL = only inflorescence characters; VEG = only vegetative characters; MPD = mean phenetic distance; SD = standard deviation; CV = coefficient of phenetic variation; P1 = Pullman #1 population; P2 = Pullman #2 population; P1 + P2 = pooled P1 and P2; A = Albion population; H = Hooper population; A + H = pooled A and H.

		Character subset						
Stat	Population	ALL	%	INFL	%	VEG	%	INFL + VEG
MPD	P1	0.52	—	0.61	—	0.52	—	0.55
	P2	0.55	—	0.54	—	0.51	—	0.60
	P1 + P2	0.69	25	0.78	30	0.56	9	0.65
	A	0.47	—	0.47	—	0.43	—	0.49
	H	0.49	—	0.45	—	0.59	—	0.53
	A + H	0.54	13	0.54	17	0.66	35	0.59
	P1 + P2 + A + H	0.88	—	0.79	—	0.98	—	0.86
SD	P1	0.10	—	0.23	—	0.12	—	0.10
	P2	0.11	—	0.21	—	0.13	—	0.12
	P1 + P2	0.21	53	0.28	25	0.16	25	0.16
	A	0.11	—	0.15	—	0.14	—	0.12
	H	0.11	—	0.13	—	0.21	—	0.12
	A + H	0.13	15	0.17	24	0.29	—	0.14
	P1 + P2 + A + H	0.36	—	0.29	—	0.45	—	0.32
CV	P1	19	—	38	—	24	—	19
	P2	21	—	39	—	26	—	21
	P1 + P2	31	—	36	—	28	—	25
	A	24	—	32	—	32	—	25
	H	22	—	30	—	36	—	22
	A + H	24	—	31	—	39	—	25
	P1 + P2 + A + H	41	—	37	—	46	—	37

overall MPDs (0.47, 0.49) and the lowest SDs for inflorescence traits (0.15, 0.13). However, H had the greatest variability among vegetative traits (MPD = 0.59; SD = 0.21). Using only inflorescence traits, pooling the two Pullman populations resulted in the greatest amount of interpopulation variation (MPD = 0.78) and the pooled data are significantly different from pooled A and H (MPD = 0.54).

The floral plus vegetative character analyses yielded biologically significant results. The Albion population exhibited the least variation, which is probably due to the small MPD exhibited by this population when the vegetative characters alone were analyzed. Omitting the four ecological characters has little effect on the statistics as there is no significant difference between analyses using this set of characters and those statistics resulting from analyses using all characters for any one population.

Discussion

The method of population sampling used in this study yields many data from few individuals and contrasts with the method of Mack and Harper (1977), which measures only three characters for a large number of individuals or the method of Hickman and Johnson (1969) who emphasized 16 variable characters (of 29) in a study of geographic variation. Common methods treat the measurements themselves as the primary data base whereas interpretations in this work are derived only from the resulting dissimilarity values.

Using vegetative traits only, A and H showed an increase in SD of 27 to 52 percent when pooled. These differences suggest responses to the environmental heterogeneity between the two sites. The two habitats are sufficiently different environmentally (Daubenmire, 1956, 1970) to produce different phenotypes. Although intermediate in size, H exhibited the greatest variability of vegetative traits (SD = 0.21). Perhaps this is due to greater microhabitat heterogeneity than in the Albion or Pullman habitats.

The two Pullman populations have differentiated a great deal (53 percent difference in SD for individual populations versus pooled populations). Inflorescence and vegetative traits contributed equally to this difference. The smaller differences in vegetative traits suggest that their habitats are more similar than those of A and H. Nevertheless, some differentiation in the inflorescence traits is apparent (30 percent difference).

This differentiation may be the result of the breeding system exhibited by *Bromus tectorum.* Hurlbert (1965) stated that he frequently observed self-pollination but that outcrossing was also common. Habitual inbreeders are commonly highly successful weeds (Harper, 1978) and, in habitually inbreeding taxa, variation between populations is often discontinuous and morphologically discrete, uniform populations may form (Davis and Heywood, 1963). Because neither discontinuous variation nor morphologically uniform populations have been found here, the results support the contention of Ehrlich and Raven (1969), who emphasize the local interbreeding population and the importance of different selection regimes over gene flow in causing evolutionarily important differentiation between populations.

Mean phenetic distance within populations of *Bromus tectorum* (average MPD = 0.50) is less than that for three species of *Agrostis* (0.73: Neighbors, 1977) and for families Asclepiadaceae, Apiaceae, and Fabaceae (Gilmartin, personal communication) but are about the same as for Bromeliaceae (Gilmartin, 1974). Moreover, the dissimilarity between populations within the species (MPD = 0.88; CV = 41) approaches that exhibited within species for the Bromeliaceae (MPD = 0.70; CV = 35: Gilmartin, 1974). Certainly four populations do not represent the variation in this wide-ranging species as shown by the range in intrapopulational MPD (0.37–0.64) of *Agropyron spicatum* (Dobrowolski, 1979) but quantification of variation can be used in taxonomic and ecologic contexts to clarify the environmental responses within and between populations of these and other plants.

ACKNOWLEDGMENTS

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REVIEW

Vegetation Dynamics. By JOHN MILES. 80 pp. Outline Studies in Ecology, Halsted Press, John Wiley & Sons, New York. ISBN 0-470-26504-3.

This small book provides a brief but comprehensive discussion of the principles of plant ecology. Although the author is British, the book presents a broad and unbiased approach to the various ideas of American as well as European ecologists. The book is written in an elementary way with simple vocabulary. The clear and uncluttered presentation of principles, concepts, and theories of plant ecology is the outstanding feature of the book, something few writers accomplish. As a result the book would be a very useful aid as the primary or supplementary text in undergraduate as well as advanced courses in plant ecology and vegetation management.

The unsatisfactory portions of the book are minor. They include too many examples from the heather (*Calluna vulgaris*) moorlands, omission of a discussion of gradients or continua in time as well as space, and inadequate discussion of seed production. In addition, the author seems to underplay the role of chance—for example, which plant species arrive first in recolonization episodes and how this relates to the season and type of disturbance; apparently doesn't acknowledge that some vegetational types are dependent upon disturbances for their continuance; and seems to be unaware of "build and tear" plant systems. But in spite of these minor deficiences, the book is refreshing to read and use because it highlights basic principles and clearly and simply presents essential similarities or differences among theories, approaches, and concepts of plant ecology.—RICHARD J. VOGL, Department of Biology, California State University, Los Angeles 90032.

ERRATA

vol. 26, p. 180, line 8. The correct address for TOM WENDT and EMILY J. LOTT is Rama de Botánica, Colegio de Postgraduados, Chapingo, Edo. de México, México.

vol. 23, p. 185, line 22. For "this species" read "the type variety".

vol. 20, p. 246, line 27. For "Texas" read "Arizona" (affects the type locality for *Oenothera platanorum* Raven & Parnell).

VEGETATIONAL CHARACTERISTICS OF TWO STANDS OF JOSHUA TREE WOODLAND

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ABSTRACT

Quantitative study of two superficially similar stands of Joshua tree woodland showed much variation. One stand included Joshua trees and junipers in the tree layer. The other stand also included piñon pine and desert scrub oak and had a different order of shrub importance values. Both stands contained shrubs characteristic of other plant associations. A list is presented of the annuals and biennials in flower in May, 1978.

Although Joshua tree is considered well known, Vasek and Barbour (1977) presented the first quantitative data published for any Joshua tree woodland—from a single stand in northeastern San Bernardino County. In May, 1978, we surveyed two stands of Joshua tree woodland on the road to Key's View, 6.4 km south of Cap Rock in Joshua Tree National Monument, Riverside County, at an elevation of 1470 meters. This paper presents an analysis of two stands of Joshua tree woodland including trees, shrubs, and those herbs flowering in May, 1978.

Joshua tree woodland is desert scrub vegetation of *Yucca brevifolia* associated at its upper levels with *Pinus monophylla, Juniperus californica,* or *Quercus turbinella,* and at its lower limits with *Larrea tridentata.* Beneath the open canopy are a variety of shrubs and, in good rainfall years, many flowering herbs. Treatments of this vegetation may be found in Webber (1953), Benson and Darrow (1954), Miller and Stebbins (1964), Jaeger (1957, 1967), and Vasek and Barbour (1977).

METHODS

We took 40 point-centered-quarter samples in each of two seemingly similar stands that we consider typical of this elevation in the Joshua tree area as studied over a period of 30 years (e.g., Juhren et al., 1956). In each 90° quarter around each point, we determined crown cover and point-to-plant distance for the nearest tree and shrub. Quarters were set on compass directions starting 50 m from the road in four transects spaced 20 m apart. Each successive point was located so that no plant was counted twice. We used crown cover rather than stem diameter because the junipers have many trunks and the diameter of Joshua trees changes in relation to stem water content. We calculated crown cover by taking the mean of the largest and smallest diameters of each tree and shrub crown. From these data we calcu-

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lated absolute density, cover, and frequency and derived an importance value (IV) based on relative density, cover, and frequency (Mueller-Dombois, 1974).

Stand one, east of the road, had a gentle (5°–8°) slope to the southeast and extended 800 m along the road and 770 m eastward. Stand two, west of the road and approximately 20 m higher, was flatter and extended 700 m along the road and approximately 600 m westward. Each was dominated in appearance by Joshua tree. Soils of both stands are fine, gravelly, decomposed granite.

The total rainfall from June, 1977 thru April, 1978 was 22.9 cm, 13.2 cm more than normal. Monthly totals with departure from mean in parentheses were: J 0.00 (−.05); J 1.42 (.10); A 9.35 (7.59); S 0.13 (−.71); O 0.00 (−1.17); N 0.00 (−.78); D 1.47 (.41); J 5.26 (4.16); F 2.31 (1.83); M 2.26 (1.61); and A 0.66 (.38) cm.

Mean annual temperature in this area is 20.2°C and this year's departure from normal was only −.5°C. Mean monthly temperatures and departure from normal beginning in June 1977 were: J 29.2 (1.8); J 31.5 (.11); A 30.2 (−.24); S 26.1 (−.79); O 21.9 (1.2); N 15.7 (1.8); D 12.6 (2.8); J 9.8 (.57); F 12.1 (.49); M 15.3 (1.24); A 17.6 (−.84)°C.

All temperature and rainfall measurements are from the Twentynine Palms weather station, 25 km northeast of the study site.

RESULTS AND DISCUSSION

Vegetational characteristics of the two adjacent stands are presented in Table 1. Stand one included Joshua trees and juniper in the tree layer and stand two included piñon pine and desert scrub oak as well. Importance values in the table are calculated for the whole stand (trees plus shrubs) for comparison with Table 24-6 in Vasek and Barbour (1977). Their IV for Joshua tree is 4 (density of 125/ha), compared with our IV of 27 (60/ha) in stand one and 19 (50/ha) in stand two.

These stands are considered phases of Joshua tree woodland as described by Munz and Keck (1940) because stands include the indicator species *Yucca brevifolia, Juniperus californica, Salazaria mexicana, Lycium cooperi, Eriogonum fasciculatum,* and *Tetradymia spinosa* var. *longispina.* Stand two has the following piñon-juniper woodland indicator species: *Pinus monophylla, Juniperus californica, Quercus turbinella* subsp. *californica, Purshia glandulosa,* and *Yucca schidigera.* Thus, stand two may be considered transitional. Other understory shrubs are characteristic of other communities. For example, Benson and Darrow (1954) indicate that *Thamnosma montana* occurs at 600–1200 m on rocky or gravelly desert slopes and mesas and *Haplopappus linearifolius* occurs in sagebrush and creosote bush deserts. Vogl (1976) lists *Purshia glandulosa* and *Yucca schidigera* for piñon-juniper woodland and states that *Ephedra viridis* occurs in higher creosote bush deserts. Other examples are *Coleogyne ramosissima, Purshia glandulosa,* and *Tetradymia spinosa* var. *longispina,*

TABLE 1. VEGETATIONAL CHARACTERISTICS FOR TWO STANDS OF JOSHUA TREE WOODLAND, LOST HORSE VALLEY, JOSHUA TREE NATIONAL MONUMENT, CALIFORNIA. Density = #/ha; Cover = m^2 crown cover/ha; Frequency = points of occurrence/(total points × 100); IV = importance value. Roman numerals identify stands.

	Density		Cover		Frequency		IV	
Taxon	I	II	I	II	I	II	I	II
Trees								
Juniperus californica	60	80	600	500	90.0	80.0	40	37
Pinus monophylla		10		200		20.0		11
Quercus turbinella subsp. californica		30		200		45.0		18
Yucca brevifolia	60	50	100	100	95.0	58.0	27	19
Shrubs								
Coleogyne ramosissima	70	80	60	800	4.0	40.0	3	60
Echinocereus mojavensis	20	20	<0.1	<0.1	2.5	2.5	1	2
Encelia farinosa		30		20		12.5		4
Ephedra viridis	60	130	350	280	37.5	17.5	31	17
Eriogonum fasciculatum	2140	960	1320	520	77.5	57.5	98	62
Gutierrezia microcephala		30		20		5.0		2
Haplopappus linearifolius	20	160	10	140	2.3	15.0	1	13
Hymenoclea salsola	290	80	230	50	12.5	15.0	16	8
Lycium cooperi	60		30		5.0		3	
Nolina parryi		50		50		7.5		6
Opuntia basilaris	60		60		2.5		4	
O. echinocarpa	130		70		7.5		7	
Prunus fasciculata		20		80		2.5		3
Purshia glandulosa		50		90		7.5		7
Salazaria mexicana	630	30	320	40	25.0	2.5	27	2
Tetradymia spinosa var. longispina	130		70		7.5		7	
Thamnosma montana	920	350	230	200	42.5	35.0	35	26
Yucca schidigera		40		20		5.0		2

indicators of sagebrush scrub, and *Hymenoclea salsola, Encelia farinosa,* and *Opuntia basilaris,* indicators of creosote bush scrub. These scrub communities are at lower elevations than the present study site and the occurrence of these species here must indicate suitable understory microenvironments.

The order of importance values for shrubs is different in the two stands. When shrubs alone are compared, the sequence in stand one is: *Eriogonum fasciculatum, Thamnosma montana, Ephedra viridis, Salazaria mexicana, Hymenoclea salsola, Coleogyne ramosissima, Haplopappus linearifolius.* In stand two the sequence is: *Eriogonum fasciculatum, Coleogyne ramosissima, Thamnosma montana, Ephedra viridis, Haplopappus linearifolius, Hymenoclea salsola, Salazaria mexicana.* The greater importance of *Coleogyne ramosissima* and *Hymenoclea salsola* and the presence of *Eriogonum fasciculatum, Gutierrezia microcephala, Prunus fasciculata, Purshia glandulosa,* *Nolina parryi,* and *Yucca schidigera* in stand 2 indicate more diverse topographic microenvironments there.

Rain was much above average, especially in August, 1977 and January, 1978, so winter annuals and some perennial herbs were in flower at the time of this study. Annuals encountered in sampling were *Anisocoma acaulis, Baileya pleniradiata, Chaenactis fremontii, Eriophyllum pringlei, E. wallacei, Layia glandulosa, Malacothrix glabrata* (Asteraceae); *Amsinckia tessellata, Cryptantha similis, Cryptantha* sp. (Boraginaceae); *Nama demissum, Phacelia crenulata, P. distans, P. fremontii* (Hydrophyllaceae); *Salvia columbariae* (Lamiaceae); *Camissonia claviformis, Oenothera deltoides* (Onagraceae); *Gilia* sp., *Langloisia mathewsii, Linanthus aureus* (Polemoniaceae); *Chorizanthe thurberi, Eriogonum pusillum* (Polygonaceae).

Perennials and biennials were *Lomatium mohavense* (Apiaceae); *Baileya multiradiata,* (Asteraceae); *Arabis holboellii* var. *pinetorum, Erysimum capitatum, Lepidium* spp. (Brassicaceae); *Euphorbia polycarpa* (Euphorbiaceae); *Astragalus lentiginosus* var. *variabilis, Astragalus* sp., *Lupinus* sp. (Leguminosae); *Mirabilis bigelovii* (Nyctaginaceae); *Castilleja* sp., *Penstemon* sp. (Scrophulariaceae).

Broader information is needed on the herbaceous species to determine whether any are indicator species for Joshua tree woodland.

It is obvious from a comparison of our two stands with that of Vasek and Barbour (1977) that much variation occurs in Joshua tree woodlands that seem superficially similar. We conclude that many more data are needed before stand variation in this association is understood.

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NOTEWORTHY COLLECTIONS

OPHIOGLOSSUM LUSITANICUM L. subsp. CALIFORNICUM (Prantl) Clausen (OPHIOGLOSSACEAE).—USA, CA, Merced Co., along Co. Rd. J-16 (Merced Falls Rd.), ca. 2.4 mi (3.8 km) w. of North Side Canal bridge, w.- to s.w.-facing slope ca. 300 m s. of road and along fence row, 25 Apr 1978, *T. Duncan* (with *W. H. Wagner, Jr., A. Smith, T. Lowrey, L. Cserr*) *2759* (UC); Mariposa Co., above Lake McSwain along Merced River at Lake McSwain Rd. and Lake McClure Rd., ca. 0.5 mi (0.8 km) e. of intersection with Co. Rd. J-16, 25 Apr 1978, *Duncan* (et al.) *2757* (UC); Stanislaus Co., ca. 1 mi (1.6 km) n. of La Grange on Co. Rd. J-59 (La Grange Rd.), gravelly s.e.-facing slope above brook ⅛ mi (0.2 km) e. of road, 25 Apr 1978, *Duncan* (et al.) *2756* (UC). Basionym: *Ophioglossum californicum* Prantl; for a taxonomic account, see Clausen [Mem. Torrey Bot. Club 19(2):1–177. 1938].

Previous knowledge. Recorded by Clausen (op. cit., p. 160) from Amador, Monterey, and San Diego cos., also from the States of Baja California Norte and Mexico, Mexico; other subspecies occur in South America, Europe, Africa, Asia, Australia, and New Zealand. Howell and Long [Four Seasons 3(3):1–18. 1970] reported a 1970 collection from near La Grange by Perry Allen, and we have relocated this or a nearby population (cited above). There is also a sight-record from Tuolumne Co. by Perry Allen in 1969 (California Native Plant Society files). [Herbaria consulted: CAS, DS, JEPS, LA, OBI, POM, RSA, SD, UC; published sources: Clausen (op. cit.); Munz, A Calif. fl. 1959; Munz, A fl. S. Calif. 1974; Witham, Ferns San Diego Co. 1972.; Howell and Long (op. cit.); Howitt and Howell, Wasmann J. Biol. 22:1–184. 1964.] The only other species of Adder's-tongue fern in California is *Ophioglossum vulgatum* L., known from a single collection near Sisson, Siskiyou Co., collected in 1894. That species differs in having much larger, more elliptical blades.

Significance. This is the first report of the species from Merced and Mariposa counties. Several old collections are known from the vicinity of Ione, Amador Co. (the most recent collection in 1948 by Wagner), but recent attempts (by Wagner, 1975, and Smith, 1978) to relocate these populations have failed. Herbarium labels and published literature indicate that in the past this species has usually been collected around (at the margins of) vernal pools. However, it now appears that this may be only a "secondary" habitat. The "primary" habitat, at least in the Sierra foothills, seems to be in the Foothill Woodland Community (Munz, 1959) on s.-facing slopes of grazed pastures, with a sparse mixture of annual grasses (*Vulpia* sp., *Bromus* sp.) and forbs (*Erodium* sp., *Crepis* sp., *Juncus* sp., *Lepidium nitidum, Selaginella hansenii, Githopsis* sp., *Orthocarpus* sp., *Trifolium* sp., *Silene* sp., *Cerastium* sp.) with scattered trees of *Quercus douglasii*. The soil has a loose granitic gravel on the surface. Nearly all collections in the Sierra foothills have been made from February through April; after that the soil dries, the plants wither, and the aboveground parts die. During the summer, the ground is hard and baked, and there is no evidence of the plants.

Ophioglossum lusitanicum subsp. *californicum* (as *O. californicum*) has been included on the rare and endangered list of plants for California (Powell, Inv. rare and endangered vasc. pls. California. CNPS Spec. Publ. 1. 1974) and is under review as threatened by the Federal Government (Federal Register 40(127):27844. 1975). In all likelihood it is simply overlooked by collectors. The young leaves are spatulate, 0.5–2.5 (5.0) cm long, often somewhat conduplicate, and appear much like leaves or cotyledons of some small monocots. Fertile spikes are produced on fewer than 25 percent of the plants (perhaps less than 10 percent). Once the "primary" habitat was discerned (quite by accident), the authors were able to find the plant at four widely separated localities in three counties. Hence, we suspect that it may be a common plant throughout the Sierra foothills (60–300 m) and perhaps also in the coastal ranges. Invariably, it is colonial, no doubt spreading by vegetative proliferation from the roots. Thomas (Southw. Naturalist 24:395–396. 1979; Sida 8:113. 1979) has recently found other species of *Ophioglossum* in Texas and North Carolina to be more common than previously supposed.

Collections from San Diego Co. have also been made from at least two different habitats. Most of the older collections are from margins of vernal pools, especially on Kearny (often spelled Kearney) Mesa. More recent collections are often from slopes in chaparral in sun or partial shade of such plants as *Rhus laurina, Salvia, Ceanothus, Cercocarpus, Adenostoma,* and *Eriogonum.* Several times it has been described as growing in mats of *Selaginella cinerascens.* Altogether, *Ophioglossum* has been collected at more than a dozen sites in San Diego Co., but many of these are now in or near areas where heavy pressure for development exists.—ALAN R. SMITH, University Herbarium, University of California, Berkeley 94720; WARREN H. WAGNER, JR., Department of Botany, University of Michigan, Ann Arbor 48109; and THOMAS DUNCAN, Department of Botany and University Herbarium, University of California, Berkeley 94720. (Received 24 Aug 1979; accepted 7 Dec 1979.)

NOTES AND NEWS

SPECIFIC STATUS FOR *Encelia californica* VAR. *asperifolia* (COMPOSITAE: HELIANTHEAE).—In 1913, S. F. Blake described a collection (*Anthony 292*; lectotype here designated: GH!; isotypes, F!, US!) from Cedros Island, Baja California Sur, as *Encelia californica* var. *asperifolia.* It is unclear to us why he chose to assign it varietal status under *E. californica* rather than specific status, as he listed a number of characters by which it was distinct from *E. californica*: bushier habit, smaller capitula and leaves, rougher pubescence on stems, leaves, and involucral bracts, and shorter involucres. To this we can add that it has more slender peduncles and, whereas the petioles of var. *californica* are stiff, straight, and diverge from the stem at an ascending 45° angle, those of var. *asperifolia* are more lax, curved, and diverge at nearly a 90° angle. In addition, preliminary evidence indicates substantial differences in the flavonoid aglycones of the two taxa.

The habitat differences are even more striking. Variety *californica* occurs in coastal sage and chaparral from Santa Barbara Co., California, south to El Rosario, Baja California. Variety *asperifolia* is found in the central desert of the Lower California peninsula, south to the Sierra Vizcaíno. The taxa marginally come in contact in the region just south and east of El Rosario; this region also marks the southernmost extent of the coastal sage and the beginning of the desert (Axelrod, Amer. J. Bot. 65:1117–1131. 1978; Shreve and Wiggins, Veg. and fl. Sonoran Desert. 1964). In this region of contact the two taxa interact in a manner like that observed for other well-differentiated species of *Encelia.* There is no gradual transition between the taxa in either morphological or ecogeographic features. Their area of sympatry consists of a very narrow zone (no more than 500 m wide on Mex. hwy 1, 8.4 mi (13.4 km) e. of El Rosario). Within this zone the taxa hybridize; the hybrid individuals (F_1's and recombinants) are essentially confined to areas of natural and man-made disturbance. We have not found any other plants having morphology intermediate between the taxa.

Considering all available information against the background of variation within the genus as a whole, we believe that the variety *asperifolia* is best treated as a distinct species.

Encelia asperifolia (S. F. Blake) Clark & Kyhos, stat. nov.

Based on *Encelia californica* Nuttall var. *asperifolia* S. F. Blake, Proc. Amer. Acad. Arts 49:368. 1913.—CURTIS CLARK and DONALD W. KYHOS, Department of Botany, University of California, Davis 95616. (Received 12 Oct 1979; revision received and accepted 19 Oct 1979.)

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FIRE ECOLOGY OF A MONTANE PINE FOREST, JUNIPERO SERRA PEAK, CALIFORNIA

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Abstract

Between 1640 and 1907 fires hot enough to produce basal scars on pines in a small isolated *Pinus lambertiana* forest in the Santa Lucia Range of central California occurred on the average of once every 21 years. Excepting two small lightning fires that were quickly extinguished, no fires occurred in the pine forest after 1907 until the lightning-caused Marble-Cone fire burned the entire forest in 1977. This was the most intense burn recorded within the life of the present forest. It caused significant loss of pines, particularly within the 40 percent of the forest on the north summit above 1600 m elevation. Changes in forest composition resulting from the Marble-Cone fire suggest that several more fires following 50–75 year intervals may eliminate *P. lambertiana* forest above 1600 m on Junipero Serra Peak.

Recurrent light fires are essential for development and maintenance of montane pine forest in the western United States (Cooper, 1960). Fires originally set by lightning and Indians removed dead and senescent trees, furnished a desirable seedbed, and thinned the subsequent regeneration. These periodic surface fires kept fuel levels so low that conflagrations were rare (Cooper, 1961). In California such low intensity fires have been documented for pine and mixed conifer forests of the Sierra Nevada (Wagener, 1961; Biswell, 1967; Kilgore and Taylor, 1979), north Coast Ranges (Biswell, 1963), Mt. Pinos region (Vogl and Miller, 1968), and San Bernardino Mts. (McBride and Laven, 1976). The role of fire in disjunct forests of the central California Coast Ranges has remained unstudied.

Junipero Serra Peak (J. S. Pk.) is the highest point (1788 m) in the Santa Lucia and adjacent ranges (Griffin, 1975a). Montane pine forest dominated by *Pinus lambertiana* covers 146 ha on the peak's north slope (Fig. 1). The J. S. Pk. and nearby Cone Peak forests are isolated from the next *P. lambertiana* stands by 220 km (Griffin and Critchfield, 1972). The J. S. Pk. pines are surrounded by a vast area of scrubby mixed hardwood forest and chaparral. We evaluate the fire history of the pine forest and examine the effect of past fires on forest composition. An analysis of forest plots before and after the severe Marble-Cone fire of 1977 is given.

Madroño, Vol. 27, No. 2, p. 49–60, 16 April 1980

LOCAL FIRE HISTORY

The fires that scarred old *P. lambertiana* trees on J. S. Pk. span four land management eras: Indian (before 1800); Spanish and Mexican (1800–1847); American settlement (1848–1906); and U.S. Forest Service (since 1907). Through all four eras both lightning strikes and humans started fires on the peak or close enough to reach the peak during hazardous fire periods.

Three Indian groups held territory around J. S. Pk.: Esselens, Costanoans, and Salinans (Kroeber, 1925). The peak had religious significance to the Salinans, and the southwestern base of the mountain is rich in Salinan materials, including two prehistoric settlements (Lick Observatory, 1977). Nothing is known of Esselen fire habits, but widespread burning in grassland and oak woodland is documented for Costanoans and Salinans (Gordon, 1977). Reports of Indians burning chaparral or forest vegetation types in the interior of the Santa Lucia Range are lacking (Burcham, 1959); however, Indian burning in grassland or oak woodland could have spread long distances to the J. S. Pk. forest during the long dry seasons.

We also know few details about the local burning practices of the Spanish and Mexicans or even the first American ranchers who replaced them. There are conflicting views on whether they started more or fewer fires than the Indians. But in the 1890's government files and newspapers began to record specific large fires in the Santa Lucia mountains. An 1894 fire burned for weeks covering the upper watershed of every permanent stream in the central Santa Lucia mountains (Plummer and Gowsell, 1905). Many settlers started fires that were "allowed to run" so as to facilitate passage of their livestock. In July, 1903, an escaped campfire in the north-central Santa Lucia mountains burned for months, covering an area about 10 km wide extending 20 km to the coast (Sterling, 1904). Another fire in October, 1906, burned about 55,000 ha stretching 39 km across the northern Santa Lucia mountains (Los Angeles Herald, 1906). While these specific fires did not reach J. S. Pk., they show that the vegetation did carry some regional fires—even when deliberate and accidental fires were so frequent that surface fuels must have been well below current levels.

Primitive fire control in the Santa Lucia Range began in 1907 with the establishment of the Monterey National Forest (now the Monterey District, Los Padres National Forest). Within the National Forest the annual burn was about 3200 ha through the 1920's but declined to about 160 ha by the 1960's (U.S. Forest Service, undated). In 1970 this trend was dramatically reversed by the man-caused Buckeye fire, which burned 24,000 ha. In 1977 the 72,000 ha Marble-Cone fire was the second largest blaze in California records (Griffin, 1978).

Until 1977 the total area burned by lightning fires in the Santa Lucia mountains was modest. About 1000 ha burned after a rash of lightning

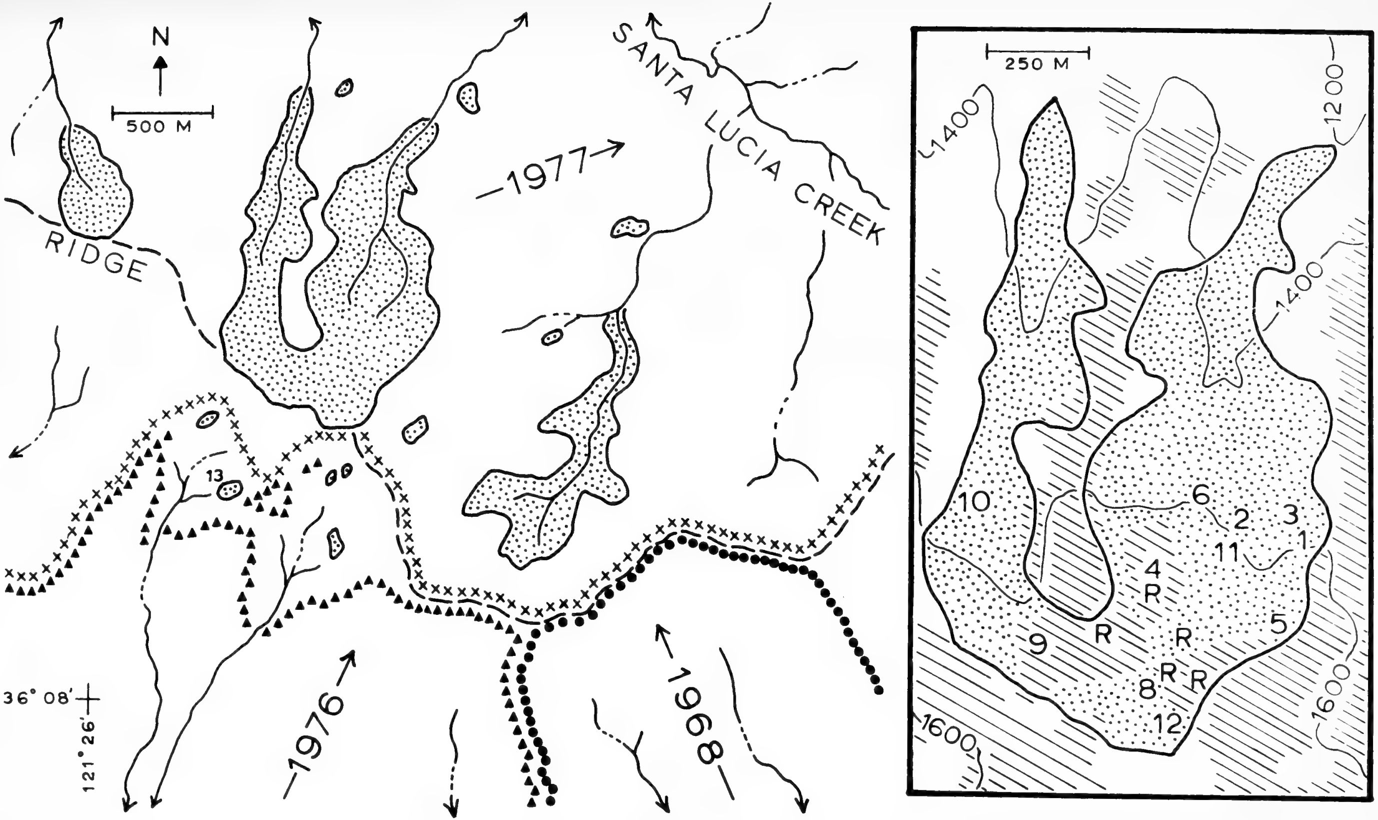

FIG. 1. Junipero Serra Peak region with distribution of *Pinus lambertiana* (stippled); edges of 1968 Rattlesnake fire (dots); 1976 Indians fire (triangles); 1977 Marble-Cone fire (×'s); and south slope outcrop plot 13. Insert shows enlargement of central pine population (stippled), 1976 stand plots (numerals), 1978 regeneration plots (R's), areas of tree and shrub canopy destroyed by crown fire (hatched), and 200-m contours.

strikes in August, 1916. Between 1931 and 1977 only 39 lightning fires were officially recorded on the Monterey District; a smaller number started on private lands adjacent to the National Forest. All these fires were extinguished while still small. If left uncontrolled, some of these could have become major fires and spread to J. S. Pk. On August 1, 1977, a lightning storm started eight fires. Four fires outside the National Forest were quickly suppressed, but four within the rugged Ventana Wilderness merged into the Marble-Cone conflagration.

Historical fires on the summit of J. S. Pk. start with a major blaze in 1901 that covered most of the mountain (Plummer and Gowsell, 1905). There are no other records until September, 1939, when lightning started a 0.4-ha fire in oak scrub on the northwest ridge. Lightning also started a 0.4-ha fire in pine forest on the north slope in September, 1959. A vehicle on Fort Hunter Liggett started the Rattlesnake fire in June, 1968. This 1300-ha fire burned up the south slope of the mountain through chaparral (Fig. 1). The man-caused 2800-ha Indians fire in May, 1976, burned up the southwestern slope of the peak through chaparral and scrubby mixed hardwood forest (Fig. 1). The Indians fire burned into the margin of the Rattlesnake burn. After burning for a week, the August, 1977, Marble-Cone fire reached J. S. Pk., skirting the Indians burn and then covering the entire north slope of the mountain (Fig. 1).

METHODS

We started mapping the J. S. Pk. pine forest on the 7.5 min Junipero Serra Peak topographic sheet in 1975 using black-and-white 1968 aerial photography and field observations. In 1976 thirteen sites representative of the pine forest diversity (Fig. 1) were analyzed using 0.07-ha plots (22.9 m × 30.5 m) with the long axis parallel to the slope direction. Shrub and herb strata were assessed using tabular comparison (Mueller-Dombois and Ellenberg, 1974). Tree species 5 cm dbh or greater were evaluated using count-plot methods for density, cover, and basal area. Heights of pines less than 5 cm were also measured. Fire dates were determined by aging fire scars on large *P. lambertiana* trees with methods similar to those of Arno and Sneck (1977).

All plots were reexamined in July, 1978, 11 months after burning. Plot 7 (not shown in Fig. 1) was unusable because of bulldozer damage during the fire, but the remaining plots were redone using 1976 methods. At this time the sampling of fire scars was increased. Patterns of fire intensity were mapped onto the same topographic sheet from color infrared aerial photography (taken 1 month after the fire) and field observations. We also established five 0.1-ha permanent plots for long-term pine regeneration studies. In 1978 and 1979, pine seedlings on each plot were counted, and shrub seedlings on plot subsamples were counted.

TABLE 1. ESTIMATED DATES OF FIRES SCARRING *Pinus lambertiana* TREES ON OR ADJACENT TO JUNIPERO SERRA PEAK STUDY PLOTS. Dates within a given row are believed to represent the same fire.

Plot 3 (1 tree)	Plot 5 (2 trees)	Plot 6 (1 tree)	Plot 8 (3 trees)	Plot 10 (2 trees)	Plot 12 (2 trees)
1977	1977	1977	1977	1977	1977
	1959				
1901	1901	1901	1901	1901	1901
	1896				1896
	1872	1872	1872	1872	1872
	1852	1853		1852	
	1840	1842	1842	1845	1843
	1820	1826	1826	1826	1825
					1812
		1809			
		1801			
1793	1791	1795	1795	1795	
	1786				
	1758	1757		1759	
				1755	
1743	1746				
	1740	1734		1739	
	1724	1717		1722	
		1707			
		1700			
	1688	1683			
		1668		1671	
		1664			
		1651			
		1640			

RESULTS AND DISCUSSION

Fire scar analysis. Intervals between fire scars on individual plots ranged from 4 to 108 years (Table 1). Eleven of the fires involved were spot fires or else not hot enough to scar trees on several plots (Table 1). Over the entire time period the average interval between scars on a given plot ranged from 19 to 78 years. Prior to fire control in 1907, 13 fires scarred trees on two or more of the six plots with an average interval between multiplot fires of 21 years (Table 1). Such fires probably would have lightly burned sizeable portions of this small pine forest. Before fire control the study tree at plot 6, which was particularly sensitive to fire, was scarred at least 18 times with an average interval of 15 years. A large proportion of the short fire intervals (10 years or less) occurred early in the record: eight before 1809, two after 1809. A decline in lightning frequency would help to explain this shift. But if the Indians started more fires than the Spanish or Mexicans, another cause could be the destruction of the Indian culture near the peak soon after 1800.

We emphasize that this sort of fire scar record is a conservative estimate of the fires in the study area. Kilgore and Taylor (1979) also stressed the difficulties in comparing fire frequencies when different sampling intensities and different habitat types were involved. Nevertheless, the 21-year average interval between multiplot fires in the J. S. Pk. pine forest before fire control may be longer than intervals in the most similar California reports: 10 years for *P. ponderosa* forest, 12 years for *P. jeffreyi* forest (San Bernardino Mts.: McBride and Laven, 1976); 6–9 years for *P. ponderosa* forest, 8–17 years for mixed conifer forest (southern Sierra Nevada: Kilgore and Taylor, 1979).

Qualitative review of the fire scar record and evidence of fire recorded higher in the boles of the pines suggest the Marble-Cone fire was the most intensive burn to occur within the J. S. Pk. pine forest during the past 3 centuries. Limb breakage from a wet snowstorm in January, 1974 (Morrison, 1976) added greatly to fuel accumulation at low and middle elevations in the Santa Lucia mountains but did not damage vegetation above 1000 m on J. S. Pk. Two consecutive drought seasons, reducing precipitation below half of normal, preceded the Marble-Cone fire and also increased fire damage. However, the absence of fire over the previous 76 years was the single most important factor contributing to the intensity of the Marble-Cone fire within the J. S. Pk. pine forest.

Pre-fire vegetation. On the south side of J. S. Pk., *P. lambertiana* is restricted to colonies on rock outcrops above 1500 m (Fig. 1). Slopes within these rock outcrops exceed 100 percent, vegetation is sparse, litter does not accumulate, and the colonies do not burn readily. They had opportunity to burn when the Indians fire ran directly up to them and again when the Marble-Cone fire ran around them (Fig. 1).

The outcrop plot 13, which did not burn in either fire, had tree and shrub strata cover of 35 percent. In order of increasing importance, the cover was composed of *P. coulteri, P. lambertiana, Arctostaphylos glandulosa,* and *Quercus chrysolepis.* Young pines were rare. Species richness is higher on south-slope outcrops than in other J. S. Pk. communities (Griffin, 1975b; Talley, 1976). The herb and subshrub strata included *Arabis breweri, Castilleja foliosa, Cheilanthes covillei, Dudleya cymosa, Galium angustifolium, G. clementis, Hieracium argutum* var. *parishii, Lotus argophyllus* var. *fremontii, Lupinus abramsii, L. hirsutissimus, Penstemon corymbosus, Polystichum munitum, Stipa coronata,* and *Yucca whipplei.*

To the north of the ridgeline, *P. lambertiana–P. coulteri* forest extends down to 1200 m in some situations (Fig. 1). North-slope outcrops are common near plot 2. Enough moss and litter accumulate on parts of these outcrops to carry a light, spotty fire. Vegetation cover does not exceed 25 percent and is dominated by slow growing *Quercus chrysolepis* and scattered *Arctostaphylos glandulosa.* Bushy *P. lam-*

Table 2. Basal Area and Density of *Pinus lambertiana, P. coulteri,* and *Quercus chrysolepis* within the Junipero Serra Peak Forest before and after the Marble-Cone Fire. *Calocedrus decurrens* is also present at plot 3 with 4.7 m^2/ha basal area, 115 stems/ha density (1-76) and 1.4 m^2/ha basal area, 86 stems/ha density (7-78).

Plot no.	Basal area (m^2/ha)						Density (stems/ha)					
	P. lam.		*P. cou.*		*Q. chr.*		*P. lam.*		*P. cou.*		*Q. chr.*	
	1-76	7-78	1-76	7-78	1-76	7-78	1-76	7-78	1-76	7-78	1-76	7-78
						Summit Forest						
12	16.2	6.8	47.8	24.2	0.4	0	717	72	516	229	57	0
8	85.2	41.9	1.4	1.3	0	0	976	158	43	14	0	0
5	57.2	56.4	6.6	6.8	2.8	1.9	244	215	43	43	115	57
4	30.8	4.4	19.3	17.3	4.9	0	1004	43	215	129	502	0
9	59.0	4.0	4.3	0	12.8	0	560	14	43	0	660	0
Ave.	49.7	22.7	15.9	9.9	4.2	0.4	700	100	172	83	267	11
						Slope Forest						
11	42.8	21.8	0	0	32.4	18.4	129	14	0	0	731	229
1	9.5	8.6	3.1	3.2	16.6	3.4	187	129	28	28	1937	488
10	71.8	44.3	0	0	5.0	1.7	158	86	0	0	187	14
6	53.8	50.2	0	0	8.6	7.0	287	201	0	0	316	143
3	21.5	19.0	0	0	24.5	22.0	144	100	0	0	631	430
Ave.	39.9	28.8	0.6	0.6	17.4	10.5	181	106	6	6	760	261

bertiana and *P. coulteri* account for only about 5 percent cover. Herb species largely restricted to north slope outcrops included *Allium campanulatum, Erigeron petrophyllus, Lomatium macrophyllum, Holodiscus microphyllus,* and *Stipa* (*latiglumis*?). *Galium clementis, Heuchera micrantha* var. *pacifica,* and *Polystichum munitum* grow on north slope outcrops and other rocky slopes within canyons.

We separated the non-outcrop pine forest on the north side into two topographic units—"summit" and "slope" forests. The summit forest was generally above 1650 m elevation with moderate slopes; plots averaged 1700 m and 42 percent slope. The slope forest had more broken topography, with plots averaging 1590 m and 57 percent slope, becoming steeper with decreasing elevation. Tree cover on summit plots was: *P. lambertiana* 52 percent, *P. coulteri* 12 percent, and *Q. chrysolepis* 16 percent. Cover data for slope plots were: *P. lambertiana* 25 percent, *P. coulteri* 1 percent, and *Q. chrysolepis* 49 percent. *Pinus lambertiana* accounted for about two-thirds of total basal area on both summit and slope forests (Table 2), but *P. lambertiana* density at slope plots was only 40 percent that of summit plots due to lower establishment on slopes after the 1901 fire. *Pinus coulteri* accounted for 23 percent of the total basal area and 15 percent of tree density at summit plots. On slope plots *P. coulteri* declined, and only a few trees grew near chaparral ecotones. *Quercus chrysolepis* increased from 6 percent basal area and 23 percent density at summit plots to 30 percent basal area and 73 percent density on slope plots (Table 2). In effect the nearly pure pine stands on the summit grade into pine-oak stands on steeper terrain. Lower slope and canyon bottom forests have some dominant *Calocedrus decurrens* trees (Table 2, plot 3); small *Calocedrus* trees were rare in the summit forest.

The only shrub common within the pre-fire summit forest was *Rhamnus californica* (Table 3). Herbs were too infrequent in the dense pine needle duff on the summit to appear in the stand survey but included *Viola purpurea, Mimulus subsecundus, Silene lemmonii,* and one small population of the rare disjunct *Cycladenia humilus* var. *venusta.*

In the slope forest, shrubs were also unimportant. A few colonies of *Arctostaphylos glandulosa* grew along with uncommon individuals of *Rhamnus* and *Ribes.* Herbs were more diverse and included *Galium clementis, Carex multicaulis, Gayophytum heterozygum,* and *Pyrola picta* ssp. *aphylla. Lupinus cervinus* grew in small groups under semi-open stands dominated by large *P. lambertiana* trees (Table 3).

Fire behavior. The Marble-Cone fire crowned through portions of the summit forest (Fig. 1). None of the plots happened to be in areas where all the aboveground vegetation was killed, but only a few stems survived in plot 9 (Table 2). Stands consumed by the crown fire had dense understories that helped carry the crown fire. The origin of these pine thickets was related to old wind-throw damage. A few years after the 1901 fire a severe southwest wind felled patches of dominant *P. lambertiana* trees, and these openings regenerated densely without any subsequent thinning by fire. The upper summit, above the wind-throw zone, had a more open understory and did not generate a crown fire. Instead a strong surface fire swept the region killing 85 percent of the pine and all oak stems (Table 2, plots 8, 12). The least vegetation damage within the summit forest occurred near plot 5, the site of the 1959 lightning fire, where basal area and density reductions were minor for the pines (Table 2).

When the fire burned downhill over the steep north slope terrain below 1650 m elevation, it changed from a crown-type to surface fire. Along the upper margin of the slope forest about half the pine and two-thirds of the oak cover were killed (Table 2, plots 10, 11). Heat generated by this surface fire generally decreased as the fire burned deeper into the pine-oak stands (Table 2, plots 1, 6) but was still sufficient to kill nearly all oaks that had sprouted after the 1901 fire. Most saplings and some large specimens of *P. lambertiana* were also killed although mortality of intermediate sized pines was nil.

Significant areas in canyon bottoms remained unburned due to the presence of local fire barriers such as steep slopes with bare mineral

TABLE 3. PRE-FIRE (1976) AND POST-FIRE (1978) CONSTANCY PERCENT/MODAL COVER-ABUNDANCE VALUES (Mueller-Dombois and Ellenberg, 1974) FOR SPECIES IN THE SHRUB AND HERB STRATA ON THE JUNIPERO SERRA PEAK STUDY PLOTS.

	Slope forest		Summit forest	
Species	1976	1978	1976	1978
Trees and shrubs from sprouts				
Quercus chrysolepis	20/+	100/1	60/+	100/+
Rhamnus californica			80/+	80/+
Ribes roezlii			20/+	60/+
Arctostaphylos glandulosa	20/1	20/+		
Trees from 1977 seeds				
Pinus spp.		100/+		100/+
Quercus chrysolepis		100/+		100/+
Calocedrus decurrens		40/+		
Shrubs and herbs largely from dormant seeds				
Ceanothus integerrimus		100/+		100/+
Mentzelia pinetorum		60/+		80/+
Hulsea heterochroma		60/+		100/+
Arctostaphylos glandulosa		40/+		60/+
Lupinus cervinus	40/+	100/+		20/+
Claytonia spathulata		40/+		
Emmenenthe penduliflora		40/+		
Gayophytum heterozygum		20/+		100/+
Claytonia perfoliata & rubra?		20/+		80/+
Phacelia brachyloba		20/+		80/+
Lupinus abramsii		20/+		60/+
Ribes roezlii		20/+		40/+
Mimulus subsecundus				40/+

soil or rock outcrops. No single fire seems capable of burning the entire area within canyons. Fires in regions that do burn may not kill mature trees depending upon elapsed time since the last fire or local fuel accumulations. Rugged terrain deep within canyons did not permit the fire to burn along a uniform front. Rather, the fire was dissected into numerous small surface fires, only a few of which reached the bottoms of canyons. Hence, portions of adjacent slopes that could carry fire did not burn.

Post-fire vegetation. Pine regeneration has been abundant. Only a few pine seedlings grew near plot 5 before the fire. Now hundreds of seedlings grow on all plots. We don't know if the seeds producing 1978 seedlings all came from normally maturing cones on trees surviving the fire or if the somewhat immature cones forced open by the crown fire contributed viable seeds. In the case of *P. coulteri,* some pre-1977 seeds stored in partially closed cones might have been involved.

On four regeneration plots in the crown fire area on the summit the mortality of 1978 seedlings has been minor. The average density of two-year old seedlings on the plots in 1979 was $0.3/m^2$ for *P. coulteri* and $0.1/m^2$ for *P. lambertiana*. All these seedlings were healthy, but the *P. coulteri* seedlings were several times taller. The largest *P. coulteri* seedlings reached 50 cm in height by August, 1979. Because *P. coulteri* represented only some 20 percent of the basal area before the fire, the three-fold density advantage of the vigorous *P. coulteri* seedlings suggests a shift toward *P. coulteri* dominance in the new summit forest, at least in the early stages.

There were no *P. coulteri* seedlings in the regeneration plot on the slope that sustained only a surface fire (Fig. 1). In both 1978 and 1979, many *P. lambertiana* seedlings started in the deep shade here, but survival was poor on this already heavily stocked plot. A few *Calocedrus* seedlings were present here and at the other slope plots (Table 3). Only one *Calocedrus* seedling was found on the summit regeneration plots in 1979.

Sprouting species responded to the fire as expected (Table 3). Burned *Q. chrysolepis* stems on all plots sprouted vigorously. On slope plots, 1977 acorns also germinated to expand the number of oaks present. The few pre-fire *Arctostaphylos glandulosa* shrubs in the slope forest sprouted, but this manzanita also came up from dormant seeds in many spots. Both *Ribes roezlii* and *Rhamnus californica* shrubs sprouted. *Ribes* seedlings appeared in some new areas; no *Rhamnus* seedlings were seen.

An important response from dormant seeds has been the impressive start of *Ceanothus integerrimus* seedlings. Although this shrub was common in chaparral around the forest, no *C. integerrimus* shrubs grew within the forest in 1976. Now *C. integerrimus* seedlings are common throughout the summit forest. *Ceanothus* seedling density on four summit regeneration plots averaged $13/m^2$ in 1978 with less than 5 percent cover; in 1979 density declined to $8/m^2$, but cover increased to more than 10 percent. These *Ceanothus* seedlings along with the lesser number of manzanita seedlings and sprouts will form a significant shrub understory. When the new pine thickets start to shade out the shrubs in several decades, a severe fuel hazard will develop again. Repeated light fires are needed to remove the dying shrubs and to thin the pine saplings without killing the remaining mature pines.

The fire triggered a dramatic increase in herbs (Table 3). Vigorous plants of the perennial *Lupinus cervinus* were seen in all old localities, and seedlings expanded old stands and started new ones. Before the fire the perennial *Lupinus abramsii* grew only on south-slope outcrops. Now it is widely scattered in the summit and slope forests. Other perennials such as *Penstemon centranthifolius* that were rare in the forest are now locally common. The most restricted species on J. S. Pk. is *Eriogonum spergulinum* var. *reddingianum*. Howitt and Howell (1964) listed this Sierra Nevada and north Coast Range disjunct annual on the summit, but we could not find it prior to the fire. However, in 1978 we found a colony covering about 50 m^2. The U.S. Forest Service aerially seeded *Lolium multiflorum* over much of the burn, but this grass was not sown over the north side of J. S. Pk. Minor amounts of seed drifted into the summit forest, but the resulting grass was negligible in terms of competition with pine seedlings and native herbs in 1978 and 1979 (the grass was a serious competitor in other portions of the burn). The major response from fire-induced annuals during the second year after the burn was a dramatic increase in *Gayophytum heterozygum* throughout the forest.

Unless periodic fire returns to the J. S. Pk. pine forest, areas burned in crown or surface fires in 1977 will produce *P. coulteri* and *P. lambertiana* thickets. Needles and dead limbs from the developing pine thickets will combine with the large number of overstory snags and the dying understory *Ceanothus* shrubs to produce a serious conflagration potential within 20–30 years. Such a conflagration would deplete further the remaining old growth pines and encourage the sprouting species. Should a 50-year or greater interval between fires be repeated several more times, the *P. lambertiana* forest on the north slope of J. S. Pk. above 1600 m, which makes up 40 percent of the forest today, may well be replaced by chaparral and scrubby oak stands. If pines remain on the summit, *P. coulteri* is the more likely to survive because of its more aggressive seedling growth. *Pinus lambertiana* may remain in the low-fire-hazard, north-slope canyons regardless of fire frequency. On the south slope of the mountain, pines apparently have been restricted to unburnable rock outcrops within the chaparral for centuries.

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ELEVATIONAL DISTRIBUTIONS OF PINUS EDULIS AND P. MONOPHYLLA (PINACEAE) IN THE NEW YORK MOUNTAINS, EASTERN MOJAVE DESERT

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ABSTRACT

The elevational range over which sympatric populations of *Pinus edulis* and *P. monophylla* occur was measured on three north-facing slopes in the New York Mountains, eastern Mojave Desert. These two species have disjunct distributions over most of their geographic range, rarely occur together, and exhibit altitudinal zonation in the New York Mountains, where *P. edulis* occurs at higher elevations than *P. monophylla*. The elevation of contact varies locally. The highest ridge provides more run-off during the year, allowing *P. edulis* to exist at lower elevations than on a drier slope. The lowest and driest slope studied does not support *P. edulis* at all.

The two most abundant species of pinyon pine in the United States are *Pinus edulis* Engelm. and *P. monophylla* Torr. & Frem. They are morphologically similar and scarcely specifically distinct (Lanner, 1974; Roof, 1978), but are parapatric in distribution. While *P. edulis* ranges from Wyoming to the northern border of Chihuahua, Mexico, and west to southeastern California, *P. monophylla* is found in Idaho, western Utah, northwestern Arizona, Nevada, California, and Baja California (Critchfield and Little, 1966). They are sympatric in a few localities, the westernmost of which is the slopes of the New York Mountains in the Mojave Desert in southeastern California (Wolf, 1938; Griffin and Critchfield, 1972).

The simplest morphological character distinguishing these two species is needle number; *P. monophylla* usually possesses single needles whereas *P. edulis* has needles in fascicles of two or three (Lanner, 1974). Yet in the New York Mountains, individual trees are found with both 1- and 2-needled fascicles. Occasionally 3-needled fascicles are found. While these species are often found over the same elevational ranges, in the New York Mountains they are separated elevationally, with *P. edulis* occurring higher than *P. monophylla*.

There is some controversy over the correct identity of the trees in the New York Mountains. Using needle number, cone size, and resin canal number, Lanner (1974) concluded that *P. monophylla* is the only species found in this mountain range. However, he sampled only 24 trees and it is possible they were all from low elevations. Roof (1978)

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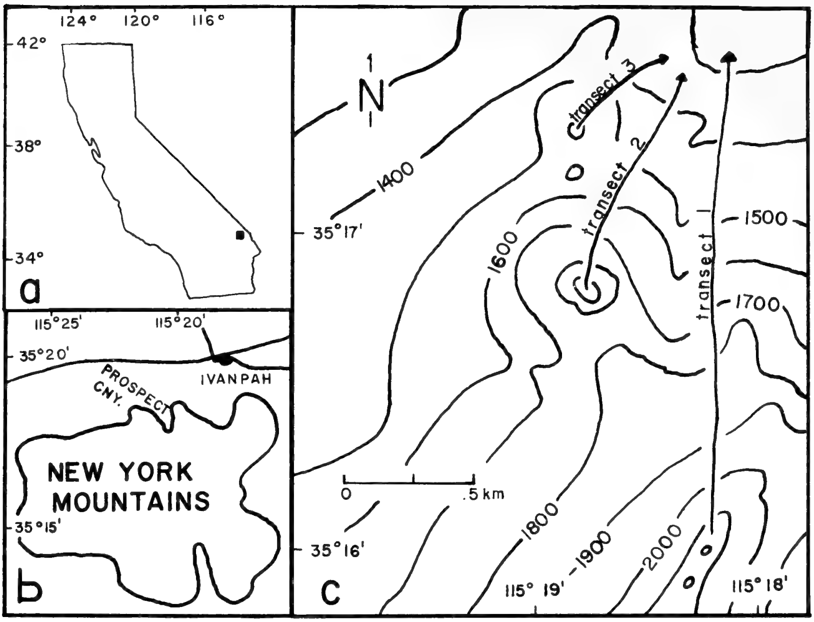

FIG. 1. Location of transects. a. Map of California, dark square shows location of New York Mountains. b. New York Mountain range. c. Topographic map with 100 m contours showing location of transects in "Prospect Canyon". Transect 1 is off the main summit ridge, transect 2 is intermediate and transect 3 is in the foothills.

claimed that *P. edulis* is the only pinyon species present based on tree color and form but not needle number.

The purpose of this paper is to document and interpret the distribution of *P. edulis* and *P. monophylla* in the New York Mountains. In this study we measured needle number per fascicle in a large number of trees from several locations. We surveyed a series of ridges from the main east–west crest north into the foothills of the range and determined the limits of the zone of overlap between the two pinyon species. We have attempted to identify the factors that affect the relative distribution of these taxa and to ascertain whether the population borders are stable or are changing over time.

METHODS

The data reported here were collected April 3–16, 1977. Three transects on the north side of the range were sampled near "Prospect Canyon", SSW of Ivanpah, CA (Fig. 1). One slope comes off the main summit ridge, one is located 2.0 km north of the summit in the foothills, and the third lies between the first two. Soil on all transects was rocky granitic sand. Elevations were determined by triangulation with a Silva Explorer Type 3 compass and USGS topographical maps (Ivanpah, CA and Mid Hills, CA quadrangles) and a Jack Dfrost altimeter.

At 15–30 m increments in elevation, three to five trees were sampled (the greater the tree density, the more sampled) and the terminal 12–15 cm of one branch 1 m above the ground was taken from the tree. Sample trees at a given site were taken as far apart as possible to control for microclimatic effects and to enhance the chance of including a broad range of tree genotypes. Slope, aspect, soil type, and degree of exposure were recorded for each tree. The needles of each sample were subsequently examined and each fascicle classified as 1- or 2-needled. No 3-needled fascicles were found in any of our samples. As fascicles were counted, those with apparently only one needle were bent to encourage separation of needles. Samples contained 71–231 fascicles. We calculated the mean percent of 2-needled fascicles at each site by averaging the percent of 2-needled fascicles on each tree at that site. We then plotted this as the dependent variable against elevation for each of the transects. From a least-squares regression of these data we have determined the median elevation where 1- and 2-needled fascicles occur in equal proportions. We then compared the curves describing the three transects.

RESULTS

Figure 2 shows the frequency of intermediate-type trees (with both 1- and 2-needled fascicles occurring on the same tree) on the northern slopes of the New York Mountains. Nearly all intermediate-type trees exhibited less than 20 percent or more than 80 percent 2-needled fascicles. No trees fell between 26 and 60 percent. Each tree can thus be classified operationally as either *P. edulis* or *P. monophylla* based on its predominant fascicle type.

Figure 3a shows the change in needle number per fascicle at each sample site along the elevational gradient of transect 1 and demonstrates the increasing proportion of *P. edulis* with increasing altitude. The fitted linear equation is $Y = -0.878 + (8.2 \times 10^{-4})X$ ($r = 0.51$, $p < 0.005$) where $Y =$ the proportion of 2-needled fascicles at each site and $X =$ elevation. The elevation at which 50 percent of the fascicles per sampled site are 2-needled ($X_{0.5}$, the turnover elevation) is 1680 m for transect 1.

Figure 3b shows a similar representation of the data for transect 2. Here $Y = -1.665 + (1.18 \times 10^{-3})X$ ($r = 0.69$, $p < 0.005$) with $X_{0.5} = 1834$ m. In transect 3 there is only one species present, so the data were not fitted to a line (Fig. 3c).

Thus transect 3 exhibits no species turnover and consisted only of *P. monophylla* while transect 2 shows a higher turnover elevation (1834 m) than transect 1 (1680 m).

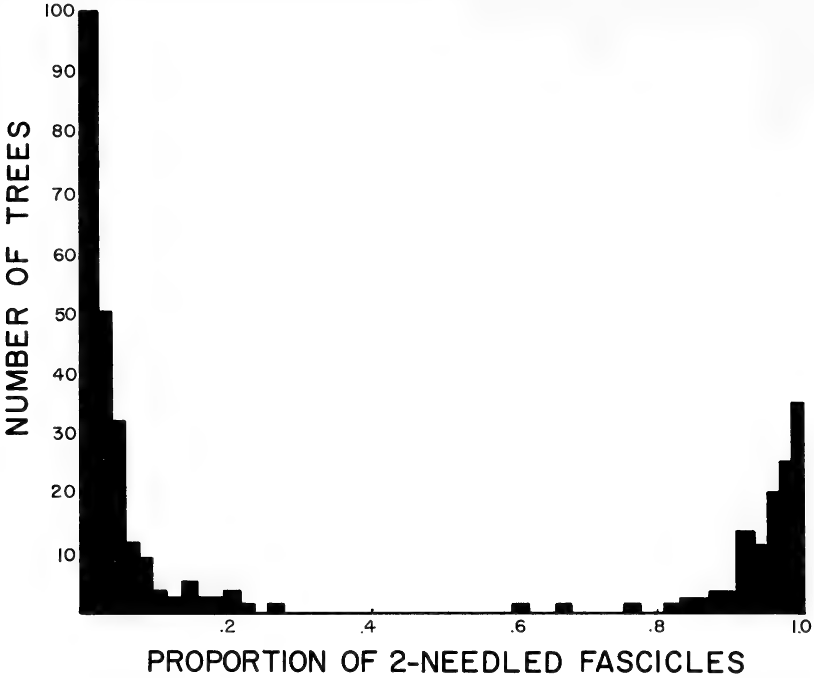

FIG. 2. Frequency distribution of intermediate-type trees in 2-percent units. All but seven of the 337 trees sampled in the New York Mountains have a proportion of 2-needled fascicles between 0 and 20 percent or between 80 and 100 percent. This allows an operational definition of *P. monophylla* as any tree with less than 50 percent 2-needled fascicles and *P. edulis* as any tree with greater than 50 percent 2-needled fascicles.

Figures 3a and 3b also show the elevations of the seven trees with 21–79 percent 2-needled fascicles. Five of these seven trees are located within 200 m of the calculated turnover point for their respective slopes. In addition, the proportion of 2-needled fascicles on each of these trees is compatible with the predictions made by the regression line—i.e., those lying below the turnover point have less than 50 percent 2-needled fascicles and those lying above the turnover point have greater than 50 percent 2-needled fascicles.

DISCUSSION

No conclusive data are presented here as to whether the intermediate-type trees are the products of convergence in response to similar edaphic conditions or to hybridization. The fact that intermediate individuals are found in isolated monospecific populations suggests that there is some developmental plasticity that affects needle number in

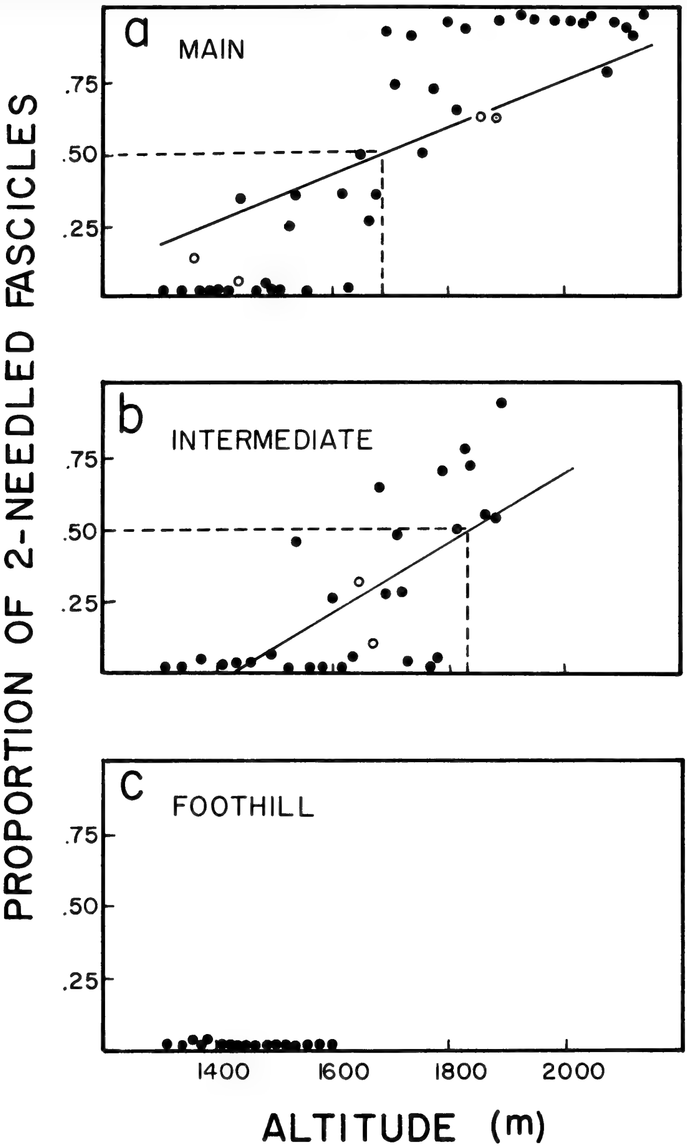

FIG. 3. Change in mean proportion per site of 2-needled fascicles with elevation on transects 1, 2, and 3. Open circles represent sites with one sampled tree that had 21–79 percent 2-needled fascicles. The dotted open circle represents a site with two such trees. a. Transect 1: *P. edulis* extends to low elevation. b. Transect 2: *P. edulis* found only at high elevations. c. Transect 3: *P. edulis* absent.

response to direct and immediate environmental pressure (Little, 1950, 1968). However, Lanner (1974) describes a slope that ranges over 400 m and several climatic zones. *Pinus monophylla* over this entire slope shows no variation in the number of needles per fascicle. In addition, much work has been attempted to answer the question of whether *P. edulis* and *P. monophylla* hybridize in nature (Lanner and Hutchison, 1972; Lanner, 1974) and it appears that such hybridization is possible.

As previously mentioned, there is some doubt that both *P. edulis* and *P. monophylla* are present in the New York Mountains. Lanner (1974), after examining needle morphology, cone size, and resin canal number, concluded that the 2-needled trees in the New York Mountains merely represented a form of *P. monophylla*. However, the discontinuous frequency distribution (Fig. 2) suggests that two distinct forms are present, and we retain both names for this material.

Figure 3 shows that, based on needle number, *P. edulis* replaces *P. monophylla* at higher elevations and the relative distribution of *P. monophylla* and *P. edulis* differs with location. *Pinus edulis* is absent from the lowest foothill slopes (transect 3), and on slopes near the main ridge (transect 2) the zone of transition between the two species occurs at a higher elevation than on the main summit slope (transect 1). This pattern may be a product of displacement competition—a process in which *P. monophylla* replaced *P. edulis* in lower, drier sites so that *P. edulis* became restricted to the high peaks of the main ridge in relictual stands. The sequence of events can be conceived as follows: *P. edulis* was once widely distributed at lower elevations in the Mojave Desert during pluvial Pleistocene climates (Wells and Berger, 1967). With glacial recession and climatic changes beginning about 20,000 years ago, *P. monophylla* began replacing *P. edulis* at lower elevations and on foothills. At present, *P. edulis* has been completely replaced on the foothill slopes, on all but the top of the intermediate slopes, and is being replaced on the uppermost main slope.

The causal factor of this altitudinal zonation is probably water availability. In general, water availability increases as one moves up the slopes of the New York Mountains. This may result from a number of factors, including more precipitation and lower evaporation rates due to cooler temperatures. Halvorson (1972) reported that narrow vegetational belts of *P. edulis, P. ponderosa,* and *Artemisia tridentata* on the north rim of the Grand Canyon are due to microclimatic effects that simulate an elevational moisture gradient even though there is no significant change in elevation. Likewise, species differences between sites at a given elevation are likely to be associated with microclimatic effects produced by topography, soil type, etc.

The altitudinal zonation exhibited by *P. edulis* and *P. monophylla* can then be interpreted as the superiority of *P. edulis* in cooler, wetter environments and the superiority of *P. monophylla* in hotter, drier environments. It is likely that the competitive dominance of each under different moisture regimes prevents either from existing over a larger elevational range. Therefore, the elevation of contact is different on each slope due to the different levels of water availability. The highest ridge provides more run-off during the year, allowing *P. edulis* to extend to lower elevations than on either of the drier slopes. The lowest slope studied does not provide enough moisture to support *P. edulis* at all.

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ANALYSIS OF TWELVE SONORAN DESERT SEED SPECIES PREFERRED BY THE DESERT HARVESTER ANT

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ABSTRACT

Twelve species of Sonoran desert seeds are shown to be the preferred food of the desert harvester ant, *Veromessor pergandei* (Mayr), at the Deep Canyon Desert Research Center, Riverside County, California. The nutrient and caloric content of these species are analyzed: stepwise extraction of (1) surface lipid, (2) inner lipid, (3) protein, and (4) carbohydrate was followed by extraction by thin layer chromatography of monoterpenoids in the surface lipid fraction. Caloric content was estimated by nutrient content. Monthly records of nutrient intake per ant colony show that with some exceptions, lipid (excluding surface lipid) is taken in greatest proportion and carbohydrate in the smallest. The amount of surface lipid is highly correlated with the content of inner lipid, protein, and carbohydrate, and with the caloric content of the seeds. The amount of surface lipid, along with the monoterpenoids therein, is suggested as possible chemical cues that could be utilized by ants in the selection of seeds.

Seeds have evolved under selection for certain physical and chemical properties to meet demands of dispersal, longevity, defense against predation, germination, and seedling establishment. Some of the chemical requirements are met by reserves of lipids, carbohydrates, and proteins stored in the cotyledons or endosperm of the seeds to provide energy and a source of carbon skeleton precursors (Levin, 1974). These stored substances make seeds an important food resource for many animals.

One of the main consumers of seeds in the deserts of southern California is the desert harvester ant, *Veromessor pergandei* (Mayr). It has been shown that granivorous ants do not select from the seed pool at random (Tevis, 1958; Box, 1960; Willard and Crowell, 1965; Eddy, 1970; Went et al., 1976; Pulliam and Brand, 1975). Although some authors suggest that selection may be based on size (Davidson, 1977), shape (Pulliam and Brand, 1975), or abundance of seeds during the foraging season (Willard and Crowell, 1965; Went et al., 1972; Whitford and Ettershank, 1975; Whitford et al., 1976), some workers believe that forage preference must be related at least in part to chemical properties of the seeds (Tevis, 1958; Nickle and Neal, 1972; Whitford, 1978). This paper reports an analysis of the nutrient content and possible sources of chemical cues available to ants in the seed species most commonly used as food by *V. pergandei.* No such study has been reported previously.

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The term "seeds" is applied here not only to true seeds but also to nutlets, achenes, and caryopses that are the functional units being used by the ants (Harper et al., 1970).

METHODS

Seeds were collected from *V. pergandei* foragers at the Deep Canyon Desert Research Station near Palm Desert, Riverside County, California. Each month, all foragers returning to a colony during a five-minute period of each hour of a complete foraging cycle were collected and separated from the items they carried. A minimum of five colonies was sampled each month. Forage items were identified, counted, and stored in glass vials, dry at room temperature. Mean weight per ten seeds of each species was determined.

The availability of seed resources was measured as the actual number of seeds of each species found in the surface litter during each month of the study. This measurement was chosen over seed production estimates because it is from the surface litter that the ants draw the great majority of seeds they collect; no buried seeds are sought or found, and only rarely are seeds harvested directly from plants (Gordon, 1978). Each month, three replicate 225-cm^2 samples of surface litter were taken along a transect from each of 11 types of foraging areas most typically used by the ants: burrow openings, rock depressions, soil depressions, under fallen cholla, under the canopy of several plant species, and from random interspaces between shrubs. Each sample was sieved, then hand sorted; all seeds and other food items were identified, examined, counted, and stored dry at room temperature. The numbers of items counted were corrected for differences in total area represented by each type of foraging area sampled. Details of these methods are given in Gordon (1978).

A set of approximately 20 seeds of each of the 12 species most commonly used by *V. pergandei* as food was taken from among samples collected from the foragers. Analysis of the seeds' nutrient content was conducted in a stepwise manner, extracting first lipids, then proteins, and finally carbohydrates from the same set of seeds.

Lipids were measured in two separate steps, because the ants may make different use of lipids from the surface than those from within the seeds. Surface lipids were extracted from preweighed seeds in chloroform:methanol (2:1 v/v) for 2–3 minutes. The solvent was evaporated, and the lipid weighed (Harborne, 1973). When the quantity of lipid was too small to be weighed, the extract was redissolved, spotted on filter paper, dried, and spotted with osmic acid to obtain an approximate reading by comparison with spots of known concentration. For some species the capsule, calyx, achene, or floret was also spot-tested with osmic acid and Sudan IV for presence of surface lipids. A similar method was used to extract lipids from inside the seeds, differing only in that the seeds were first macerated and allowed to stand for six hours before each of three extractions.

Proteins were measured with the Folin-phenol reagent (Lowry et al., 1951; Vasu, 1965). Only soluble proteins were measured; structural proteins, such as in the pericarp or testa, are discarded by ants and were not measured. Samples were read in a spectrophotometer at $\lambda = 660$ nm, and values were calculated from a standard curve.

Carbohydrates were determined by colorimetric methods using phenol in the presence of concentrated sulfuric acid (Dubois et al., 1956). Samples were read in a spectrophotometer at $\lambda = 490$ nm, and values were calculated from a standard curve of known concentrations.

Terpenoids were separated from previously-extracted surface lipids using thin layer chromatography on silica gel adsorbant with a benzene:chloroform (1:1 v/v) solvent, followed by a detection spray of vanillin/H_2SO_4 (Attaway et al., 1965; Stahl, 1969; Harborne, 1973).

An estimate of caloric content was made based on the nutrient constituents rather than by calorimetric methods in an attempt to include only seed parts actually consumed (Spector, 1952; Levin, 1974).

Spearman rank-correlation tests were applied to nutrient and caloric content values of all species.

Mucilage exudation on wetting was tested by placing intact seeds in water with India ink.

RESULTS

Monthly seed use by foragers, compared with a monthly frequency distribution of seed availability in the litter, is summarized in Table 1. A detailed account of the ants' diet and of food availability, including 100 seed species as well as insects and other nonseed material, is given in Gordon (1978).

Seed weight, content of protein, carbohydrate, internal lipid, surface lipid, and calories of the 12 species are shown in Table 2. Protein content in all but three species is below 12 percent by weight. High protein species are *Cryptantha angustifolia* (20.1 percent), *Hyptis emoryi* (16.8 percent), and *Ambrosia dumosa* (12.8 percent). The content of carbohydrate is relatively low for all species, with the highest amount present in the grass *Schismus barbatus* (9.3 percent), followed by *Oenothera claviformis* (6.5 percent). The other species have less than four percent carbohydrate. The internal lipid content is greater than 19 percent in all but three species; the low species are *Plantago insularis* (5.5 percent), *Larrea tridentata* (10.9 percent), and *Schismus barbatus* (4.8 percent). The two lowest of these have no measurable surface lipid; however, qualitative spot tests on the capsule, carpel, and floret of the three indicate a small amount of lipid on the external structures, which are typically encountered by foraging ants prior to or concurrently with the seeds contained therein.

TABLE 1. MONTHLY SEED USE OF 100 SPECIES BY THE DESERT HARVESTER ANT AT DEEP CANYON, RIVERSIDE CO., CA. First number is percent of total seeds foraged, by species (N = 6144); second number is percent of total seeds in litter samples, by species (N = 36,305). Species are designated by initials: *Larrea tridentata*; *Euphorbia micromera*; *Plantago insularis*; *Cryptantha angustifolia*; *Hyptis emoryi*; *Oenothera claviformis*; *Ambrosia dumosa*; *Bebbia juncea*; *Encelia farinosa*; *Perityle emoryi*; *Psathyrotes ramosissima*; *Schismus barbatus*; All Other Species. "p" = less than 1 percent. "*" = no data for month immediately following.

Species	1975						1976						
	JUN	JUL*	SEP	OCT	NOV	DEC*	MAR	APR*	JUN*	AUG	SEP*	NOV	DEC
L. t.	2, 4	5, 12	31, 16	17, 37	9, 14	43, p	1, p	1, 22	1, 1	1, 12	11, 34	1, 12	0, 8
E. m.	0, 5	0, 11	0, p	2, 1	0, 2	10, 1	10, 6	0, p	0, p	1, 12	0, 2	0, 17	48, 30
P. i.	1, 2	17, 1	13, 1	3, 1	17, p	10, p	28, 4	71, 2	1, 1	1, p	25, p	10, 1	14, 1
C. a.	32, 7	0, 1	2, 5	1, 1	26, 2	0, 2	16, 10	8, p	2, 19	64, 1	0, 6	10, 3	0, p
H. e.	4, 53	3, 21	8, 5	42, 8	2, 20	1, 5	12, 36	0, 18	11, 39	3, 3	14, 13	0, 39	0, 11
O. c.	0, p	11, p	14, 1	0, 0	0, p	2, p	0, p	1, p	0, p	2, 1	15, p	0, 0	0, 0
A. d.	0, 2	0, 2	1, 1	0, 2	0, 6	0, 1	5, 2	0, 4	7, 8	2, 4	13, 4	0, 3	0, 1
B. j.	11, 6	1, 6	3, 8	3, 5	8, 1	5, 4	2, 11	1, 1	14, 7	1, 6	3, 4	58, 13	4, 40
E. f.	27, p	22, 5	0, 1	3, 14	0, 2	0, 7	0, 4	0, 23	53, 12	10, 25	5, 23	1, 8	28, 2
P. e.	1, 2	17, 1	1, 6	0, 2	0, p	0, p	4, 4	0, 4	1, p	0, p	1, 3	2, p	0, p
P. r.	1, 3	0, p	3, 1	2, p	23, p	15, p	7, 1	0, p	0, p	2, 1	5, 1	14, 1	0, p
S. b.	7, 9	5, 30	6, 51	9, 26	1, 51	6, 49	5, 3	1, 24	5, 12	5, 20	0, 2	3, 1	5, p
A.O.S.	7, 7	5, 10	6, 4	9, 3	1, 2	6, 31	5, 19	1, 2	5, 1	5, 15	0, 8	3, 2	5, 7

Table 2. Weight of Ten Seeds (W/10); Percent Composition by Weight of Protein (P), Carbohydrate (CHO), Internal Lipid (L), and Surface Lipid (SL); Calories per Ten Seeds (Cal/10); and Calories per Gram (Cal/gm) of 12 Species of Sonoran Desert Seeds. Standard deviation in parentheses. $\bar{x}$ = 3224 (1583) Cal/gm.

Plant species	W/10 (mg)	P	CHO	L	SL	Cal/10	Cal/gm
Larrea tridentata	31.27 (.87)	3.5	2.1	10.9	9.5	62 (1.0)	2013 (56)
Euphorbia micromera	1.35 (.04)	3.5	1.1	36.8	14.7	6 (0.1)	4628 (138)
Plantago insularis	9.88 (.40)	6.5	3.5	5.5	0.0	9 (0.3)	982 (39)
Cryptantha angustifolia	0.65 (.02)	20.1	1.2	29.2	8.9	2 (0.1)	4421 (132)
Hyptis emoryi	2.97 (.13)	16.8	1.0	28.8	29.3	17 (0.7)	5921 (266)
Oenothera claviformis	0.77 (.05)	7.4	6.5	23.1	0.6	1 (0.1)	2323 (81)
Ambrosia dumosa	21.96 (.55)	12.8	1.1	36.8	26.5	120 (3.0)	5494 (37)
Bebbia juncea	8.74 (.26)	8.5	1.5	29.9	24.5	45 (1.4)	5172 (155)
Encelia farinosa	7.56 (.38)	7.3	2.6	23.5	8.4	24 (1.2)	3233 (161)
Perityle emoryi	1.43 (.07)	7.0	1.9	20.9	14.1	5 (0.3)	3440 (172)
Psathyrotes ramosissima	7.14 (.29)	4.3	3.5	19.9	0.0+	15 (0.6)	2083 (83)
Schismus barbatus	0.67 (.03)	4.3	9.3	4.8	0.0	1 (0.0)	1037 (42)

Species with higher lipid content generally show higher surface lipid amounts. In *Hyptis emoryi*, for example, surface lipid constitutes nearly one-third of total seed weight. Not only is the amount of surface lipid highly correlated with that of inner lipid ($r = 0.96$, $p < 0.01$), but also with the amount of protein ($r = 0.92$, $p < 0.01$), carbohydrate ($r = -0.74$, $p < 0.01$), and caloric content ($r = 0.99$, $p < 0.01$) of the seeds.

There are other strong correlations among the nutrient constituents. Protein and internal lipid content of the 12 species are positively correlated ($r = 0.92$, $p < 0.01$); protein and internal lipid contents are each negatively correlated with carbohydrate content ($r = -0.75$, $p < 0.01$; $r = -0.70$, $p < 0.05$, respectively). Jones and Earle (1966) showed that, on a family basis, there is a strong positive correlation between average oil and protein content in seeds. Their data indicate that families low in seed oils and proteins are more likely to include species with starchy seeds than are families rich in oils and proteins. Their generalizations are supported by the data reported here.

Earle and Jones (1962), Kleiman et al. (1964), and Jones and Earle (1966) reported values within 3 percent of those shown in Table 2 for the families represented in the present study, and some are as close as 0.04 percent.

Caloric content of the seeds is expressed for units of ten seeds, and for a gram of seeds for each species (Table 2). There is a wide range of values among the 12 species (982–5921; $\bar{x}$ = 3224, s.d. = 1593). Reichman (1976) reports a higher mean for 18 species of Sonoran desert seeds ($\bar{x}$ = 4579, s.d. = 736), measured by microbomb calorimetry. His direct measure should yield higher values, because structural ma-

TABLE 3. MONTHLY NUTRIENT INTAKE (90–99 PERCENT) AND CALORIC INTAKE (100 PERCENT) PER COLONY PER DAY. Percent nutrient intake is based on total mg of edible material.

	Nutrient intake (mg)			Nutrient intake (%)			Caloric intake
Month	Protein	Lipid	CHO	Protein	Lipid	CHO	Calories
Jun 75	312.5	732.3	857.9	16	39	45	13,804
Jul 75	396.5	848.8	143.4	29	61	10	10,051
Sep 75	270.7	680.2	136.0	24	63	13	12,686
Oct 75	106.5	251.4	37.3	27	64	9	5,425
Nov 75	162.0	402.7	102.2	24	60	16	6,799
Dec 75	115.6	352.6	71.0	21	65	14	6,830
Mar 76	53.9	96.7	54.5	27	47	26	2,614
Apr 76	136.1	126.0	78.3	40	37	23	2,500
Jun 76	388.4	1164.0	92.9	23	71	6	18,067
Aug 76	582.9	983.8	339.6	30	52	18	22,196
Sep 76	257.0	633.5	75.5	27	65	8	10,062
Nov 76	167.5	532.3	51.2	22	71	7	8,618
Dec 76	169.9	519.9	68.7	22	69	9	7,306

terials are burned along with the soluble nutrients. Although Reichman concludes that caloric as well as chemical and nutritional content of the seeds vary independently of seed weight, in the present sample the caloric content is highly correlated with seed weight ($r = 0.83$, $p < 0.01$) as well as internal lipid content ($r = 0.98$, $p < 0.01$).

The 12 preferred species represent 90–99 percent of seeds gathered each month by *V. pergandei* (Table 1). Based on the nutritional content of these species, I calculated the partial monthly nutrient intake per colony per day (Table 3). In addition, I calculated the total calories taken in per colony per day using the determined caloric values of the 12 preferred species and an average caloric value for the remaining 1–10 percent of other seed species gathered each month (Table 3).

Data on terpenoids extracted from seed and fruit surfaces are summarized in Table 4. Although the identity of the compounds could not be determined from these data alone, it is clear that there are five distinct substances present among the species tested. The thin layer chromatography R_f values are given in the table; characterization of the spots with detection spray at 1 min and 30 min is as follows: spot 1, tan to green; spot 2, tan to brown; spot 3, blue to violet; spot 4, blue to violet; spot 5, only at 30 minutes, colored mauve. Only spot 1 showed in UV light. All compounds appear to be monoterpenoids, which are characteristically colorless, water-insoluble, steam-distillable liquids with fragrant odor (Robinson, 1975).

Mucilaginous species include only *Plantago insularis* and *Euphorbia micromera*.

TABLE 4. R_F VALUES OF FIVE TERPENOID SUBSTANCES OF SEEDS AND FRUITS OF 12 SONORAN DESERT SPECIES. Compounds were extracted in petroleum ether and separated by thin layer chromatography using benzene:chloroform (1:1 v/v) solvent.

Plant species	Plant part	$R_f \times 100$				
		1	2	3	4	5
Larrea tridentata	carpel	—	12	—	72	—
Euphorbia micromera	capsule	—	12	—	—	—
	seed	—	12	26	—	streak
Plantago insularis	capsule	0	12	—	77	streak
Cryptantha angustifolia	calyx	—	12	26	72	streak
	nutlet	—	12	27	—	streak
Hyptis emoryi	fruit	0	13	—	77	streak
	nutlet	0	12	26	—	streak
Oenothera claviformis	capsule	0	12	—	77	streak
	seed	—	12	—	—	—
Ambrosia dumosa	achene	—	—	—	—	—
Bebbia juncea	achene	0	12	—	—	streak
Encelia farinosa	achene	—	—	—	—	—
Perityle emoryi	achene	—	12	—	—	—
Psathyrotes ramosissima	achene	0	12	—	72	—
Schismus barbatus	floret	—	12	—	—	—

DISCUSSION

Of the 100 species available in the litter at Deep Canyon, only 50 are ever collected by *V. pergandei* (Gordon, 1978), and of these, only the 12 species discussed here are used with regularity. In certain months, one or a few of these 12 species dominate. For example, in April, 1976, *Plantago insularis* made up 71 percent of all seeds collected; it is a species low in lipid, high in carbohydrate. In August, 1976, 64 percent of all seeds taken were *Cryptantha angustifolia,* the species highest in protein content.

The frequency of occurrence of seeds in the surface litter reflects the frequency with which they are encountered by the foraging ants. Chi-square tests show that there is a highly significant difference between the number of seeds collected in each month ("observed") and the frequency of seeds encountered in the litter ("expected"), regardless of whether the data are pooled by season, by year, or by month (Gordon, 1978, tables 5-5, 5-6). The ants are clearly selective of the seeds they gather, and thus the 12 species used most frequently can be termed "preferred".

Although detailed nutrient requirements of ants are not known, in general the workers take a large share of carbohydrates as an energy source, growing larvae as well as workers take lipids as a source of energy and reserve, while egg-laying queens and growing larvae make most use of proteins for production of new tissue (Abbott, 1978). Thus the seeds, or portions thereof, may be partitioned among members of an ant colony, depending on their particular needs. Further, nutrient requirements may change with season, depending on the type of activity in which members are engaged, and upon the composition of the colony in terms of age and caste. Monthly or seasonal changes in nutrient use, therefore, are more interesting than the annual total, since these variations should relate to cycles within the colony.

The array of preferred seed species offers the ants a source of all three fundamental nutrients. In most months, lipid is taken in the greatest proportion, and carbohydrate in the smallest (Table 3). Exceptions were in June, 1975, when carbohydrate accounted for 45 percent of nutrient intake and lipid only 39 percent; and in April, 1976, when only 37 percent lipid was taken in along with 40 percent protein and 23 percent carbohydrate. In March, 1976, although lipid was in the highest proportion (47 percent), the amount of carbohydrate taken in was slightly higher than that of protein (27 and 26 percent, respectively). Although these figures might suggest a relation of nutrient intake to worker activity, such as intense worker activity during early summer requiring high carbohydrate intake, or of reproductive effort in April requiring a higher protein intake, there is a major obstacle to such interpretation: the dynamics of seed storage are unknown. Neither the quantity of seeds stored in a nest at any one time, nor the proportion of seeds used immediately is known. Only small numbers of seeds have been recovered from nest excavations (Tevis, 1958; Wheeler and Rissing, 1975) due to the difficulty of exploring *V. pergandei* nests, which exceed 3.5 m depth and 15 m breadth in sandy desert soils (Tevis, 1958). In addition to the factors of colony needs and partitioning of nutrients among castes, the storability of different seed species, with regards to physical and chemical properties of the seeds, probably influences patterns of seed storage and use. Until these patterns are quantified, the basis of seed selection, the seasonal use of nutrients, and food utilization cannot be fully understood in relation to the activity and reproductive cycles of ant colonies.

It is clear, however, that granivorous ants do select particular seed species from among the available seed pool. If their selection is based upon chemical cues, it is important to determine their nature, and to address the question of whether such cues could provide the ants any information about the nutrient contents of the seeds. *V. pergandei* foragers have been shown experimentally to select seeds by chemical cues alone, without benefit of visual or tactile cues (Gordon, 1978). Ants can perceive at least some components of lipids *via* chemical receptors, because certain fatty acids are among the chemicals used as communication signals or as "releasers". For example, necrophoric behavior is released by the "death scent" of deceased ants, which in *Solenopsis saevissima* consists of a mixture including oleic, linoleic, myristoleic, and palmetoleic acids (Wilson et al., 1958). Further, monoterpenoids are among the compounds used by ants for defense and for attraction of nestmates (Cavill and Robertson, 1965; Gabba and Pavan, 1970). Thus, the surface lipids measurable on the seeds and fruits under consideration, as well as the five monoterpenoid substances present on seed surfaces, are candidates as chemical cues that could be utilized by ants in the selection of seeds.

Essential oils may provide cues for recognition of particular seed species, learned by experience (Tevis, 1958). Indication of nutrient content, however, could rest on detection of the amount of surface lipid present: the amount of surface lipid is highly correlated with the amount of internal lipid, protein, and carbohydrate available in the seed. The ants may, however, simply be attracted to some lipid and/or terpenoid component. Based on what is known of their feeding methods, ants are not likely to utilize surface lipids as a food source (Went et al., 1972). This question warrants further study, both by experimentation and by examination of discarded seed coats for the presence of surface lipids after seed extraction by the ants.

In the coevolution of plants and the animals with which they interact, some secondary plant substances have come to serve as repellents of pest species, while others are attractants to animals acting as dispersal agents (Fraenkel, 1959; Janzen, 1969; Whittaker and Feeny, 1971). Ants are known to be a major nonpassive dispersal agent for the seeds of many species that have elaiosomes (Berg, 1969, 1975; Handel, 1976). Harvester ants collect seeds for food and carry them up to 100 m from the parent plants (Gordon, 1978). Seeds are frequently dropped by foragers and not recovered; partially eaten but still viable seeds, along with intact seeds that were collected but subsequently rejected, are deposited on the refuse pile outside the nest; and seeds may be abandoned in shallow chambers (Went et al., 1972; Wheeler and Wheeler, 1973). By all these methods, *V. pergandei* and other harvester ants inadvertently disperse seeds of some desert plants. This may provide an advantage to the seed species attractive to them, even though many seeds are eaten. Whether or not the surface lipids serve some other function for the seeds, such as acting as an antiwetting agent, for example, to prevent premature germination in desert soils, there may be selection for their presence simply for chemical communication with potential dispersal agents—the ants.

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BOOKS RECEIVED AND LITERATURE OF INTEREST

Hortulus Aliquando: a sometime journal on historical and current horticultural and allied subjects. Published by GRANT DAHLSTROM at Castle Press, 516 N. Fair Oaks Ave., Pasadena, CA 91103. Three numbers have been published to date. Titles include "Plants in the works of Albrecht Dürer (1471–1528)" by W. A. Emboden; "William Roxburgh's plants of the coast of Coromandel" by Ray Desmond; and "Richard Spruce still lives" by Richard E. Schultes.

A Guide to Botanical Resources of Southern California. By JANICE R. BARTEL and SAGE CULPEPPER BELT. Castle Press, Pasadena. Developed by docents and volunteers of the Natural History Museum of Los Angeles County, 900 E. Exposition Blvd., Los Angeles, CA 90009 and available from the museum for $4.74 postpaid. Reviewed (Hortulus Aliquando 2:2. 1977) by W. A. Emboden.

GEOLOGIC CONTROL OF VEGETATION IN THE PURISIMA HILLS, CALIFORNIA

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ABSTRACT

Five plant communities are recognized from the western Purisima Hills, Santa Barbara Co., California: closed-cone pine forest, douglas-fir forest, oak grassland, chaparral, and coastal sage scrub. The distribution of each community with respect to substrate type, fire history, and exposure was examined by mapping a 9.3 km^2 area. Bedrock geology and exposure were the principal factors affecting the distribution of the closed-cone pine forest and douglas-fir forest. Both communities were found primarily on north slopes of diatomaceous shale. To a lesser extent the other communities were most common on particular aspects and substrates: oak grassland grew mainly on gentle slopes, chaparral was predominant on south slopes of sandstone, and coastal sage scrub occurred on argillaceous substrates. The one recorded fire within the area had no recognizable affect on the sharp ecotones between communities.

The Purisima Hills of western Santa Barbara County, California, support a rich assemblage of vegetation types. Five distinct plant communities form mosaic patterns across rolling hills (Fig. 1). Coastal sage scrub, chaparral, oak grassland, closed-cone pine forest, and douglas-fir forest occur as discrete communities, usually with sharp ecotonal boundaries.

While the mosaic patterns of vegetational units in coastal California are readily apparent, the reasons for these patterns have been the subject of much discussion. They have been explained as successional (Cooper, 1922); a polyclimax controlled by different substrates (Shreve, 1972); the result of fire (Wells, 1962); and the result of differential moisture availability (Harrison et al., 1922). The sharp ecotones between some communities have been described as the result of volatile growth inhibitors produced by some aromatic shrubs (Muller et al., 1964) and herbivore impact between the communities (Bartholomew, 1970; Halligan, 1976). Some ecotones have been shown to be constant for at least 40 years (Bradbury, 1978).

Bishop pine (*Pinus muricata*), the dominant species of the closed-cone pine forest, forms a homogeneous cover with abrupt boundaries. Its distribution has been shown to be strongly influenced by edaphic factors (Lemmon, 1900; Westman, 1975), but stands have been reported on a variety of substrates (Wells, 1962; Griffin, 1964).

The variety of plant communities and substrate types present within a small area makes the Purisima Hills an ideal location for investigating relationships between substrate and community patterning. The sedimentary rock units are relatively undeformed allowing for a

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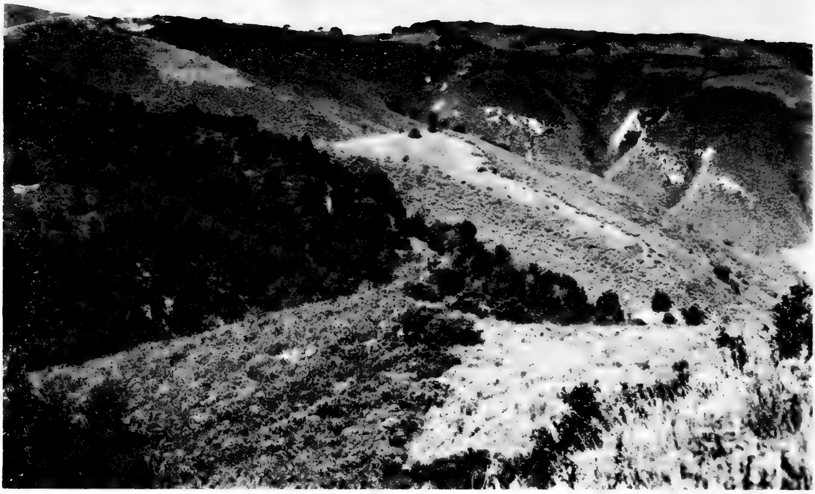

FIG. 1. Vegetation patterns in the Purisima Hills. In the left foreground, chaparral grows on diatomaceous shale. Coastal sage scrub grows on mudstone in the right foreground. In the middleground, bishop-pine forest grows on diatomaceous shale on the left with coastal sage scrub and grassland on mudstone to the right. In the background, oak grassland grows on a sandstone terrace deposit.

clear understanding of stratigraphic relationships. This permits better understanding of soil origins because parent rocks are often obscured by thick soils and subtle lithologic differences could go unnoticed in the field.

The study area consists of rolling hills 190 to 400 m in elevation, 15 km east of the Pacific Ocean. The climate is greatly influenced by proximity to the ocean and frequency of summer fogs that offset the small amount of summer precipitation (Azevedo and Morgan, 1974). Rainfall is concentrated during the winter months (97 percent of recorded annual precipitation), while fog is concentrated in the summer (73 percent of foggy days/year: Cole, 1974). Precipitation has varied from a minimum of 8.5 cm in 1947 to a maximum of 97 cm in 1941 at the nearest long-term weather station (Santa Maria). The average annual precipitation 5 km south of the ridge is 33 cm. Temperatures do not fluctuate widely from day to night or seasonally.

METHODS

In this study, I compared vegetational, geologic, and topographic features by plotting them on a 1:8000 base map of the 9.3 km^2 study area. The vegetation and geology were mapped through observation and stereo aerial photography (U.S.G.S.). Five plant communities

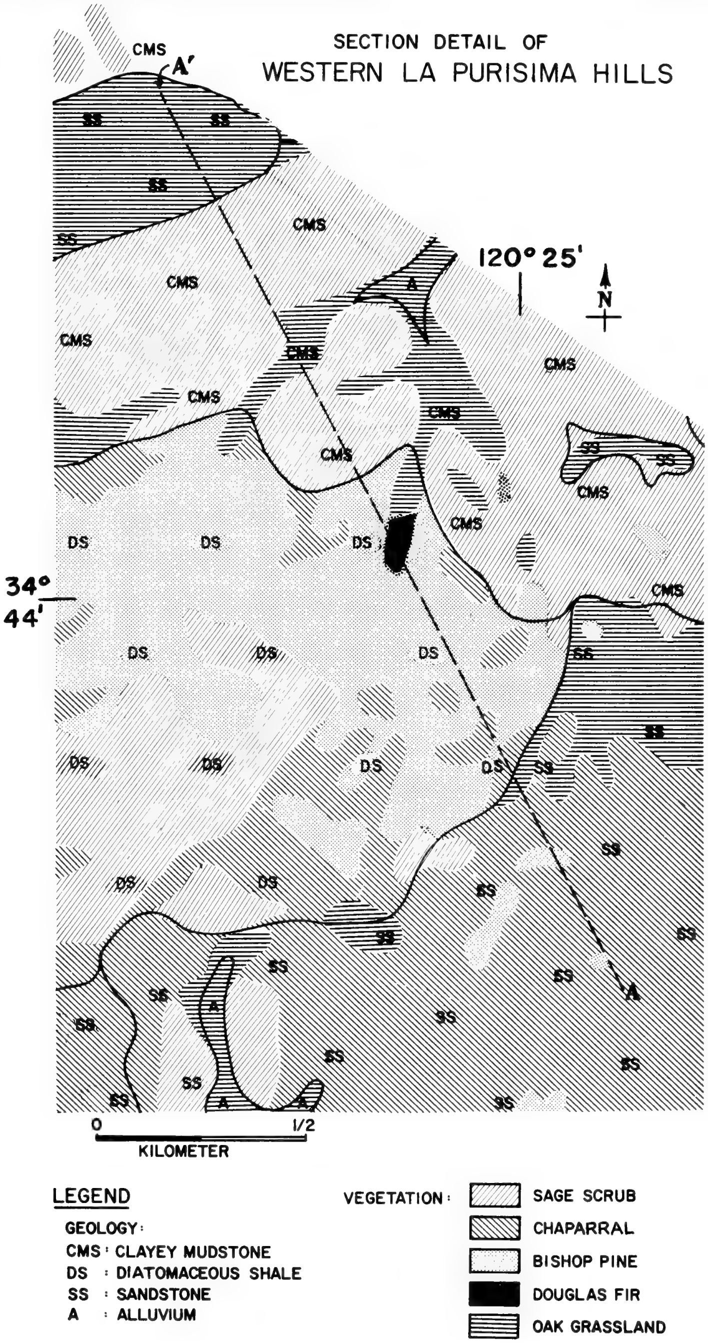

FIG. 2. Detail (about 25 percent) of vegetation-geologic map of the Purisima Hills.

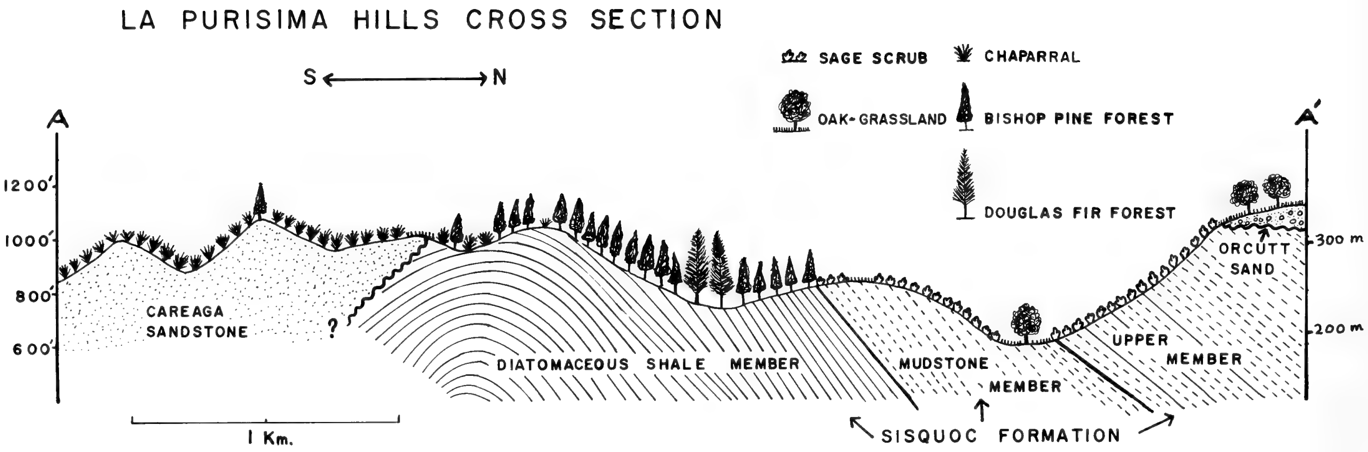

FIG. 3. Cross-section through line A-A′ of Fig. 2.

were recognized and mapped. Forty-one 30-m line intercepts provided quantitative data on the coverage of common plants in each vegetational unit. Taxonomic nomenclature follows Munz (1959).

Two composite soil samples from each substrate were made by combining 5 subsamples of surface soil from along a 30-m line intercept. Soil samples were tested using La Motte Soil Test Kit Model ST-1013. Eight distinct substrate units were mapped using the geologic nomenclature of Woodring and Bramlett (1950). The orientation of bedding planes was measured using a Brunton compass. The area occupied by each community type on each substrate was measured with a compensating polar planimeter from the map. These data were then split into north-facing slopes (270° to 90°) and south-facing slopes (90° to 270°).

Oven-dried rock samples from different substrates were tested for their water-retaining capacity by soaking in water for 30 minutes. The rocks were weighed several times as they dried to measure the remaining water. Rock volumes were measured by placing the rocks in plastic bags, submersing them in a filled container, and measuring the overflow.

RESULTS

Figure 2 is a portion of the map produced in this study. This portion was selected because it includes all five plant communities and an assortment of substrates. A cross-section through this area is illustrated in Fig. 3. The distribution of communities is discussed below.

Closed-cone pine forest. A dense forest dominated by bishop pine (*Pinus muricata* including some *P. remorata*) occurred on diatomaceous shale and sandstone. Only those areas where the coverage of these pines exceeded 50 percent were mapped as forest, even though isolated trees were spread over the entire area. The codominants in this forest were (in order of decreasing cover): *Quercus agrifolia, Heteromeles arbutifolia, Arctostaphylos crustacea, Vaccinium ovatum,* and *Rhus diversiloba.*

The majority (97 percent) of the area mapped as pine forest had diatomaceous shale substrates. Eighty percent of the mapped pine forest was located on north-facing slopes. Patches of forest were located on exposed sandstone hilltops accounting for 2.0 percent of the total forest cover. Not all diatomaceous shale substrates were covered by bishop pine. Good examples of both chaparral and sage scrub communities were found nearby on this substrate. The relative coverage of each community on each substrate is shown in Table 1. Bishop-pine forest covers a much larger percentage of the diatomaceous shale unit than any other substrate.

Douglas-fir forest. A small patch of douglas-fir forest (*Pseudotsuga*

Table 1. Relative Coverage of Five Purisima Hills Communities on Three Substrates. Percent coverage = area of community in substrate and slope class/total area in substrate and slope class. Community areas in hectares from which percent coverage values were calculated are given in parentheses. N = north-facing slope; S = south-facing slope.

	Diatomaceous shale		Sandstone		Mudstone	
Community	N	S	N	S	N	S
Bishop-pine forest	72% (99)	19% (24)	2.5% (1.7)	0.27% (0.90)	0.68% (0.83)	0.24% (0.22)
Douglas-fir forest	0.51% (0.70)	—	—	—	—	—
Oak grassland	1.7% (2.3)	—	40% (28)	14% (47)	15% (19)	5.7% (5.2)
Chaparral	11% (15)	43% (55)	40% (28)	71% (242)	4.1% (5)	—
Sage scrub	15% (21)	38% (48)	17% (12)	15% (49)	80% (98)	94% (85)

menziesii) was located in a shaded canyon on diatomaceous shale. The douglas-fir had a coverage exceeding 50 percent and was associated with *Vaccinium ovatum* and *Polystichum munitum*.

Oak grassland. The oak grassland community was dominated by introduced grass species with *Bromus rigidus, B. mollis,* and *Avena barbata* covering more than 70 percent of the ground. *Quercus agrifolia* reached its greatest concentrations (greater than 20 percent cover) in this community, although scattered oaks were present in every community. Seventy-four percent of the oak grassland was located on sandstone. This community is extensive in areas of low slope angle, and is probably underrepresented in this study because the flat areas adjoining the hills were mostly under cultivation.

Chaparral. The chaparral unit was defined as those areas dominated by chamise (*Adenostoma fasciculatum*) or manzanita (*Arctostaphylos* spp.). Chamise cover ranged from 30 percent on sandstone to greater than 80 percent on south slopes of diatomaceous shale. *Arctostaphylos pechoensis* var. *viridissima* was located predominantly on south slopes of sandstone, while *Arctostaphylos crustacea* dominated north slopes of diatomaceous shale. Chaparral was most common on southerly aspects and sandstone. Sandstone underlay 73 percent of the chaparral.

Coastal sage scrub. Areas of subligneous scrub vegetation were dominated by *Artemisia californica,* which usually had greater than

TABLE 2. CHARACTERISTICS OF FOUR SOILS FROM THE PURISIMA HILLS. Numbers are averages of 2 samples from each substrate.

	Diatomaceous shale	Porcelaneous shale	Clayey mudstone	Sandstone
pH	4.7	4.9	6.9	5.8
Nitrate (NO_4) (kg/ha)	29	21	18	9
Available potassium (kg/ha)	348	280	258	196
Replaceable calcium (ppm)	100	1250	2100	775
Chloride (ppm)	37.5	37.5	275	75
Sulfate (ppm)	50	50	75	50

40 percent cover. Other prominent species in this community were *Salvia mellifera, Brassica hirta, Lotus scoparius, Elymus condensatus,* and *Antirrhinum multiflorum.*

The coastal sage scrub community was most predominant on south slopes of clayey mudstone, covering 94 percent of these slopes. The community had a stunted appearance and lower total cover where it occurred on diatomaceous shale.

Soil tests (Table 2) suggest that soil pH is a factor in edaphic control on diatomaceous shale. Four samples taken in the closed-cone pine community, the chaparral community, and the coastal sage scrub community, all on diatomaceous shale, had pH values ranging from 4.6 to 5.0. The diatomaceous soils had relatively high nitrate and potash values and low calcium values.

In some cases geologic controls on plant distribution were apparent but no substrate or soil differences could be found. For example, bedding planes along the Purisima Anticline (Fig. 4) demonstrate that a chaparral community and a sage-scrub community are distinctly separated along a stratigraphic horizon. The pattern would appear fortuitous, or due to an aquifer, except for the fact that it continues through several hills and valleys as far as these rock strata are exposed. Both communities are growing on the same rock type, porcelaneous shale, a siliceous rock similar to the diatomaceous shale. The two soil samples taken from this substrate (one from each community) do not differ greatly. Comparison of 1954 and 1967 photos show that the boundary is stable and was not affected by a 1959 fire that burned both communities. No conclusion seems possible except that these communities are controlled by some unmeasured edaphic factor.

Substrate types differed in their ability to absorb and retain moisture. After one hour of drying, six samples of diatomite averaged 0.6 g H_2O/cm^3, or 60 percent retention. This compares with 32 percent for mudstone, 10–28 percent for sandstones, and 7 percent for granite.

FIG. 4. Sharp contact between chaparral (middle) and coastal sage scrub. This contact follows a stratigraphic horizon within the porcelaneous shale unit along the Purisima Anticline through several hills and valleys.

The diatomite samples still retained 30 percent water by volume after 135 hours. This compares favorably with previous reports on diatomite (Oakshott, 1957).

DISCUSSION

Diatomaceous shale as a unique substrate type. The diatomaceous shale within the upper portion of the Sisquoc Formation ranks high on a world scale for thickness and purity. The Johns Manville Quarry, the largest diatomite quarry in the world, excavates the Sisquoc Formation 32 km south of the study area, in what used to be an extensive bishop-pine forest (Wieslander and Jensen, 1945). This substrate is composed almost entirely of the siliceous tests of diatoms with very few clay particles. Thus, the purity of the substrate determines both its unique biological nature and its economic value. Shallow, acidic soils are formed on diatomaceous substrates regardless of the plant community type. The substrate has a spongelike ability to absorb and retain water, but the availability of this water for plants remains an interesting area for further research.

Most outcrops of high quality diatomite support unique vegetation. In the Purisima Hills, bishop-pine forest and douglas-fir forest grow almost exclusively on diatomaceous substrates. Chaparral and coastal sage-scrub communities have lower species richness on diatomite than on adjacent substrates.

The diatomaceous substrates in the Purisima Hills support a large percentage of plants near the southern limits of their ranges (Cole, 1974). The population of douglas fir is disjunct 150 km south from its next occurrence along the coast (Griffin, 1964). Similarly, *Polystichum munitum, Vaccinum ovatum, Arbutus menziesii,* and *Lupinus arboreus* were found only on diatomaceous substrates in the area. The diatomaceous shale substrate in the Purisima Hills supports a large percentage of plants also located on the northern Channel Islands (21 out of 62 plants collected on this substrate). It is noteworthy that much of Santa Cruz Island is underlain by diatomaceous shale.

Edaphic control of the distribution of bishop pine. The distribution of *Pinus muricata* is strongly influenced by substrate type. Although stands of forest are located on all substrates, the densest and most extensive forests are on diatomaceous shale. The sandstone substrate supporting pine forest is similar to the diatomaceous shale substrate in that the forests are located in pockets of quartz-rich sand with little clay content.

Other localities in Santa Barbara County conform well to the model of edaphic control in the Purisima Hills. At the Johns Manville Quarry and Pine Canyon at Graciosa Ridge, extensive forests grow (or grew) on diatomite of the Sisquoc Formation. The bishop pines on nearby Vandenburg Air Force Base are less restricted to the diatomite units with the most extensive groves located on adjacent sandstones (Paul Zedler, pers. comm., 1979).

Pinus muricata is distributed discontinuously along 1400 km of Pacific coastline from near Oregon to Baja California. It occurs on a variety of soils, but most are shallow, acidic, and poorly drained (Vogl et al., 1977).

Substrate restriction in the study area is probably the result of reduced competition from the surrounding chaparral and sage communities, rather than an inability of the pine forest to survive on other substrates. The situation is similar to that of other moisture-loving species that are restricted to acidic substrates in xeric habitats (Kruckeberg, 1969).

Edaphic control of other communities. Wells (1962) also concluded that chaparral communities dominate on siliceous substrates while coastal sage-scrub communities dominate on argillaceous substrates. This has been explained as a result of moisture availability (Harrison et al., 1971). Oak grassland is best developed on gentle north slopes with deep soils.

Fire roads plowed during the last 20 years were invaded by coastal scrub communities even in dense chaparral thickets. This may support Cooper's (1922) suggestion that coastal sage scrub is successional to chaparral. However, an extensive fire in 1959 did not affect the ecotonal placement between the communities. The only recognizable change occurring in the area since the first stereo aerial photographs were taken in 1954 was a thinning of the closed-cone pine forest in the fire area. Although this fire had no affect on community patterning, a more (or less) severe fire might.

Edaphic restrictions of these more widespread communities are not as definite as those of the closed-cone pine forest. Perhaps the best explanation for the patterning between these communities lies in the past; events have occurred that allowed one community to expand at the expense of another, while each community has maintained a core where it is most favorably adapted to substrate and microclimate. The present distributions could be described as: (1) stable, changing only with long-term climatic or other changes; (2) stable, dominant plants controlled by some edaphic or climatic factors yet unmeasured; or (3) changing so slowly that 24 years of aerial photography could not demonstrate a change.

Geologic control of vegetational patterns. Vegetational boundaries on steep slopes in temperate habitats often correlate strongly with underlying geology. Deep soil development is prevented by steep topography and climatic limits on vegetation are less controlling than in more severe habitats. As a result, plants compete for dominance on a variety of substrates. Although each community could probably occupy any substrate successfully, only the most competitive community will dominate any given substrate.

The importance of these relationships has been obscured in the past by comparison of substrates and vegetation over large areas. There is no reason to expect a community restricted to a particular substrate to exhibit this restriction 50 km away because many climatic factors may have changed over that distance. Another problem is the variable nature of rocks themselves. A formation of sandstone may include layers of shale or limestone not indicated on a large-scale geologic map. Stratigraphic knowledge and the ability to do simple, projective geological mapping will often uncover plant-rock relationships that would otherwise escape notice. One last complication is that two very different substrates can yield similar soils and vegetation. For example, diatomite and siliceous sandstone both can produce shallow acidic soils capable of deep water percolation.

The vegetational mosaics of coastal California provide unique opportunities for the study of the interrelationships between substrate and vegetation. Unfortunately, many plant ecologists have turned away from this kind of study because the variability inherent in rocks is probably as great as the variability within the vegetation itself. Nevertheless, there is great potential in the study of these correlations.

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GERMINATION, GROWTH, AND WATER RELATIONS OF ASTRAGALUS LENTIGINOSUS VAR. NIGRICALYCIS (FABACEAE)

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Abstract

Astragalus lentiginosus var. *nigricalycis* Jones is a leguminous, drought-evading hemicryptophyte endemic to the San Joaquin Valley of California. Germination in the growth chamber was 0–13 percent by day 20 over a wide range of temperatures (from constant 3°C to alternating 35/20°C) and photoperiods (8–14 hr, 225 W/m^2). In a Temblor Range plot, we obtained 7.5 percent establishment with 115 mm precipitation. Eighteen hr light and 21 ± 4 °C provided optimal conditions for vegetative growth. Davis, CA, field conditions led to flowering by early March. Seed vernalization was not effective in bringing this variety into flowering. Summer dormancy was moisture-dependent. Onset of wilting occurred at −3.8 MPa xylem pressure potential.

Astragalus lentiginosus Dougl. is a complex and variable species, containing many perennial and some annual varieties. Munz (1959) stated that this species is a "group of reticulately interrelated forms, and most of them intergrading freely at the edge of their ranges with vicariant relatives."

A. lentiginosus var. *nigricalycis* Jones is a San Joaquin Valley endemic (Twisselmann, 1967), growing in Mediterranean-type arid and very arid climates (Sankary, 1971) and found as a frequent companion of the Atripleto-Brometum community. It becomes only occasional in the Junipereto-Stipetum community in the Temblor Range, California. Selected strains of var. *nigricalycis* might become an important spring forage legume in arid and very arid zones throughout the world. Its toxicity is debatable. Keeler (1975) in Utah indicated that *Astragalus lentiginosus* is particularly potent in inducing congenital deformities in sheep, but California field observations by Twisselman (pers. comm., 1970) indicate little, if any, toxicity.

In this paper, we examine some factors that affect germination, establishment, growth, reproduction, and water relations of *Astragalus lentiginosus* var. *nigricalycis*. This paper is part of a series of ecological studies on dominant species of comparable Syrian and Californian arid zones (Sankary, 1971; Sankary and Barbour, 1972a, 1972b, 1972c). Plant nomenclature follows Munz (1959).

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METHODS

Germination experiments. Seeds of *Astragalus lentiginosus* var. *nigricalycis* were collected in June, 1969, from the Elkhorn Experimental Site, Kern County, in the southern portion of the San Joaquin Valley at approximately 35°10′N. The climate is Mediterranean-type arid with variable precipitation, averaging 145 mm per annum, none falling June through August. The mean maximum/minimum temperatures are estimated as 36/20°C for July and 11/2°C for December (Sankary, 1971).

Seeds were collected in paper bags, then stored in open glass jars at room temperature and exposed to room light. Germination is considered in this work as protrusion of the radicle from the seed coat. When a sand cover was used over sown seeds, all seedlings that appeared above the sand surface were considered established.

To examine the effect of temperature and light on germination, we used growth chambers (Percival PGW-108) for the following treatments: 14 hr light and 12°C, 8 hr light and 23°C, 14 hr light and 30/15°C, and 14 hr light and 35/20°C. We used a cold room for darkness and 3°C, and a germinator for darkness and 30°C. In all experiments we used 7 × 7 × 7 cm plastic pots filled with sterile sand and subirrigated with distilled water. Germinated seeds were counted daily during the first 20 days and a final count was made on the 40th day.

Germination and establishment in the field were followed in a Temblor Range plot located within an exclosure established by the Temblor Range research team of the University of California at 35°10′N, 119°30′W, 200 m elevation. The soil in this plot is a crusty loam of pH 7.2. Soluble salt content is low (0.55–0.63 mmhos/cm), boron is 0.5–1.4 ppm, and $CaCO_3$ is 4.0–4.5 percent. The climate is typically Mediterranean with variable precipitation that averaged 200 mm per annum for 1955–1970. The soil was plowed on 16 December 1969 with a 10 cm cultivator shovel, but the vegetation, mulch, and seeds present were not removed. We employed four replicates, each consisting of a 1 × 1 m plot with four furrows, sown with 400 seeds about 0.5 cm deep and 4 cm apart. Observations on establishment were first made on 29 April 1970.

Growth, reproduction, and dormancy. Growth and reproductive aspects were studied at different thermophotoperiodic regimes at little water stress. The regimes imitated daylength and/or temperatures of all seasons in the natural habitat: 8 hr light and 23°C, 12 hr light and 21 ± 4°C, 14 hr light and 35/20°C, and 18 hr light and 21 ± 4°C. The 8-hr light regime was produced in a growth chamber with light intensity of 290 W/m^2 at plant level (both fluorescent and incandescent bulbs). All other regimes were produced in a greenhouse, with the photoperiod artificially extended (fluorescent and incandescent bulbs, 65 W/m^2 at plant level).

The seedlings for these experiments were raised from seeds germinated in 7 × 7 × 7 cm plastic plots filled with sterilized sand and subirrigated with half-strength Hoagland's solution. As seedlings attained an age of 30–40 days, they were transplanted into subirrigated 18 × 15 cm plastic pots filled with sterilized sand. The pots were watered by distilled water from the top once every 10 days to prevent salt accumulation. Soil solutions never exceeded 1.5 mmhos/cm in electrical conductivity and generally were 1–1.3 mmhos/cm (about −0.05 MPa osmotic potential). Notes on height and phenology were taken at 10 day intervals for 4 months except when specified otherwise. Three plants were used per treatment.

Water relations. The Scholander bomb (Scholander et al., 1965) was used to measure water stress. The data are expressed in megapascals (MPa) of negative water potential (xylem pressure potential). For each measurement, we used a 7–10 cm twig with several leaves. Whenever permitted by the branching pattern and size of the plant, twig sampling was performed systematically from base to top, in order to detect differences in water potential with height. The twig was sealed in a pressure chamber and pressure was applied with compressed nitrogen. The pressure is generally considered equal to the water potential of the leaf cells (Boyer, 1969).

Plants either were subirrigated continuously or were allowed to dry. Four subirrigated plants were used for each thermophotoperiodic regime employed. These plants were 4–5 months old and had been kept for that time in these same regimes. The regimes and the planting and subirrigation methods were identical to those used for studying growth and reproduction.

Additional plants grown in a greenhouse in sandy loam were allowed to dry. Eight 4-month-old plants were divided into four groups, each group composed of two plants in a 15 × 18 cm pot. Initially, for 25 days, all plants were watered at 2 day intervals. The first determination of twig water potential was made at field capacity about 16 hr after the last watering. From then on, no water was given to the plants and moisture determinations were taken periodically (noontime) until wilting occurred. The experiment took place between February and April, with natural photoperiods of 11–12.5 hr.

RESULTS AND DISCUSSION

Germination experiments. Germination generally was very poor. By day 20, it ranged from 0 to 13 percent and it was not much higher by day 40. The speed of germination increased with temperature (Table 1). The optimum germination temperature was 35/20°C, which was similar to the pattern for *Astragalus oxyphysus* from California and *A. spinosus* from Syria (Sankary, 1971). Hammouda and Bakr (1969) found that maximum germination of the Egyptian nanopha-

TABLE 1. EFFECT OF TEMPERATURE ON GERMINATION OF *A. lentiginosus* VAR. *nigricalycis*. Average of 3 replicates, 20 seeds each.

Temperature (C°)	Photoperiod (hr at 1800 ft-c)	First day of germination	Germination (%) 10th day	20th day	40th day
3	0	24	—	—	5
12	14	5	3	5	7
23	8	5	7	7	7
30	0	5	3	7	7
30/15	14	5	10	13	13
35/20	14	3	10	13	15

nerophyte *A. sieberi* and the winter annual *A. hamosus* occurred at 30–35°C. This optimum is somewhat anomalous because such temperatures do not occur in nature when there is appreciable soil moisture.

As with many other arid zone species studied by the senior author (Sankary, 1971), sand cover improved germination and aided establishment. Germination was indifferent to photoperiod, however, so the effect of sand may have been improvement of moisture relations around the seed, rather than attrition of light.

In the field plot, *A. lentiginosus* var. *nigricalycis* exhibited an ability to germinate and establish itself with only 115 mm rain, and its rate of establishment was almost equal to that of the Syrian species *Salsola vermiculata* var. *villosa,* seeded at the same time (Sankary and Barbour, 1972a). On 29 April 1970, we recorded 7.5 percent establishment, which is modestly high when compared with 15 percent at optimum temperature in controlled conditions where moisture was not limiting.

The seedlings grew slowly, reaching 2–2.5 cm in April, with 4–5 leaves each. Two naturalized annuals were present in the same plot: *Bromus rubens* and *Erodium cicutarium*. Their growth was also slow, *B. rubens* attaining a height of 5 cm with 1–2 spikelets, and *E. cicutarium* reaching 4 cm with 1–2 fruits per plant. In September, 1978, the plot was revisited. No *Astragalus* survivor was observed, possibly because of competition with *Salsola vermiculata* var. *villosa*. Approximately 5000 *Salsola* plants were present in a 1-ha area about the plot, so it is clear that this species is spreading aggressively and is offering competition that *Astragalus lentiginosus* does not normally encounter in California.

Growth, reproduction, and dormancy. As with 17 other species from the Mediterranean-type arid zones of California and Syria, the 8 hr light and 23°C regime was not effective in bringing *Astragalus* into flowering (Table 2). This regime imitated spring or fall temper-

TABLE 2. EFFECT OF TEMPERATURE AND PHOTOPERIOD ON HEIGHT AND FLOWERING OF *Astragalus lentiginosus* VAR. *nigricalycis*. Average of 3 plants/treatment. FB = formation of visible floral buds; Fr = fruiting. Plants in thermophotoperiod columns 2, 3, and 5 were germinated and grown for 40 days in 14-hour light, 30/15°C before receiving the treatments described.

		Photoperiod (hr) and temperature (C°)				
	hr:	8	12	14	14	18
	C°:	23	21 ± 4	35/20	35/20	21 ± 4
Day:	10	Height (cm): 1.5	13	14	3.5	10
	20	3	15	16	5	13
	30	4.5	18	18	7	19
	40	6	22	29	10	25
	50	9	26	22	14	29
	60	12	30	24	20	34
	70	15	34 FB	26	23	38
	80	20	38	29	25	42
	90	25	44 FB	32	28	46
	100	31	48	35	30	50
	110	—	48 Fr	36	32	55
	120	—	48	38	34	60
Flowering (% by day 120)		0	100	0	0	0

atures and short photoperiods. Three plants that had germinated and grown for 100 days in this regime formed visible floral buds within 2 months when transferred into a 14 hr light and 12°C regime. Plants raised from seeds in 14 hr light and 30/15°C for 40 days, then transferred to 12 hr light and 21 ± 4°C (imitating late winter), flowered and fruited by day 90 (Table 2).

At Davis field conditions (4 plants, pot experiment planted on December 5 at age of 1 month), plants formed visible floral buds very early in February, and all were in full bloom by early March. *Astragalus oxyphysus* flowered in a similar pattern, following a relatively long juvenile stage of about 1 year. *Astragalus spinosus* from Syria also flowered in nature by February. Apparently, all these species are short-day plants (Sankary 1971, 1977).

Plants raised from seeds in 14 hr light and 30/15°C for 40 days, then transferred to 14 hr light and 35/20°C (imitating early summer) grew well and did not enter summer dormancy. This regime did not promote flower induction, whether the seeds were vernalized or not, although the vegetative growth was good (Table 2). Under Davis field conditions with maximum daily temperatures above 40°C, *Astragalus* continued growing all summer, as long as moisture was available. This indicates that summer dormancy is controlled by moisture, not by temperature.

Plants raised from seeds in 14 hr light and 30/15°C for 40 days, then

TABLE 3. RELATIONSHIP BETWEEN TWIG WATER CONTENT AND WATER POTENTIAL WITH PROGRESSIVE DECREASE IN SOIL MOISTURE. Average of two readings from two plants.

Plant water content (% dry weight)	Twig water potential (MPa)	Average plant condition
78.2	−1.1	All leaves turgid, soil at field capacity
75.8	−1.6	
71.2	−1.9	
62.0	−2.8	Lower leaves permanently wilted
60.0	−3.8	95% of leaves dried, only two youngest leaves still unwilted (all leaves recovered upon rewatering)

transferred to 18 hr light and 21 ± 4°C (long photoperiod, spring or fall temperatures) grew optimally and neither flowered nor entered summer dormancy (Table 2).

A final group of plants was exposed to a gradual change of temperature, imitating a change from winter to early summer, with a constant photoperiod of 14 hr. Eight seedlings were grown for their first 2 mo at 12°C. Shoot growth was slow, height reaching only 2 cm and only two leaves per plant developing. Root growth was 10–15 cm, however. By the end of the second month, seedlings reached a height of 5 cm and developed six leaves. Then three plants were selected and temperatures raised to 30/15°C for 2 months, then raised again to 35/20°C for one additional month.

This sequential change did not induce flowering or dormancy, but did result in rapid shoot growth: 15 cm height the third month, 28 cm the fourth, and 36 cm the fifth.

Water relations and drought endurance. Plants continuously subirrigated showed an average predawn water potential of −0.3 MPa and an average noon water potential of −1.0 MPa, with relatively little difference among the four thermophotoperiodic regimes used. This average was about 50–60 percent less negative than those of such summer-active shrubs as *Atriplex polycarpa, A. lentiformis, A. lencoclada, Salsola vermiculata,* and *Haloxylon articulatum* (Sankary, 1971; Sankary and Barbour, 1972a, 1972b, 1972c).

When those plants were allowed to dry, twig water content and water potential dropped gradually until there was a sharp decrease as the soil approached the permanent wilting point (Table 3). On 29 April 1970 (a dry year), *Astragalus* plants in the arid zone of California were dry, while adjacent *Atriplex polycarpa* plants were still actively growing. Field measurements showed that *A. polycarpa* endured very low twig water potentials of −6.9 MPa (Sankary and Barbour, 1972a), while Table 3 shows that *Astragalus* did not tolerate noon values below −3.8 MPa. In relative terms, *Astragalus* is a drought evader.

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A NEW SPECIES OF CYMOPTERUS (UMBELLIFERAE) FROM THE TOIYABE RANGE, LANDER COUNTY, NEVADA

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ABSTRACT

Cymopterus goodrichii Welsh & Neese is described from the Toiyabe Range in Lander County, Nevada.

In the course of field studies leading to a floristic treatment of the Toiyabe, Toquima, and Monitor ranges of Nevada, Sherel Goodrich has discovered a series of unique taxa occurring predominantly at high elevations. The species herein described is such a plant. Populations are scattered within a 13-kilometer region in the Big Creek–Kingston area of the Toiyabe Range at elevations between 2230 and 3400 m. Plants grow in talus of angular slate and limestone. The slopes are steep (40–50 percent) and the colluvial talus creeps downslope under influence of gravity and climatic factors. Plants of this *Cymopterus* accommodate the change in position of the slope by producing elongate pseudoscapes that penetrate the talus gravels to the surface.

Pseudoscapes arise singly from the summit of a caudex that is either simple or branched. Caudex branches are clothed with marcescent leaf bases. The taproot is fusiform to subcylindric and penetrates deeply into the fine substrate below the angular gravels.

Material was sent to Dr. Lincoln Constance, long-time student of the genus. He noted (pers. comm., 1979) "We do not have nor have I ever seen anything like it."

The Goodrich cymopterus is distinct from other species in the genus in its long, flexuous, narrow pseudoscape, small leaves, and short rays. It is compared in the diagnosis with both *Cymopterus acaulis* and *C. fendleri* because those taxa, while apparently not closely allied to *C. goodrichii,* are the most similar to it. It simulates those taxa with its short rays, but is separable by the purplish involucellar bractlets, longer pseudoscape, and smaller leaves.

It is a pleasure to name the species in honor of Sherel Goodrich, enthusiastic collector and botanist, and specialist in diverse aspects of plant taxonomy.

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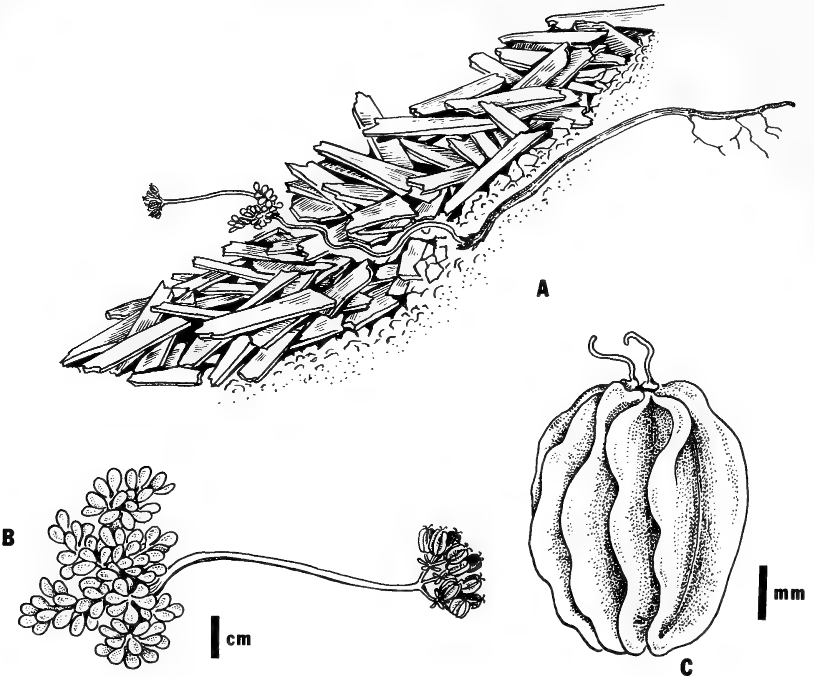

FIG. 1. *Cymopterus goodrichii* Welsh & Neese. A. Habit. B. Detail of leaves and inflorescence. C. Fruit.

Cymopterus goodrichii Welsh & Neese, sp. nov.

Ab specibus caeteris generis differt pseudoscapo longo flexuoso gracili foliis parvis radiis brevibus; similis *Cymoptero acaulis* (Pursh) Raf. et *C. fendleri* A. Gray radiis brevibus sed ab ambibus bracteis involucellis purpurescentibus pseudoscapo longiore et foliis parvioribus; et differt ad specibus caeteris pseudoscapo gerentibus radiis brevioribus et foliis parvioribus.

Herbae perennes, radice palari gracilibus fibrosa elongata; pseudoscapi flexuosi 4–15 (23) cm longi, saepe purpurascentes; folia subsessilia vel petiolis 3–50 mm longis caulina vel caudice enanescenti et 5–12 cm longi laminae 0.5–2 cm longae ovatae dissectae glaucae segmenta ultima 1–7 mm longa 0.5–2 mm lata congesta spatulata vel elliptica; pedunculi 1–6 cm longi; involucrum nullum; bracteole involucelli 3–4 mm longae lineares vel ellipticae anguste; radii 2–5 mm longi; pedicelli 2–4 mm longi in fructum; flores albidi vel purpurascentes; fructus 5–8 mm longus corpus circa 1.5 mm latum alae dorsales et laterales plerumque bene evolutae 1–2 mm latae (Fig. 1).

Perennial herbs from long, slender, fibrous taproots; pseudoscapes flexuous 4–15 cm long, often purplish; leaves cauline, subsessile or with petioles 3–50 mm long or arising from the caudex and 5–12 cm long, the blades 0.5–2 cm long, ovate, dissected, glaucous, ultimate segments 1–7 mm long, 0.5–1 mm wide, crowded, spatulate or elliptic; peduncles 1–6 cm long, involucre none; bractlets or involucel 3–4 mm long in fruit; flowers whitish or purplish; fruit 5–8 mm long, the body about 1.5 mm wide, lateral and dorsal wings usually well-developed, 1–2 mm wide.

TYPE: USA, NV, Lander Co., Toiyabe Natl. For., Toiyabe Range, crest of range between Frenchman Creek and Kingston Canyon, about 3 km n.e. of Bunker Hill, 24 km s. and slightly w. of Austin, T16N R43E S2 SE¼, 3320 m, 40 percent slope, loose slate talus of gravel- and cobble-sized fragments over gravelly soil slightly vesicular at surface, growing with or near *Ribes cereum, Haplopappus macronema, Erigeron compositus, Agropyron scribneri, Leucopoa kingii,* and *Leptodactylon pungens,* 14 Jul 1975, *S. Goodrich 11,816* (Holotype: BRY. Isotypes: UC, NY).

PARATYPES: USA, NV, Lander Co., Toiyabe Natl. For., near crest of Toiyabe Range, about 22 km s. and slightly w. of Austin, T17N R43E S36 NW¼ NE¼, w. exposure, slope 40–50 percent, shallow talus over gravelly soil, talus of limestone with some quartzite intrusions, 3170 m, growing with *Draba arida,* 21 Jul 1978, *S. Goodrich 11,874* (BRY); crest of range between Big Creek and Globe Canyon, 22.5 km s. and slightly w. of Austin, near corners of TN R43E S35–36 and T16N R43E S1–2, 3540 m, in 5–10 cm of elongated gravel- and cobble-sized slate over very gravelly sandy loam soil, pH 7.8, with slight vesicular crust, 20 percent slope, e. exposure, one plant of *Crepis nana* associated in a small area of loose talus, *Leucopoa kingii* nearby, 14 Jul 1978, *S. Goodrich 11,795* (BRY); along crest of range between Kingston Canyon and Frenchman Creek, T16N R43E S2 SE¼, 25 km s. and slightly w. of Austin, 3230 m, 14 Jul 1978, *S. Goodrich 11,831* (BRY); above head of Big Creek drainage, about 23 km s. and slightly w. of Austin, T16N R43E S2 NE¼, 3200 m, shallow slate talus over gravelly soil, w. exposure, growing with *Gilia congesta,* 21 Jul 1978, *S. Goodrich 11,866* (BRY); North Fork Big Creek, 18 km s. of Austin, 39°20′37″N, 117°6′53″W, 2230 m, gravelly slopes and very unstable gravel- and cobble-sized talus on 50 percent slope, 9 Jul 1979, *S. Goodrich 13,310* (BRY); w. side of Bunker Hill, 27 km s. of Austin, 39°15′18″N, 117°7′35″W, 3400 m, steep talus slopes of gravel- and cobble-sized limestone, associated with *Erigeron compositus, Polemonium viscosum, Gilia congesta, Astragalus platytropis, Poa rupicola,* and *Ribes cereum,* 10 Jul 1979, *S. Goodrich 13,344* (BRY); steep w. exposure near crest of range above Big Creek, 24 km s. of Austin, 39°17′5″N, 117°6′15″W, 3130 m, gravel- and cobble-sized talus of slate, with *Draba arida, Haplopappus macronema, Ribes mon-*

tigenum, Artemisia michauxiana, 10 Jul 1979, *S. Goodrich 13,318* (BRY, NY); steep s.w. exposure at crest of range between Kingston and Santa Fe Creeks, 24 km s. of Austin, 39°16′30″N, 117°6′20″W, 3230 m, gravel- and cobble-sized talus of slate, 10 Jul 1979, *S. Goodrich 13,324* (BRY, RENO, UC, UTC); near crest of range above Kingston Creek, 24 km s. of Austin, 39°16′45″N, 117°6′15″W, 3300 m, gravel- and cobble-sized talus of slate over clay loam soil with vesicular crust, soil strongly effervescent with 10 percent HCl, pH 8.0, parent material slightly effervescent, with *Ribes montigenum, Haplopappus macronema,* and *Artemisia michauxiana,* 10 Jul 1979, *S. Goodrich 13,322* (BRY, UT).

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THE GENUS NEMACAULIS NUTT. (POLYGONACEAE)

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ABSTRACT

Nemacaulis Nutt. (Polygonaceae) is a monotypic genus belonging to the subfamily Eriogonoideae. The genus is restricted to the coastal and desert regions of extreme southern California, southwestern Arizona, and adjacent northwestern Mexico. The species, *N. denudata* Nutt., consists of two variants, the coastal var. *denudata* and the inland var. *gracilis* Goodman & Benson. The two variants are distinct throughout much of their ranges but tend to merge in northwestern coastal Baja California where the desert comes in contact with the Pacific coast. *Nemacaulis* is most closely related to *Eriogonum* Michx., and probably evolved from the subgenus *Ganysma,* near *E. gossypinum* Curran.

This paper is a continuation of our review of the genera belonging to the subfamily Eriogonoideae Benth. (Polygonaceae Juss.) begun with the discovery of the genus *Dedeckera* Reveal & Howell (1976). So far, the genus *Stenogonum* Nutt. has been reestablished (Reveal & Ertter, 1977a) and *Goodmania* Reveal & Ertter (1977b) proposed for the discordant *Oxytheca luteola* Parry. Reviews of *Eriogonum* Michx. (Reveal), *Oxytheca* Nutt. (Ertter), *Hollisteria* S. Wats., *Gilmania* Coville, and at least one more new genus are presently being prepared by us separately or jointly. The present paper brings our understanding of *Nemacaulis* Nutt. up to date.

TAXONOMY

NEMACAULIS Nutt., Proc. Nat. Sci. Philadelphia 4:18. 1848.—LECTOTYPE: *N. denudata* Nutt., by implication in Nuttall (1848b).

Plants erect to prostrate annual herbs arising from thin woody taproots; leaves basal and cauline, the basal completely sheathing the short stem and forming a basal rosette, the cauline usually present at least at proximal nodes; stems solitary, erect, short, covered by petiole-bases; inflorescences compound, many-branched at the first node, dichasially thereafter, often becoming spiciform distally due to tardy development of the second branch, each node usually bearing three cauline bracts subtending the cauline leaves and a single sessile or pedunculate glomerule consisting of a number of involucral bracts each subtending a single sessile or pedicellate flower and 2 bractlets;

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involucral bracts in whorls of 5, sometimes only the outer fertile, glabrous without, densely lanate within, the margins scarious; flowers perfect, campanulate, the tepals 6, ± united with a smooth or papillate thickened ridge at the inside base of the free lobes, the margins broadly scarious; stamens 3, included, attached opposite the outer tepals on the inner ridge; pistils solitary, 3-carpellate, the ovary 1-celled, the styles 3, short, each terminated by a subcapitate stigma; fruits ovoid, indistinctly 3-angled achenes falling free from the tepals at maturity; embryos curved, with abundant endosperm.

A monotypic genus of dry sandy places in the desert and along the Pacific coast of the American Southwest and adjacent northwestern Mexico.

Nemacaulis was first collected in 1836 along the ocean beaches of San Diego, California (then Alta California), by Thomas Nuttall, who was in San Diego from 15 April to 7 or 8 May. Nuttall had traveled westward with Nathaniel J. Wyeth, a Boston merchant, from Philadelphia to the mouth of the Columbia River in 1834, and was on his way home via the Horn when he visited California (McKelvey, 1955; Graustein, 1967). The genus was described in the Proceedings of the Philadelphia Academy of Natural Sciences (Nuttall, 1848a), but as he failed to characterize either of the two species proposed at the time, the genus was without a valid species. Later in that year, a second edition of Nuttall's paper appeared, and in the Journal Nuttall (1848b) proposed two species, *N. denudata* and *N. foliosa* (Reveal and Spevak, 1967). Bentham (1856), in his revision of Eriogonoideae, lumped the two species into a single species which he termed *N. nuttallii,* a superfluous substitute. Torrey and Gray (1870) followed Bentham in this practice, but the proper name, *N. denudata,* was soon in use amongst California workers.

Nemacaulis, like *Hollisteria, Gilmania, Goodmania,* and *Lasterriaea* Remy in Gay, is one of the minor eriogonoid genera whose exact placement in the subfamily Eriogonoideae is uncertain. It bears a superficial resemblance to *Eriogonum gossypinum* Curran, which led Curran (1885), Stokes (1936), and Roberty and Vautier (1964) to place it in that genus. However, *Nemacaulis* has only three stamens (not nine as in *Eriogonum*) and lacks the tubular involucre that is characteristic of *Eriogonum* (Reveal and Howell, 1976; Reveal, 1978). Yet *N. denudata* and *E. gossypinum* are the only species in the subfamily that have flowers imbedded in a dense tomentum. *Goodmania* shares with *Nemacaulis* its free involucral bracts, though not in such abundance. *Hollisteria* has densely woolly vegetative parts like *Nemacaulis,* while *Gilmania, Lasterriaea,* and a few species of *Eriogonum* have the inner floral ridge of *Nemacaulis* flowers.

It would seem that the ideas of relationship suspected by Curran (1885) are correct and that *Nemacaulis* probably evolved from the subgenus *Ganysma* (S. Wats.) Greene of *Eriogonum,* the same subgenus from which *Oxytheca, Stenogonum, Gilmania, Goodmania,* and perhaps *Hollisteria* arose (Reveal, 1978). *Nemacaulis* has probably undergone rapid evolutionary development in the hot deserts of southern California and adjacent Mexico since diverging from *Eriogonum.*

Nemacaulis now appears to be more distantly related to *Eriogonum* than is *Oxytheca.* For the most part, *Oxytheca* has retained its gross morphological similarities with *Eriogonum* subg. *Ganysma* far more and over a broader spectrum of features than has *Nemacaulis.*

The single species may be characterized as follows:

NEMACAULIS DENUDATA Nutt., J. Acad. Nat. Sci. Philadelphia II, 1:168. 1848.—For synonymy and typification see the varietal headings.

Plants erect to prostrate or decumbent, 2–8 dm across and 0.4–2.5 (4) dm tall; leaves linear to spatulate, densely white-tomentose on both surfaces, the margins undulate, the apex blunt, the base tapering to a long, narrow petiole, the basal leaves 1–8 cm long (including the petiole), 0.1–1.5 cm wide, the cauline leaves 0.5–4 (7) cm long, 0.1–1 cm wide; stems solitary, (0.2) 0.5–2 (4) cm tall; inflorescences diffuse, 2–8 dm across or 0.3–3 dm tall, the branches wiry or thread-like, glabrous to glandular or sparsely lanate, (2) 4–10 at the first node, 1–2 (3) thereafter, the glomerules 2–6 cm wide, sometimes deciduous at maturity; cauline bracts usually 3, sometimes fewer, triangular to obovate or linear, 1–5 mm long, 0.5–2 mm wide, basally connate to half-united, glabrous to glandular without, lanate within, herbaceous, dark red to light greenish-brown; peduncles lacking, or if present then 0.5–3 mm long and slender; involucral bracts oblanceolate to broadly spatulate, 2–4 mm long, 0.5–2 mm wide, dark red to light greenish-brown, glabrous without, densely lanate within, the tomentum white or tawny, the margins broadly scarious, the bractlets linear and hyaline, sparsely lanate, 1 mm long, sometimes tinged with pink, the pedicels lacking or 1 mm long, slender; flowers 5–30 per glomerule, narrowly to broadly campanulate, 0.8–1.5 mm long, at least partially buried in the tomentum of the involucral bracts, the tepals united ¼–⅓ their length, the inner 3 linear to oblong, slightly longer than the linear to oval outer 3, dark red to light brown or greenish-white, glabrous or more frequently sparsely covered with narrow, gland-tipped hairs without, the scarious margins white to yellowish or pink; stamens 0.5–1 mm long, the filaments glabrous, the anthers round, 0.2 mm wide, light red to dark pink; achenes light brown to dark red or black, shiny, 1 mm long, the 3 angles of the short acute beak becoming indistinct in the plump ovoid body.

Key to *Nemacaulis*

Plants decumbent; leaves usually spatulate, sometimes linear; involucral bracts broadly spatulate, dark red, the tomentum white;

glomerules sessile, (2) 4–6 mm wide; flowers usually more than 10 per glomerule, the outer tepals broadly obovate; coastal beaches. . . . . 1a. var. *denudata*.

Plants erect; leaves linear; involucral bracts oblanceolate, light greenish-brown, the tomentum often tawny; glomerules often pedunculate, 2–4 mm wide; flowers usually 5 (12) per glomerule, the tepals linear; inland. . . . . lb. var. *gracilis*.

1a. NEMACAULIS DENUDATA Nutt. var. DENUDATA.—*Nemacaulis nuttallii* Benth. in DC., Prodr. 14:23. 1856, a superfluous name.—*Eriogonum denudatum* (Nutt.) Curran, Bull. Calif. Acad. Sci. 1:274. 1865, non Nutt., 1848.—*Eriogonum nemacaulis* S. Stokes, Gen. Eriog. 39. 1936.—TYPE: USA, CA, San Diego Co., In sandy places near the sea shore, San Diego, Apr–May 1836, *Nuttall s.n.* (Holotype: BM!; isotypes, GH!, K!, NY!).

Nemacaulis foliosa Nutt., J. Acad. Nat. Sci. Philadelphia II, 1:169. 1848.—USA, CA, San Diego Co., "With the above [*N. denudata*], from which it is perhaps not distinct," Apr–May 1836, *Nuttall s.n.* (Holotype: BM!; isotypes: K!, PH!).

Plants prostrate to decumbent, 2–8 dm across; leaves usually spatulate, sometimes linear, the basal leaves 2–8 cm long, 0.3–1.5 cm wide, the cauline leaves usually well-developed, 1–4 cm long, 0.2–1 (1.3) cm wide; inflorescences very diffuse, 2–8 dm across, the branches thick, wiry, thread-like only at the extremities, dark red, the glomerules usually sessile, (2) 4–6 mm wide, firmly attached; cauline bracts usually 3, sometimes fewer, broadly triangular or obovate to elliptic, 1–5 mm long, 0.5–2 mm wide, often unequally sized and spaced, basally connate or irregularly united, dark red; peduncles usually lacking; involucral bracts numerous, broadly spatulate or divided into a distinct orbicular blade and petiole, 1.5–3.5 mm long, 1–2 mm wide, dark red, all usually alike, fertile, and concave, the tomentum white, the pedicels 1 mm long; flowers (5) 12–30 per glomerule, broadly campanulate, 1–1.5 mm long, half-exposed, the tepals dark red with white or pink margins, the outer 3 oval to obovate.

Locally common on sandy beaches along the Pacific Coast from Los Angeles County and Santa Catalina Island south to San Quintín, Baja California Norte, Mexico, mostly below 5 m. Flowering from late March in Baja California Norte to August farther north (Fig. 1A–D).

1b. NEMACAULIS DENUDATA Nutt. var. GRACILIS Goodman & Benson in Munz, Aliso 4:89. 1958.—TYPE: USA, CA, Riverside Co., Agua Caliente, Palm Springs, desert base of San Jacinto Mountains, 150–200 m (500–700 ft), 4–13 Apr 1896, *S. B. Parish 4140*. (Holotype: UC!; isotypes: DS!, GH!, LAM!, MO!, NY!, PH!)

Plants ascending to erect, 0.4–2.5 (4) dm tall, delicate; leaves linear

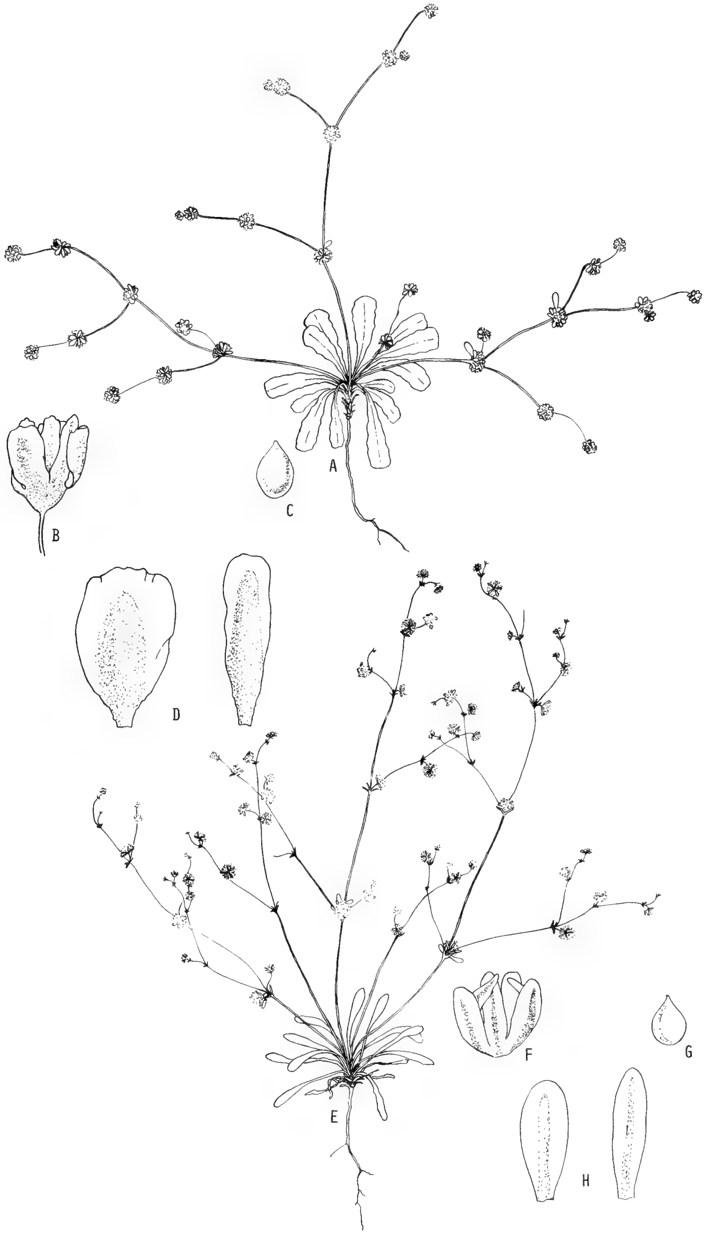

FIG. 1. *Nemacaulis denudata*. A.–D. var. *denudata*. A. Habit. B. Flower. C. Achene. D. Outer (left) and inner (right) tepal. E.–H. var. *gracilis*. E. Habit. F. Flower. G. Achene. H. Outer (left) and inner (right) tepal.

or narrowly spatulate, the basal 1–7 cm long, 0.1–0.6 cm wide, the cauline often undeveloped, 0.5–2 cm long, 0.1–0.3 cm wide; inflorescences more compact than in var. *denudata,* 0.3–2.5 (4) dm tall, most branches except the lower ones slender, thread-like, and light brown, most glomerules distinctly pedunculate, 2–4 mm wide, often deciduous at maturity leaving bare branches; cauline bracts regularly 3, narrowly triangular or linear to oblanceolate, 1–4 mm long, 0.2–1 mm wide, all equally sized and spaced, basally connate, light brown or greenish; peduncles usually present and slender, 0.5–3 mm long, easily deciduous; involucral bracts few, oblanceolate, 2–4 mm long, 0.5–1 mm wide, light brown to yellowish-green, sometimes tinged with red, the outer 5 bracts fertile and spreading out in a single plane, the inner bracts often sterile and curled inwardly, the tomentum white or more often tawny, the pedicels lacking or up to 1 mm long; flowers commonly 5 (12) per glomerule, narrowly campanulate, 0.5–1.2 mm long, usually buried in the tomentum, the tepals light brown or green with white, yellow, or pink scarious margins, the outer 3 linear to oblong, the inner 3 linear to oblong.

Rare to locally common on sandy or gravelly soils, mostly inland, from San Diego and Riverside cos., California, eastward to western Yuma Co., Arizona, and south to west-central Baja California Sur and northwestern Sonora, Mexico, from below sea level to 450 m. Flowering from January in Mexico to May farther north (Fig. 1E–H).

The two varieties are more distinct than might be expected from the original description (Munz, 1958) or floristic treatments (Munz, 1959; Shreve and Wiggins, 1964; Munz, 1974) and might deserve specific distinction were it not for the hybridization that occurs where the two meet along the Pacific Coast. Nearly all plants of either variant from San Diego to Soccoro, show some signs of genetic contamination from the other variety. Delicate plants with *gracilis* tepals and oblanceolate involucral bracts will be found with numerous flowers and dark red coloration, while wiry-stemmed prostrate plants with *denudata* flowers and large glomerules will have narrowly obovate greenish involucral bracts and distinct peduncles. Collections from the Descanso Dunes in Baja California Norte are particularly frustrating to place in either variant. In fact, Nuttall's original collection of *N. denudata,* while predominantly var. *denudata,* shows some characteristics of var. *gracilis*. Nuttall's type of *N. foliosa* is more typical of what we now recognize as var. *denudata*. In spite of this evidence of genetic exchange, differences in blooming time and preferred habitat keep the two variants reasonably distinct so that unmistakable var. *gracilis* can be found in San Diego near the coast, while perfectly good var. *denudata* abounds in the San Quintín area even in the presence of the other variety.

We have noted on the distribution map (Fig. 2) several collections

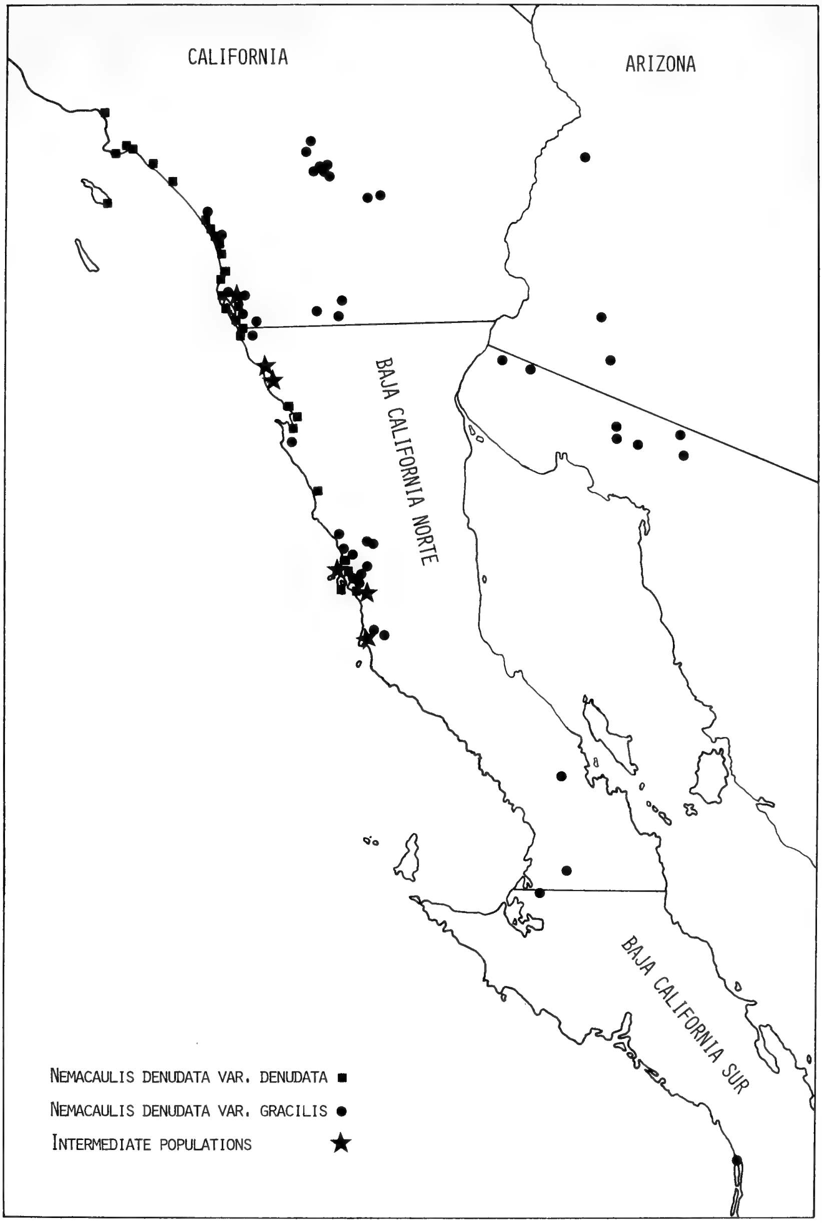

FIG. 2. Distribution of *Nemacaulis denudata* var. *denudata, N. denudata* var. *gracilis,* and intermediates.

that we are unable to place in either variant or that consist of both phases.

The two varieties do not merge gradually one into the other, but instead maintain some distinctiveness along their entire interface regardless of their propensity to intergrade. This, combined with the constancy of var. *gracilis* in the Colorado and Sonoran deserts, suggests that the two did not diverge from each other along the coast. The var. *denudata* probably evolved along the coast, while var. *gracilis* probably evolved inland, perhaps on the shores of the Pleistocene lake then in the Salton Sea basin. Only after the two varieties had evolved, but before internal isolation barriers developed, did they mingle in northern Baja California. The var. *denudata* was probably already well-established here, because it has maintained itself so well in San Quintín and San Diego while being swamped by var. *gracilis* around Descanso. The inland variant apparently has a much broader habitat tolerance as evidenced by its more scattered range. This may well be due too to its much greater dispersal capability as witnessed by the easily detached glomerules that might be blown from place to place by winds.

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(Received 18 Jul 1979; revision received 9 Nov 1979; accepted 31 Dec 1979.)

NOTEWORTHY COLLECTIONS

ALLIUM GEYERI Wats. var. GEYERI (LILIACEAE).—USA, OR, Wallowa Co., along n. side lower Imnaha R. ca. 0.5–1.5 km from its juncture with the Snake R. (T4N R48E S24 NE¼ W½), 350–400 m, 30 Apr 1979, *Meinke 2266, Meinke 2271* (OSC, BLM-USFS Herbarium, Baker, OR). A discontinuous series of small colonies extending for ca. 1.0 km on basaltic shelves adjacent to the river. Associated with *Glossopetalon nevadense* var. *stipuliferum, Sedum leibergii, Phlox colubrina, Lomatium dissectum, Festuca idahoensis, Penstemon deustus,* and *Selaginella wallacei.* Most plants were in full flower.

Previous knowledge. Known from e. WA, s. and e. to n. ID. Also in n.e. NV, extending e. to SD and s. to AZ and TX. (Herbaria consulted: ID, IDF, OSC, WS, LAGO, CIC, BS; published sources: Hitchcock et al., Vasc. pl. Pac. Northw. I. 1969.)

Diagnostic characters. Flowers not replaced by bulbils, differentiating this from var. *tenerum* M. E. Jones.

Significance. First record for OR; a disjunction of ca. 50 km westward. Var. *tenerum,* equally widespread but not known to be sympatric with the typical phase, occurs to within 40 km of the Imnaha var. *geyeri* population, along the Grande Ronde R. to the w. in the Blue Mts. This is the closest reported point between the ranges of these taxa, their distributions otherwise quite dissimilar.

MYOSOTIS LAXA Lehm. (BORAGINACEAE).—USA, OR, Wallowa Co., spring seepage, ca. 1.5 km e. of jct of Hess Rd. and USFS Rd. S393 (T5S R48E S34 NW¼ SW¼, 1310 m, 9 June 1977, *Meinke 1526* (BLM—USFS Herbarium, Baker, OR). Open coniferous forest (*Abies grandis–Pseudotsuga menziesii*) in moist soil with *Ranunculus glaberrimus, Floerkea proserpinacoides, Mimulus guttatus, Habenaria saccata, Mertensia ciliata,* and *Polemonium occidentale.* Plants were in flower and fruit, very scarce.

Previous knowledge. Reportedly circumboreal; in n.e. USA and adjacent Canada, w. to s. BC, s. in Pacific states to n.w. CA, from the Cascades to the coast; S. Amer.

(Herbaria consulted: ID, IDF, OSC, WS, LAGO, CIC, BS; published sources: Hitchcock et al., Vasc. pl. Pac. Northw. IV. 1959; Munz, A Calif. fl. 1959.) *Diagnostic characters.* Calyx strigose, hairs appressed, neither uncinate or spreading; corolla limb 2–5 mm.

Significance. First record e. of the Cascade Range in w. N. Amer., a disjunction of ca. 380 km. Certain members of this genus tend to establish as waifs in more or less weedy habitats. This species occurred on an apparently undisturbed site and, considering its circumboreal pattern of distribution, would seem to be indigenous. Additional collecting in this floristically little known area may help in substantiating this assumption.

GEUM ROSSII (R.Br.) Ser. var. TURBINATUM (Rydb.) Hitch. (ROSACEAE).—USA, OR, Baker Co., w. slopes adjacent to Willow Creek Lk., Elkhorn Ridge of the Blue Mts. (T8S R38E S17 SE¼ NW¼), 2470 m, 17 Aug 1977, *Meinke s.n.* (BLM-USFS Herbarium, Baker, OR); ca, 0.8 km e.s.e. of Willow Creek Lk., on shifting granodiorite talus, w. slope and along ridge (T8S R38E S17 SE¼ SE¼), 2550 m, 8 Aug 1979, *Meinke, Bafus, and Leary 2427* (OSC, ORE, BLM-USFS Herbarium, Baker, OR). Harsh subalpine sites with *Bupleurum americanum, Selaginella watsonii, Draba paysonii* var. *treleasii, D. densifolia, Sedum roseum, Arabis lyallii,* and *Claytonia megarhiza* var. *bellidifolia.* Populations isolated and extremely local.

Previous knowledge. Rocky Mts. from MT to NM; also in NV and AZ. Reported as disjunct in the Wallowa and Blue Mts. of n.e. OR (Herbaria consulted: ID, OSC, IDF, WS, LAGO, CIC, BS; published sources: Hitchcock et al., Vasc. pl. Pac. Northw. III. 1961.) Known from only three collections in OR, the last collection made in 1936.

Significance. Only recent collection of this species in OR. Occurred as a component of an unusual and probably undescribed plant community, reminiscent of alpine associations in the Rocky Mts. Tentatively referred to var. *turbinatum* although they appear to display consistent morphologic disparity from the bulk of the plants traditionally placed here. Hitchcock (op. cit) acknowledged that plants of n.e. OR are generally taller and more sericeous than average. He stated, however, that they do not seem significantly different from those of the Rockies. This observation was apparently based on the examination of one or two collections and without the benefit of field work. In light of this new material and field scrutiny, a reevaluation of the taxonomic status of these plants may be desirable. Further research is necessary to establish their affinities clearly.

CRYPTANTHA THOMPSONII Johnst. (BORAGINACEAE).—USA, OR, Baker Co., along Pine Lakes tr., ca. 4.0 km n.w. of Cornucopia, near the s. boundary of Eagle Cap Wilderness Area (T6S R48E S16 NW¼ SE¼), 1750 m, 23 July 1978, *Meinke 2139* and 1 Sept 1979, *Bafus 418* (OSC, BLM-USFS Herbarium, Baker, OR). Dry, loose, granitic talus, on steep s. slopes within a subalpine forest mosaic. Associate species included *Sedum lanceolatum* var. *rupicolum, Pellaea bridgesii, Aspidotis densa, Pinus albicaulis, Abies lasiocarpa, Castilleja viscidula,* and *Arenaria aculeata.* Collections from 1978 were in early flower, those from 1979 in late fruit.

Previous knowledge. Endemic to the Wenatchee Mts. of c. WA, Kittitas and Chelan cos.; especially on serpentine at middle elevations (Herbaria consulted: ID, IDF, OSC, WS, LAGO, CIC, BS; published sources: Hitchcock et al., Vasc. pl. Pac. Northw. IV. 1959.) *Diagnostic characters.* Perennial; corolla limb 4–8 mm; nutlets roughened dorsally, smooth ventrally, attachment scar open full length.

Significance. First record for OR; range extension of ca. 340 km to the s.e. This is the second endemic of the Wenatchee Mts. area recently found in the Wallowas. The first, *Sedum lanceolatum* var. *rupicolum,* is associated with *C. thompsonii* at this site and has been previously reported from the Wallowas at higher elevations. It is also said to occur, with some degree of uncertainty, from the mts. of adjacent w.c. ID (Bingham, Ann. list rare native pls. Hells Canyon NRA, report on file, USFS. 1979). The restricted geographic distribution of *C. thompsonii* has been a factor contributing to its designation as a Candidate Threatened species (U.S. Fish and Wildlife Service, Fed. Reg. 40 (127):27824–27924. 1975). This population is small but maintaining itself and in no apparent jeopardy.—ROBERT J. MEINKE, U.S. Dept. of the Interior, Bureau of Land Management, Baker, OR 97814. (Received 11 Sep 1979; accepted 31 Dec 1979.)

CHAMAEBATIA AUSTRALIS (Bdg.) Abrams (ROSACEAE).—USA, CA, San Diego Co., San Marcos Mts., 5 km n.e. of Vista, n.w. slope, 305 m (near 33°13′10″N, 117°11′15″W), 20 Apr 1978, *Armstrong s.n.* (SD 99509). Covering at least 18.5 ha of rocky San Marcos gabbro on slopes and ridges between 300–509 m, in some areas forming almost pure stands. Associated with *Tetracoccus dioicus, Cneoridium dumosum, Xylococcus bicolor, Comarostaphylis diversifolia, Adenostoma fasciculatum, Heteromeles arbutifolia,* and *Rhus integrifolia.*

Previous knowledge. Known from s. San Diego Co., including San Miguel, McGinty, Elena, Jamul, and Otay mts., Tecate Pk., and s. in Baja California to Cerro San Miguel at 1225 m. Locally common, forming dense stands with associated chaparral species. (Herbaria consulted: RSA, SD; published sources: Higgins, San Diego Soc. Nat. Hist. Occ. Pap. 8. 1949.)

Significance. First record in n. San Diego Co. and n.-most location in CA, a 62 km n.w. range extension from San Miguel and McGinty mts. Considered "rare and not endangered" (Powell, ed., Inventory rare endang. vasc. pls., Calif. Native Pl. Soc. Spec. Publ. 1. 1974). Some slopes are threatened due to clearing for avocado orchards.—WAYNE P. ARMSTRONG, Palomar College, San Marcos, CA 92069. (Received 17 Sep 1979, accepted 30 Dec 1979.)

NOTES AND NEWS

NOMENCLATURAL CHANGES IN *Ipomopsis congesta* (POLEMONIACEAE).—Regional variation in *Ipomopsis congesta* is apparent in herbarium material from throughout its range in the western United States . This is reflected historically in numerous described taxa, largely within the earlier framework of *Gilia.* A difficult complex, it involved also the *Gilia spicata* group. The problem was clarified by Constance and Rollins who, in their revision of the group (Amer. J. Bot. 23:433–440. 1936), found the means to separate *Gilia congesta* from *G. spicata,* and these from a third species *G. roseata. Gilia congesta* in this treatement included four distinctive varieties.

Cronquist (Hitchcock et al., Vasc. pls. Pac. Northw. 4:105–107. 1959) followed a similar course in his treatment of *G. congesta* for the Pacific Northwest except in certain details, and added two more varieties. He did not take up Grant's transfer of *G. congesta* to *Ipomopsis* (Grant, V., Aliso 3:361. 1956), instead placing Grant's *Ipomopsis* combinations in synonymy under *Gilia.*

Grant (op. cit.) had set up the genus *Ipomopsis* "as a working unit" in a new, more inclusive state, by his transfer of 23 related *Gilia* species to the segregate genus. The *Ipomopsis congesta* complex was represented by *I. congesta* (Hooker) V. Grant, *I. c.* subsp. *montana* (Nelson & Kennedy) V. Grant, and *I. frutescens* (Rydb.) V. Grant. I here expand *I. congesta* by making five new combinations based upon the works on *Gilia* cited above as well as my own studies. One of these combinations reduces *I. frutescens* to subspecific rank.

1. **Ipomopsis congesta** (Hook.) V. Grant subsp. **crebrifolia** (Nuttall) stat. et comb. nov.—*Gilia crebrifolia* Nuttall, J. Acad. Nat. Sci. Philadelphia II, 1:156. 1848.—*Gilia congesta* var. *crebrifolia* Gray, Proc. Amer. Acad. Arts 8:274. 1870.—TYPE: "Big Sandy Creek of the Colorado of the West", *Nuttall s.n.* (Isotype: NY). From records of Nuttall's travels reported by McKelvey (Bot. Expl. Trans-Mississippi West, 1790–1850. 1955), the collection data have been determined as: WY, Sweetwater Co., Sandy Creek near its confluence with the Green River, late June, 1834.
2. **Ipomopsis congesta** (Hook.) V. Grant subsp. **frutescens** (Rydberg) stat. et comb. nov.—*Gilia frutescens* Rydberg, Bull. Torrey Bot. Club 40:471. 1913.—*Ipomopsis frutescens* V. Grant, Aliso 3:361. 1956.—*Gilia congesta* var. *frutescens* Cronquist, Vasc. pls. Pac. Northw. 4:107. 1959.—TYPE: UT, Washington Co., Springdale, *Jones 5247* (Holotype: NY). Reduction of *I. frutescens* to a subspecies is justified because, although typically well marked, it intergrades marginally with *I. congesta*. This intergradation was reported earlier by Constance and Rollins (loc. cit.) but they differed in their view of relationships. They associated *Gilia frutescens* with *G. congesta* var. *burleyana,* a form occurring in Idaho. Thus regarded, due to rules of priority. *G. frutescens* became a synonym of the latter. In the interpretation taken here, similar to that of Cronquist (loc. cit.), *Gilia burleyana* is considered closer to the typical form and therefore is synonymized with *Ipomopsis congesta*.
3. **Ipomopsis congesta** (Hook.) V. Grant subsp. **palmifrons** (Brand) comb. nov.—*Gilia congesta* subsp. *palmifrons* Brand, Pflanzenr. 4, 250:122. 1907.—*Gilia congesta* var. *palmifrons* Cronquist, Vasc. pls. Pac. Northw. 4:105. 1959.—Because Brand did not name a type I here designate the following lectotype from among his cited specimens: USA, NV, Esmeralda Co., Miller Mt., 2440 m (8000 ft), *W. H. Shockley 535*. (Lectotype: UC!). This specimen resembles the figure accompanying Brand's protologue of his subspecies, and is apparently a duplicate of his cited specimen "West-Nevada: Esmeralda County (Shockley n. 585, Herb. Boissier)." The number "585" probably corresponds with "535", handwritten, of the lectotype. This specimen is characteristic of the widespread Great Basin form that has palmately-parted leaves. *Ipomopsis c.* subsp. *palmifrons* intergrades with *I. c.* subsp. *montana* in the mountains of the western Great Basin. The habit of *I. c.* subsp. *palmifrons* in its most common aspect, however, is so different from the extreme, cushion-like form of typical *I. c.* subsp. *montana* that it seems useful to recognize both. This concept is in agreement with Cronquist (op. cit.) but differs from Constance and Rollins (op. cit.), who circumscribed *Gilia congesta* var. *montana* to include much of what Brand had placed in his *G. c.* subsp. *palmifrons*.
4. **Ipomopsis congesta** (Hook.) V. Grant subsp. **pseudotypica** (Constance & Rollins) stat. et comb. nov.—*Gilia congesta* var. *pseudotypica* Constance & Rollins, Amer. J. Bot. 23:439. 1936.—TYPE: SD, Fall River Co., Hot Springs, Black Hills, 13 June 1892, *Rydberg 886*. (Holotype: US; isotypes: NY). Constance and Rollins (loc. cit. p. 439) were the first to determine the true relationships of this taxon which, due to its basal cluster of elongate, entire leaves, appears superficially close to *Ipomopsis spicata*.
5. **Ipomopsis congesta** (Hook.) V. Grant subsp. **viridis** (Cronquist) stat. et comb. nov.—*Gilia congesta* var. *viridis* Cronquist, Vasc. pls. Pac. Northw. 4:107. 1959. TYPE: ID, Boise Co., 9.7 km (6 mi) s. of Lowman, 1830 m (6000 ft), 1 Jun 1944, *Hitchcock and Muhlick 8620* (Holotype: NY; isotype: CAS!). This subspecies is close to typical *Ipomopsis congesta* but differs in its greener, subglabrous herbage and denser habit.—ALVA G. DAY, Botany Department, California Academy of Sciences, San Francisco 94118. (Received 21 Mar 1979; accepted 14 Nov 1979; final version received 22 Nov 1979.)

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ARCHITECTURE AND THERMAL RELATIONS OF VERATRUM CALIFORNICUM (LILIACEAE), A SNOWBANK EMERGENT

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Abstract

Early in the growing season, *Veratrum californicum* Durand, a snowbank plant, displays two morphologies: a "closed" bud-like form and an "open" form with unfolded leaves. This variability enables quantitative assessment of the thermal consequences of the enlarged closed bud that characterized the early growth of these species at the edge of snowbanks. Temperatures at the center of "closed" plants are higher and more stable than leaf temperatures of "open" plants. Though "closed" plants present little leaf area for photosynthetic accumulation, they should realize an enhanced rate of early expansion growth at the expense of reserves through architecturally rather than metabolically generated overtemperature.

Veratrum californicum, corn lily, is a common and characteristic plant of wet meadows and snowmelt gullies below 4000 m in the mixed conifer forests of the Sierra Nevada, North Coast Ranges, Transverse Ranges, and Peninsular Ranges. It is one of the first perennials to emerge in these habitats in the spring. *Veratrum* overwinters as a carbohydrate-rich rhizome. This perenniating organ produces an underground "bud" composed of a tightly packed whorl of pleated, unexpanded leaf blades. The "bud" pushes above ground with the melting of the overlying snow.

The bud-like folded form may persist for several weeks or until the plant is approximately 0.2 m tall. Early growth results in the development of a large mass of folded leaves, tightly pleated into an acute-ovoid form (Fig. 1). The morphological mechanism for the maintenance of the closed or folded form lies in the differential development rate between the leaf lamina and base. Leaf lamina are preformed and expand to almost full size prior to any expansion of the leaf bases. Subsequent expansion of the lower portion of the leaf appears responsible for leaf orientation. The pattern of the early growth of *Veratrum* is illustrated in Fig. 2, which shows the relationship between plant height, distance from the edge of a receding snowbank (an estimate of the snow-free growth period), and leaf angle.

Here we discuss the thermal relations of the morphology of *Veratrum,* using the natural variation in early growth form found within local populations. Experiments were designed to test the hypothesis

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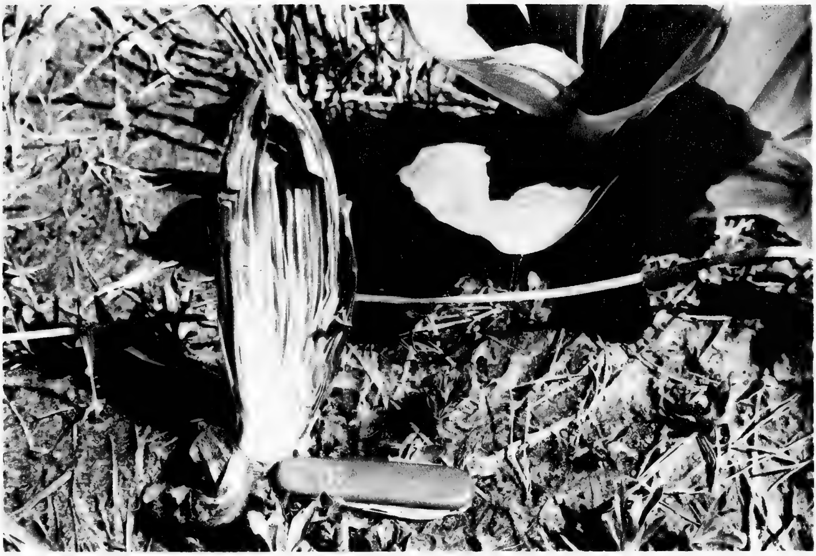

FIG. 1. Left: longitudinal section of a 'closed' *Veratrum* plant showing layers of pleated inner leaves. Right: an 'open' *Veratrum*.

that the closed form results in a more favorable thermal regime for early spring growth in a snowbank habitat. The site chosen for experiments in May and June of 1977 and 1978 was a wet meadow at Crane Flat (1830 m) in Yosemite National Park. Temperatures were measured with fine, 38-gauge thermocouples imbedded into the tissue and radiation was measured with Li-Cor sensors.

METHODS AND RESULTS

Temperature relations of snowbank emergent plants. Core or central temperatures were measured in closed plants just emerging from the edge of a snowbank (0.05 m tall) and about 1.5 m from the snowbank edge (0.14 m tall) (Fig. 3). The plants were emerging through soil covered with fir duff that appeared dry even next to the snowbank.

The measurements given in Fig. 3 were made during a partly clear morning. The plant at the edge of the snowbank had core temperatures that exceeded duff temperatures by about 5°C. This plant attained a temperature of nearly 30°C at 1030 hr. As radiation decreased, the temperature differential between the duff and plant disappeared.

The temperature relations of the larger plant were somewhat more complex. In the early morning the core temperature exceeded air temperature at the same height by about 5°C. The plant-air differential decreased even though incoming radiation increased between 0900 and

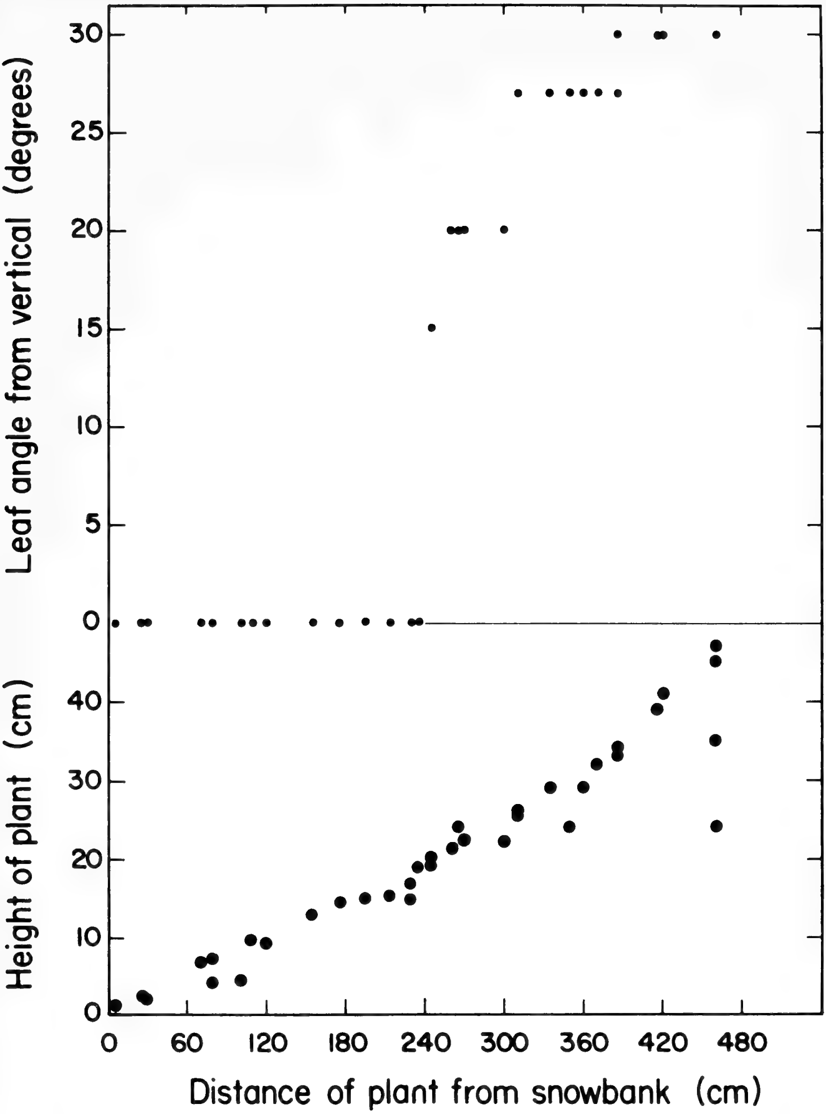

FIG. 2. Height and leaf angle of *Veratrum* plants at various distances from the edge of a snowbank. Leaf angle in degrees from vertical represents extent of unfolding. Distance from snowbank estimates snow-free interval.

0930, presumably because radiation absorbed by the plant body decreased as the zenith angle of the sun decreased. Air temperature decreased when the sun was obscured by clouds, but the plant core remained warmer than the air for an hour into the cloudy period.

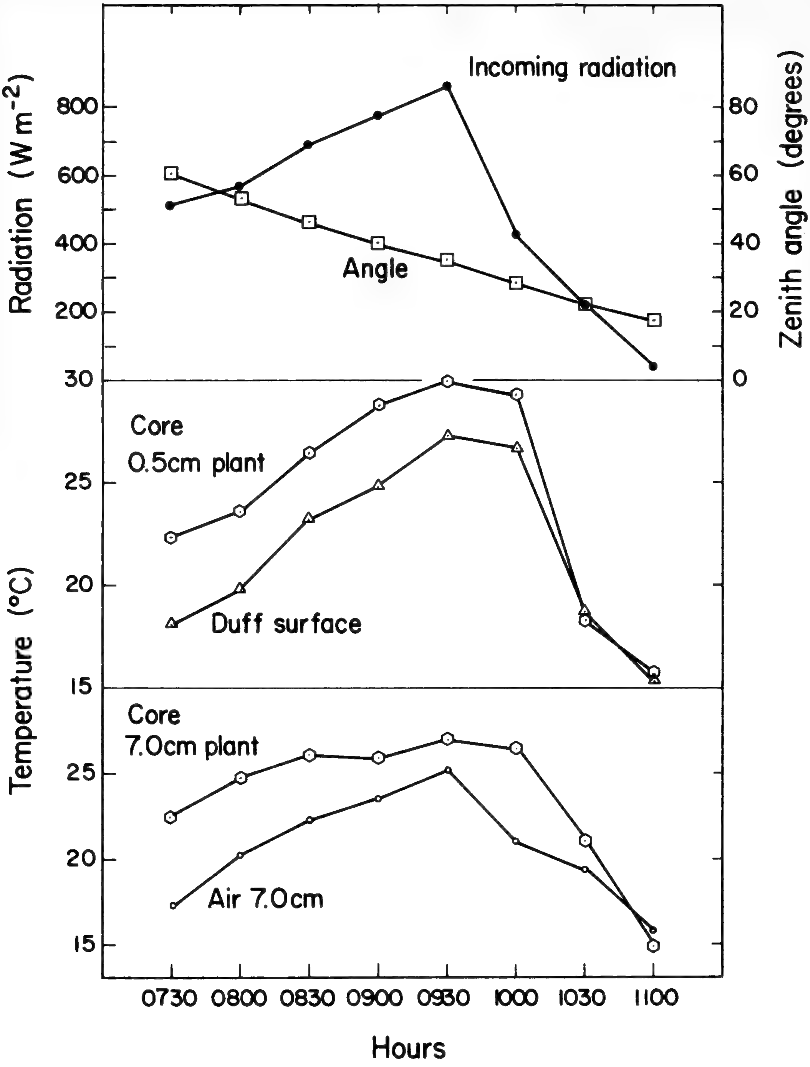

FIG. 3. Incoming radiation, solar angle, and environmental vs. tissue temperatures of two different-sized *Veratrum* plants, both in the closed 'bud' state.

Temperature relations of open versus closed plants. In snow-free areas of wet meadows, plants differing in both size and degree of leaf unfolding occur in close proximity. These experiments examined adjacent open and closed plants.

Our first series of temperature measurements compared the temperature of the underside of a leaf of an open plant with the temper-

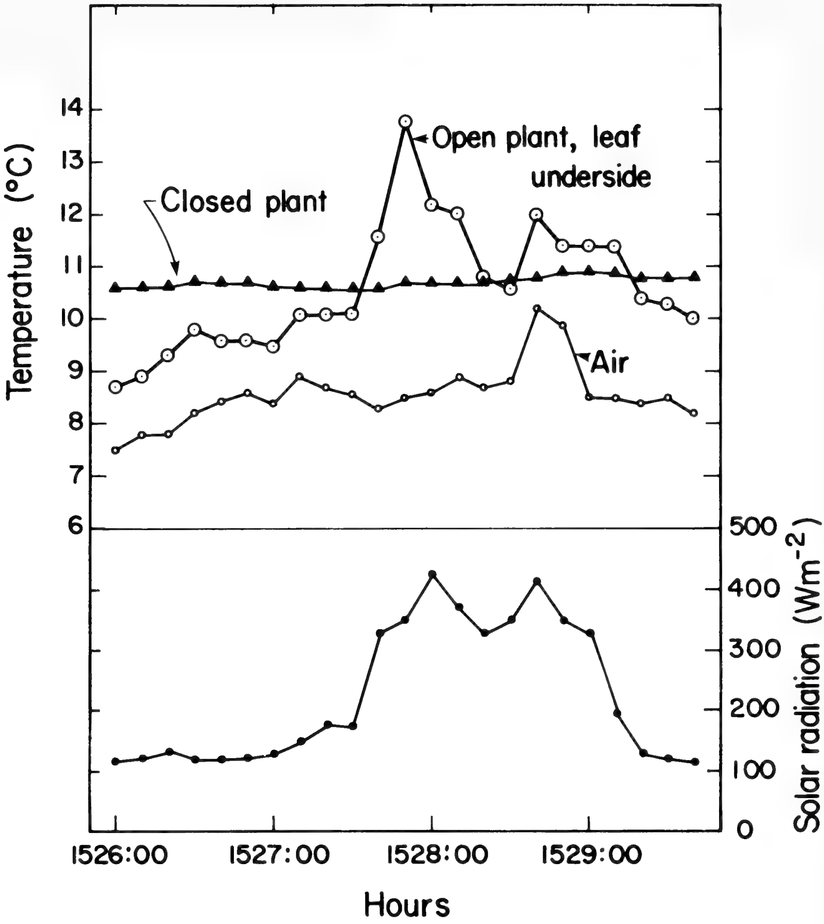

FIG. 4. Temperatures of leaves of closed and open *Veratrum* plants and of the air immediately adjacent to them during a brief period of rapidly fluctuating incoming radiation.

ature of an adjacent closed plant 1 cm from the outermost surface of the plant. Both plants were approximately 0.25 m tall. Simultaneous measurements were made at 10-sec intervals of closed-plant temperature, open-plant temperature, air temperature, and solar radiation. During the four minutes of monitoring, temperature in the closed plant varied by 0.4°C, whereas leaf temperature of the open plant varied by 5.1°C. Closed-plant temperatures were fairly constant, buffered against rapid fluctuations in air temperature, while open plant temperatures paralleled fluctuations in solar radiation and air temperature. Average temperature and average leaf overtemperature (leaf minus air temperature) during the interval were higher in the closed

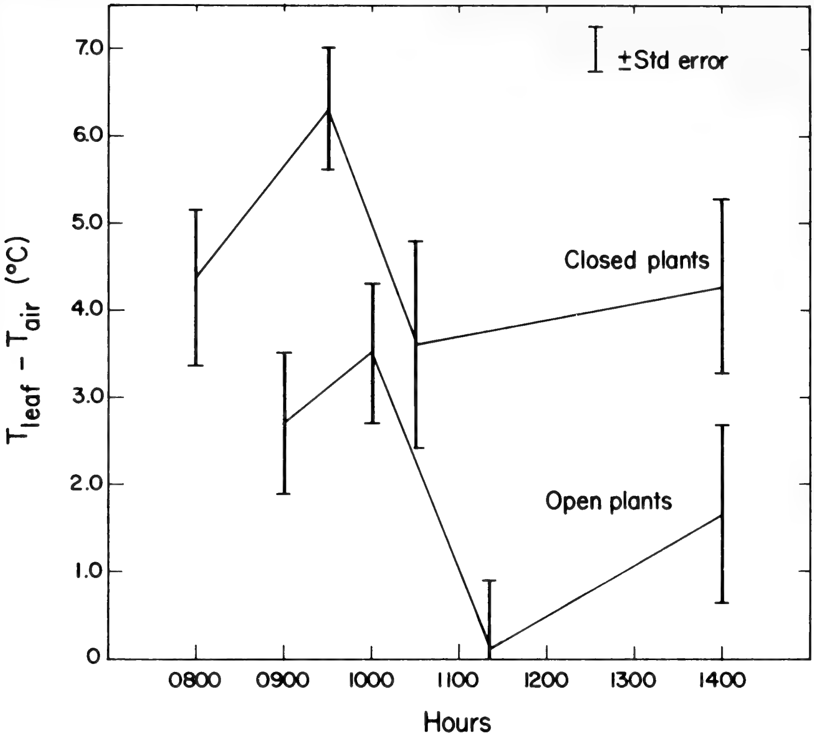

FIG. 5. Leaf-air temperature differentials of eight size-matched pairs of open and closed plants of *Veratrum*.

plant (Fig. 4). However, this was not consistently observed in other 5-min temperature comparisons of closed and open plants. Temperature buffering can maintain greater overtemperatures in closed than in open plants during brief cloudy periods, but during periods of high solar radiation open plants exhibited larger overtemperatures. The frequency and duration of cloudy periods determine which morphology confers higher daily average temperatures.

To evaluate the longer-term significance of variations in growth form, we monitored temperatures of air, sunlit side, and center leaf on eight closed and eight open plants chosen as matched pairs spanning the complete range of sizes represented in the study site. Four scans taken over most of a day revealed an average core-air overtemperature of 4.6°C in the closed plants and an average leaf-air overtemperature of 2.1°C in the open plants. Over the entire sampling period, the average overtemperature difference between open and closed

TABLE 1. TEMPERATURE COMPARISON OF VERTICAL (CONTROL) AND HORIZONTAL (REORIENTED) PLANTS. T_{air} = air temperature at 0.125 m; T_{sunny} = surface temperature on the sunny side of a vertical plant at 0.125 m; T_{core} = core or central temperature of vertical or horizontal plants; T_{top} = temperature of upper or sunny surface of horizontal plant at ca. 0.1 m; T_{bottom} = temperature of lower or shady surface of horizontal plant at ca. 0.01 m.

		T_{air}	T_{sunny}	T_{core}	T_{top}	T_{bottom}
Pair 1	Vertical plant	22.1	23.7	27.0		
	Horizontal plant	22.1		33.1	32.9	25.1
Pair 2	Vertical plant	21.2	23.8	24.4		
	Horizontal plant	21.2		32.3	34.3	22.9

plants is significant at the 5 percent level by Wilcoxon's signed-ranks test for two groups arranged as paired observations.

At each scan (Fig. 5), closed plants maintained a greater overtemperature than open plants, even at midday when the solar-projected surface area of the open form is much greater than that of the closed form. One possible explanation for the near elimination of the open-plant overtemperature near noon is the tight convective coupling between the leaves of that form and air temperature. As the wind rose near noon, open-plant overtemperatures disappeared.

Temperature relations of manipulated plants. To quantify the differences in the temperature buffering or thermal inertia between growth forms, we shaded adjacent open and closed individuals and observed the cooling dynamics. Under windless conditions near midday, leaf temperature of the open plant stabilized around 2.2°C below air temperature after 5 min in the shade. The center of the closed plant stabilized near air temperature after 28 min in the shade. The cooling rate of the center leaf of the open plant was 0.79°C/min/degree above stabilization temperature, while that of the closed plant was 0.20°C/min/degree above stabilization. A *t*-test shows the difference between these buffering capacities to be significant at the 5 percent level (t_s = 2.34, d.f. = 17).

The acute-ovoid shape of the closed plants presents a much larger surface area in horizontal than in vertical projection. Thus, absorbed radiation should reach maxima in the morning and afternoon, passing through a low at midday when low sun zenith angles minimize the cosine-corrected solar projection. Comparing matched pairs of closed plants, one oriented normally and one tied horizontally, allowed us to evaluate the interaction between closed-plant temperatures and solar angle. At midday, horizontal plants had core temperatures 6.1 and 5.9°C above core temperatures of equal-sized but vertical plants (Table 1). Evidence that differences in convective cooling cannot account for the greater overtemperature in the horizontal plants comes from the close correspondence between air temperature and the temperature at the bottom of horizontal plants.

DISCUSSION

Plants characteristic of snowbanks generally produce most of their early growth at the expense of stored reserves (Mooney and Billings, 1960). Growth is dependent primarily on energy supplied by the breakdown of carbohydrates through temperature-dependent respiration. In a cold environment, adaptations conferring elevated tissue temperature increase growth.

In certain snowbank plants (e.g., eastern skunk cabbage) high internal tissue temperatures are generated metabolically (Knutson, 1974). *Veratrum* achieves the same effect structurally. The delayed expansion of leaf bases produces a form that is very efficient at trapping radiation, particularly during morning and afternoon. It is during these cool hours that a tissue-temperature increase would be most beneficial. Near midday, when temperatures and overall radiation loads are highest, significant overtemperatures would produce high-temperature damage.

In retaining the closed form, a plant sacrifices the display of photosynthetic surface but realizes an average leaf temperature above that of similar-sized open plants. To the extent that early season growth is dominated by respiratory metabolism rather than photosynthetic accumulation, closed plants should grow faster than their open counterparts.

The other phenomenological difference between growth forms involves thermal inertia, the rates at which plants heat and cool in response to radiation load. We first observed temperature buffering in closed plants under partly cloudy skies with rapidly moving clouds. Subsequent day-long meteorological scans suggested that late-spring radiation levels commonly fluctuate between full sun and heavy overcast at intervals ranging from one to several minutes. This is the time window over which closed plants are well buffered to radiation changes, whereas open plants are not. Temperature buffering is unlikely to result in higher average temperatures for closed than for open plants except under mostly clear skies with scattered, rapidly moving clouds or moderate to high winds. Our data do not allow precise estimations of the frequency of these conditions, but experience suggests that they are very common. The thermal inertia of the closed growth form may produce a temperature advantage over a significant fraction of the early growing season. We cannot speculate on the significance of the variability found in early growth forms within local populations of *Veratrum,* or even whether this represents intraclonal variation.

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ANNOUNCEMENT

BOTANICAL ART SHOW

The Desert Botanical Garden invites botanical artists to exhibit their work in its Third Botanical Art Show, 22–30 November 1980. The show will include historical botanical prints as well as original contemporary works (excepting photography and offset lithography) of cacti, other succulents, and native desert plants. Preliminary submissions of 35 mm slides, due by 22 September 1980, will be screened for technique and botanical accuracy. Further details are available from Charles A. Huckins, Director, Desert Botanical Garden, PO Box 5415, Phoenix, AZ 85010.

EMMENANTHE PENDULIFLORA (HYDROPHYLLACEAE): FURTHER CONSIDERATION OF GERMINATION RESPONSE

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ABSTRACT

Scarification of seeds as well as the presence of burned remains of *Adenostoma fasciculatum* can serve as germination triggers for the post-fire annual herb *Emmenanthe penduliflora* in the chaparral of southern California. Seeds from desert populations of *E. penduliflora* respond primarily to scarification. Such germination mechanisms may be an evolutionary response to the differing frequency of fire in these two ecosystems.

Emmenanthe penduliflora Benth. (Hydrophyllaceae) is a common annual herb that germinates abundantly in the chaparral only during the first years after fire (Horton and Kraebel, 1955; Christensen and Muller, 1975). Various mechanisms have been postulated to explain this common post-fire response: heat shock stimulation, seed coat scarification and/or the removal of germination inhibiting substances from the soil (Sweeney, 1956; Muller et al., 1968). Fire may act to scarify seed coats and enable the seeds to imbibe water; however, Sweeney (1956) has shown that *E. penduliflora* seeds imbibe water without scarification but still require mechanical scarification for germination. Whereas washings from live foliage of *Adenostoma fasciculatum* have been shown to inhibit the germination of several herbaceous species, Christensen and Muller (1975) were not able to show a definite inhibitory effect of leachate on germination of seeds of *E. penduliflora*. Wicklow(1977) obtained only 1 percent germination of *E. penduliflora* under control conditions and in the presence of living stem segments of *A. fasciculatum*; however, when partially-ashed stem segments were added to petri dishes containing seeds on chaparral or potting soil, up to 49 percent germination was observed. He was able to extend these findings to the field where *E. penduliflora* commonly appeared in chaparral plots that had been clear-cut but spread with burned brush remains, or burned and the brush remains left in place. Only occasional *E. penduliflora* plants were seen on clear-cut zones that did not receive burned plant remains and no plants were seen in the undisturbed chaparral control area. Wicklow suggested that the ger-

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mination trigger in *E. penduliflora* may involve the "interaction between burned plant remains and certain components of the soil or soil microflora" (1977, p. 204).

In this study our first objective was to attempt to confirm the laboratory results obtained by Wicklow in chaparral populations. Also, because *E. penduliflora* occurs in deserts of creosote bush (*Larrea tridentata*) scrub (Burk, 1977) that rarely if ever experience fire, we examined the germination of seeds from a desert population of *E. penduliflora*. We know of no attempt to differentiate populations of this species at a subspecific level (e.g., Munz, 1974).

METHODS

Seeds of *Emmenanthe penduliflora* from a coastal chaparral population were collected on 18 Jun 1979 from the Santa Monica Mountains, Los Angeles County. The site was a west-facing slope dominated by *Adenostoma fasciculatum* at an elevation of 350 m, 5 km south of Highway 101 along Decker Road. This area was part of 10,300 ha that burned the previous October. Branches of *A. fasciculatum* for use in germination tests were collected on the same date from a 14-year-old stand in the Santa Ynez Mountains.

Seeds from a desert population were collected on 2 Jun 1979 in the Eagle Mountains of Riverside County, about 7.2 km northwest of Desert Center and more than 100 km east of the chaparral-desert transition in southern California. Seeds were gathered from *E. penduliflora* growing beneath *Olneya tesota* along a wash that traversed a southeast-facing slope dominated by *Larrea tridentata*. Branches of live and dead *O. tesota* less than 20 mm diameter were also collected here. At this site there was no evidence of fires, including campfires.

Methods of Wicklow (1977) were followed as closely as possible throughout this experiment; only specific details are elaborated here. Whatman #42 ashless filter paper or unwashed soils, sieved to pass 2-mm mesh, were placed in 5-cm diameter plastic petri dishes. Shrub stems were then added as an additional experimental treatment. There were four replicate dishes of each combination of substrate and shrub stem, each dish with 25 seeds (Table 1). Seeds of the scarified treatment received a shallow scratch running the length of the seed. All seeds were incubated for 30 days at 10°C with 12-hour light and dark periods provided by cool-white fluorescent lights. They were then moved to a growth chamber at 25°C, with 12-hour light and dark periods provided by both incandescent and fluorescent bulbs. Through the entire period of incubation, the contents of the dishes were kept moist by the addition of glass-distilled water. At weekly intervals the segments of stems in each dish were haphazardly rearranged. The final germination count was made after 10 days of incubation at 25°C.

TABLE 1. EFFECTS OF SCARIFICATION, PLANT PARTS, AND SOIL ON THE GERMINATION OF *E. penduliflora*. The data are percent germination, the mean of four replicate petri dishes per treatment. (** = $p < 0.05$ in one-tailed t-test for significant increase in germination over control; * = $p < 0.10$.)

			Non-scarified with stem segments			
			Adenostoma			
					Partially-ashed	
	Scarified	Non-scarified	Living	Ashed	This study	Wicklow
Chaparral seeds						
Filter paper	69**	0	1	0	57**	0
Potting soil	31**	0	1	2	32**	49
Chaparral soil (unburned)	11**	3	3	3	18**	33
			Olneya		*Adenostoma*	
			Living	Dead	Partially-ashed	
Desert seeds						
Filter paper	55**	2	1	1	7*	
Potting soil	29**	0	1	1	11*	
Desert soil	39**	0	1	2	6	

RESULTS AND DISCUSSION

Results of the germination experiments are shown in Table 1. Germination of scarified seeds was observed within 1 week at 10°C; after 30 days at 10°C, up to 62 percent of scarified seeds germinated. The response of our seeds to this treatment confirmed viability of the seeds we tested.

The results support Wicklow (1977) in showing an increased germination response over controls when chaparral seeds of *E. penduliflora* were placed in the presence of partially-ashed stem segments of *A. fasciculatum* (Table 1). Unlike the results of Wicklow, however, our most significant response in all treatments was observed with filter paper; 57 percent of the chaparral seeds germinated on filter paper with partially-ashed stems of *A. fasciculatum*. Therefore, Wicklow's suggestion that germination is triggered by an interaction between soil and burned plant remains was not supported. In fact, our weakest response of chaparral seeds in both scarified and partially-ashed stem treatments occurred on chaparral soil collected from unburned stands. Perhaps this was the result of substances inhibitory to germination still present in the soil.

Wicklow (1977) suggested that burned stem segments of *A. fasciculatum* might absorb a germination inhibitor from the seeds; however, he found that leaching *E. penduliflora* seeds for 24–48 hours in running water did not increase germination. Also, he was not able to increase germination by incubating the seeds on filter paper with activated charcoal.

We also noted a slight response of desert seeds to added stem segments of partially-ashed *A. fasciculatum* and a high response of these seeds to scarification. This difference in response between seeds collected from chaparral and desert populations implies slight ecotypic differences between these populations in mechanisms of germination. Scarification may occur commonly in the desert where coarse soils and wind-driven sheet erosion may scratch many seeds. Differences in the sizes of the seeds were also noted; desert seeds were significantly longer (2.46 mm ± 0.06 s.e. vs. 1.70 mm ± 0.04; $t = 10.1$, $n = 20$, $p < 0.05$) and heavier (0.796 mg ± 0.02 vs. 0.449 mg ± 0.02; $t = 12.0$, $n = 30$, $p < 0.05$) than chaparral seeds.

The results of this experiment confirm Wicklow's (1977) suggestion of a germination trigger present in partially-ashed stem segments of *A. fasciculatum* for populations of *E. penduliflora* in chaparral, an ecosystem with relatively frequent fires. However, in desert areas it appears that seeds depend more on scarification to trigger germination. The differences in germination mechanisms may indicate an evolutionary response to differing frequencies of fire in these two ecosystems.

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ALLUVIAL SCRUB VEGETATION OF THE SAN GABRIEL RIVER FLOODPLAIN, CALIFORNIA

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ABSTRACT

Composition, physiognomy, and development of floodplain vegetation are presented for three age zones of alluvial scrub on the San Gabriel River floodplain. The 19 species sampled are associated with the coastal sage scrub community, but the floodplain vegetation contains an unusually large proportion of arborescent, evergreen shrubs. Dominant species include *Rhus laurina, R. integrifolia, Lepidospartum squamatum, Eriogonum fasciculatum,* and *Opuntia* spp. The term "alluvial scrub" is suggested for this type of coastal sage scrub which is common on alluvial fans and floodplains along the San Gabriel and San Bernardino mountains. Mature stands are unusually diverse and appear to represent a climax vegetation that develops following severe, periodic flooding.

Gravelly alluvial fans and floodplains flanking the southern base of the San Gabriel and San Bernardino mountains support a distinctive assortment of shrubs and subshrubs characteristic of both coastal sage scrub and chaparral communities. This type of vegetation once covered much of the Los Angeles Basin (Ted L. Hanes, pers. comm., 1978) but is now confined to scattered remnants as a result of urbanization.

Although there are several references to this vegetation in the literature, no description of its composition or ecology is available. Hanes (1976) viewed it as a physiognomically unique expression of coastal sage scrub. Unlike typical coastal sage scrub composed of scattered drought-deciduous subshrubs and only occasional evergreens, this vegetation contains numerous evergreen chaparral shrubs in addition to a rich assemblage of subshrubs. In a description of structural and floristic variation within the coastal sage scrub, Kirkpatrick and Hutchinson (1977) mentioned an association occurring on fans and washes in cismontane southern California. They characterized this type by the tall stratum of evergreen shrubs and emphasized the "unrivalled structural complexity" of the association in comparison with the rest of the coastal sage scrub. In this study I surveyed the composition, physiognomy, and development of floodplain vegetation along the San Gabriel River.

STUDY SITE

Physiography and climate. The San Gabriel River floodplain has been isolated from urban impact since 1949 by a flood control dam

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and consequently retains an extensive stand of relatively undisturbed native vegetation. The San Gabriel River originates in the San Gabriel Mountains, Los Angeles County, and has a drainage area of 180,780 ha. After heavy rainstorms, the river carries debris eroded from unstable slopes, stream banks, and channels and deposits it where the river emerges from a narrow gorge onto the broad San Gabriel Valley. Thousands of years of flooding have created a gently sloping rocky plain underlain by alluvium up to 660 m thick.

The climate of the San Gabriel Valley and foothills is dry Mediterranean. The closest weather station to the study area is in San Gabriel, California, about 13 km from the flood basin. This station reports an average annual precipitation of 43 cm, most of which falls between November and April. Rainfall in the San Gabriel Mountains often falls in several extremely intense storms, which cause the destructive floods typical of the foothill regions. The two most recent floods on the San Gabriel River occurred in 1938 and 1969. Both of these were catastrophic, that in 1938 exceeding all previous floods on record by a considerable margin. These and older torrents have created a diverse alluvial topography consisting of a sparsely vegetated wash and higher, shrub-covered terraces.

Zonation. Aerial photographs of the flood basin reflect the presence of three physiographic zones of different ages, supporting distinct types of vegetation. The youngest zone, the wash, developed since the 1969 flood and supports scattered, short-statured, pioneer species. This wash contains remnants of a higher alluvial terrace destroyed by erosion during the 1939 flood. These older "islands" support large shrubs.

The terrace immediately above the wash supports dense scrub vegetation that developed since dam construction 30–37 years ago. The surface of this intermediate-level terrace represents an artificially altered substrate, as it was graded during construction.

The highest zone of the floodplain consists of an alluvial terrace that supports the diverse combination of shrubs and subshrubs that distinguish the fan and floodplain vegetation. The exact age of this stage of the floodplain community is not known, but shrub sizes and growth rings suggest 40 to 50 years.

METHODS

Forty 30-m line intercepts were established randomly throughout the floodplain, and height class, frequency, and cover were recorded for each perennial species and for bare ground at 3-m intervals. Annual species were recorded but not sampled. Pairwise resemblance among the 40 intercepts was determined using the Bray-Curtis distance index for species composition. Intercepts were clustered using a flexible sorting strategy based on a sorting coefficient of −0.25 to

TABLE 1. RELATIVE COVER OF ALLUVIAL SCRUB SPECIES FOR EACH SITE SAMPLED. Site numbers correspond to those given in Fig. 1. Values are based on total plant cover, bare ground excluded.

	Sites																			
	Pioneer Zone										Intermediate Zone									
Species	1	2	3	8	9	10	24	34	35	36	4	5	6	21	37	38	39	40	41	42
Lepidospartum squamatum	27	25	27	100	68	21	10	21	23	89	—	—	21	14	13	19	—	10	—	13
Eriogonum fasciculatum	—	73	—	—	—	46	39	26	36	—	100	66	79	86	87	80	94	90	96	89
Chrysopsis villosa	—	—	30	—	27	32	33	10	11	—	—	—	—	—	—	—	—	—	—	—
Baccharis glutinosa	57	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Penstemon spectabilis	—	—	37	—	—	—	—	18	17	11	—	—	—	—	—	—	—	—	—	—
Lotus scoparius	—	—	—	—	—	—	18	24	12	—	—	—	—	—	—	—	6	—	2	—
Yucca whipplei	—	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhus laurina	—	—	—	—	—	—	—	—	—	—	—	31	—	—	—	—	—	—	—	—
Rhus integrifolia	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Salvia mellifera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ribes aureum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gutierrezia bracteata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Opuntia occidentalis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Opuntia parryi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Haplopappus pinifolius	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Marah macrocarpus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhamnus crocea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Eriodictyon trichocalyx	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Artemisia californica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 1. Continued.

Species	Mature Zone																			
	7	11	12	13	14	15	16	17	18	19	20	25	26	27	28	29	30	31	32	33
Lepidospartum squamatum	4	—	—	—	3	—	—	1	—	5	12	10	4	29	3	20	2	14	5	—
Eriogonum fasciculatum	70	2	21	—	11	2	40	—	4	7	12	17	54	7	—	—	8	17	5	23
Chrysopsis villosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Baccharis glutinosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Penstemon spectabilis	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Lotus scoparius	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Yucca whipplei	—	—	—	—	—	—	—	—	4	6	—	—	—	24	—	—	3	4	6	50
Rhus laurina	—	26	5	27	50	—	40	—	48	40	—	—	—	24	87	18	63	21	—	—
Rhus integrifolia	25	—	—	16	2	95	—	—	—	—	30	23	—	—	—	52	—	30	39	—
Salvia mellifera	63	5	19	3	—	—	11	71	35	21	—	—	—	—	—	—	—	—	—	—
Ribes aureum	—	41	55	24	—	—	3	6	—	21	7	—	—	5	—	1	18	12	13	—
Gutierrezia bracteata	—	—	—	8	—	—	—	—	—	—	—	20	33	—	—	—	—	—	—	—
Opuntia occidentalis	—	11	—	17	21	2	6	3	—	2	21	1	3	—	4	6	3	5	19	27
Opuntia parryi	—	12	—	—	—	—	—	15	—	—	—	—	—	—	—	—	—	—	1	—
Haplopappus pinifolius	—	—	—	—	—	—	—	3	—	—	12	—	—	—	—	—	—	—	—	—
Marah macrocarpus	—	—	—	5	—	—	—	—	9	—	11	—	2	—	—	—	—	—	—	—
Rhamnus crocea	—	2	—	—	—	—	—	—	—	—	—	24	—	—	—	—	—	—	12	—
Eriodictyon trichocalyx	—	—	—	—	14	—	—	—	—	—	—	—	—	11	2	1	—	—	—	—
Artemisia californica	—	—	—	—	—	—	—	—	—	—	—	—	3	—	2	—	—	—	—	—

make group entry more difficult as the group enlarged. This method facilitates formation of numerous, distinct clusters (Smith, 1977).

To approximate the maximum age of each vegetation type, increment cores were taken from *Rhus laurina* (nomenclature follows Munz, 1974), the largest species occurring in all three zones. All perennial plants sampled were classified by lifeform (Mueller-Dombois and Ellenberg, 1974).

Quantitative measures of species diversity and lifeform diversity were made for each zone according to the Shannon-Wiener diversity function (Pielou, 1974).

To characterize the substrates of the three different zones, contents of three pits (0.3 m on each side and 0.3 m deep) from each zone were sorted into five size classes ranging from fine sand to rocks greater than 20 cm in diameter, and the relative volume of each class determined by water displacement. Soil texture and organic content were determined from a minimum of four samples in each zone, the former by standard hydrometer technique, and the latter by ash-free combustion at 500°C for 12 hours. Differences in species diversity, lifeform diversity, and soil among the three vegetation types were tested by ANOVA at $\alpha = 0.05$.

RESULTS

Composition

Sample plots on the alluvial plain supported 19 perennial species, although others were observed outside the 40 plots (Table 1). All species observed except *Juniperus californica* were common, native elements of either chaparral or coastal sage scrub communities.

Cluster analysis based on plant cover generated three major groups of sites that corresponded to vegetation zones observed in the field with only two discrepancies, sites 25 and 26 (Fig. 1). The dendrogram indicates relative uniformity of vegetation in the pioneer and intermediate zones. In contrast, dissimilarity of sites in the mature zone is high.

Pioneer zone. This zone consisted of young perennials, forming an average total plant cover of only 10 percent (Fig. 2). The zone supported seven of the 19 perennials sampled (Table 1), and had an intermediate species diversity ($H' = 0.37$).

Intermediate zone. Vegetation of the intermediate zone was uniform and relatively dense, with an average plant cover of 51 percent, dominated by *Eriogonum fasciculatum* (Fig. 2). Dead material made up a conspicuous fraction of this vegetation. Scattered tall shrubs overtopped the scrub layer (Fig. 3), but were infrequent and, with the exception of *Rhus laurina,* did not occur on sample plots. Only four

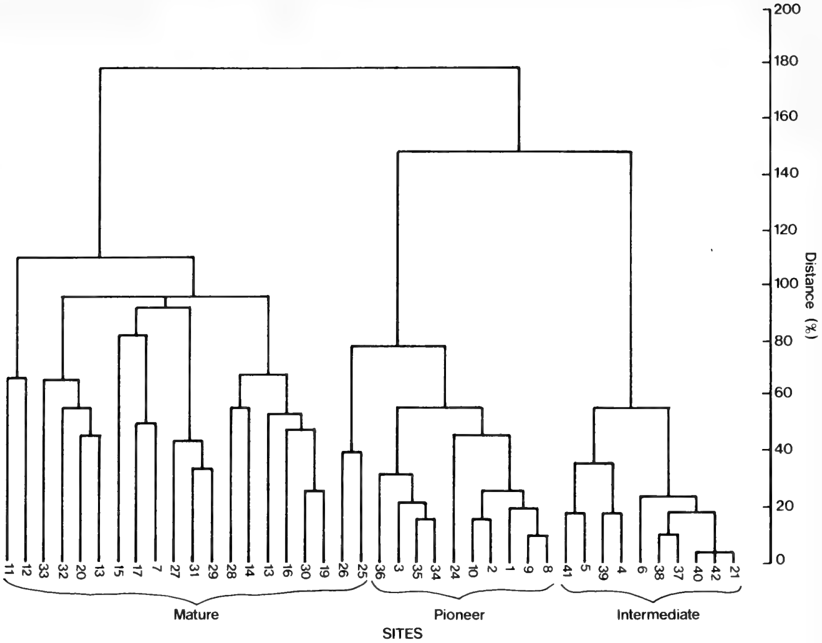

FIG. 1. Dendrogram generated from Bray-Curtis cluster analysis.

of the 19 dominant perennials were sampled in this zone (Table 1), attesting to its low diversity (H′ = 0.15).

Mature zone. The mature terrace flanking the wash and the uneroded alluvial "islands" left intact within the wash supported the greatest number of species (16) and the highest plant cover (Fig. 3, Table 1). This assemblage was not only rich in species, but had the most complex vertical structure with three distinct strata (Fig. 3).

Patterns in species composition on the mature terrace were associated with topography. The terrace consisted of two levels: higher, undissected portions and shallow drainages that once served as flood channels. Higher portions were dominated by large evergreen shrubs, predominantly *Rhus laurina* and *R. integrifolia*. *Ribes aureum, Rhamnus crocea, Sambucus mexicana,* and *Juniperus californica* also contributed to this stratum. *Ribes aureum* was the only tall shrub represented by seedlings and saplings as well as mature individuals. Subshrubs and cacti formed a variable stratum between larger, scattered shrubs (Fig. 3). This stratum was especially well developed in shallow drainages dissecting the terrace where larger shrubs were absent.

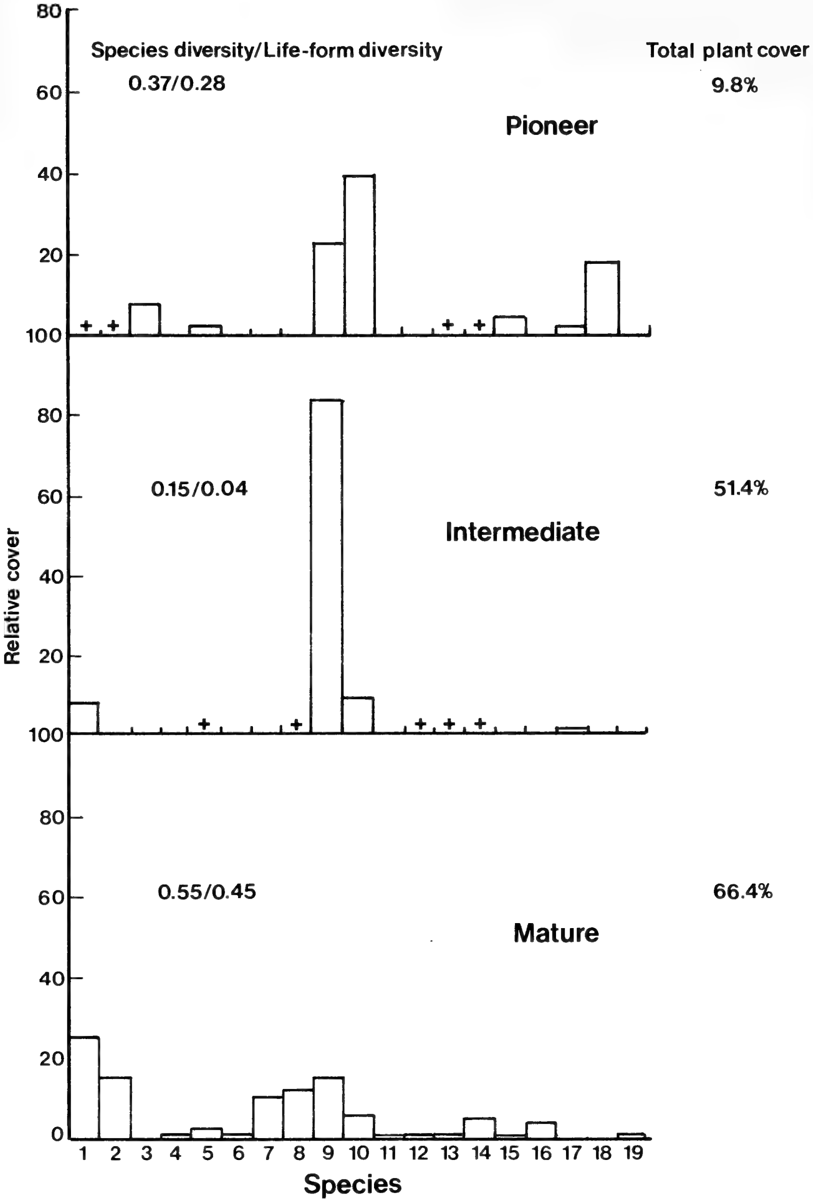

FIG. 2. Average relative cover of floodplain species and diversity of each zone. "+" indicates species observed but not sampled. Values are based on total plant cover, bare ground excluded. Key to plant species: 1) *Rhus laurina*; 2) *Rhus integrifolia*; 3) *Baccharis glutinosa*; 4) *Rhamnus crocea*; 5) *Yucca whipplei*; 6) *Eriodictyon trichocalyx*; 7) *Ribes aureum*; 8) *Salvia mellifera*; 9) *Eriogonum fasciculatum*; 10) *Lepidospartum squamatum*; 11) *Artemisia californica*; 12) *Haplopappus pinifolius*; 13) *Opuntia parryi*; 14) *Opuntia occidentalis*; 15) *Penstemon spectabilis*; 16) *Gutierrezia bracteata*; 17) *Lotus scoparius*; 18) *Chrysopsis villosa*; 19) *Marah macrocarpus*.

Seven of the 16 species encountered on the mature sites had an average relative cover greater than 5 percent of the total plant cover (Fig. 2). This distribution of dominants resulted in the heterogeneous appearance of the mature floodplain vegetation, which was reflected in relatively high diversity ($H' = 0.55$).

In portions of the mature community, the arborescent and subshrub strata formed impenetrable thickets but nearly 34 percent of the terrace consisted of open patches supporting only annual plants, particularly *Camissonia bistorta, Cryptantha muricata, Phacelia distans,* and *Schismus barbatus*. This zone was the only one with a dense herbaceous layer.

Trends in lifeform composition of the three zones paralleled those of species composition (Fig. 2). The greatest number and most even distribution of lifeforms occurred on the mature terrace.

Ages

Stand ages based on analysis of *Rhus laurina* increment cores indicated the largest individuals in the intermediate zone developed since approximately 1951 with a maximum age of 25–30 years. Individuals in the pioneer zone were 7–14 years old, indicating that some survived the record floods of 1969. Ring counts showed the largest individuals in the mature zone were 35–47 years old. Because *Rhus laurina* is a resprouting species, underground parts are potentially much older. The presence of dead snags and rotten root crowns toward the center of the multi-stemmed trees was evidence that some crowns were resprouts from much older, underground lignotubers.

Eriogonum fasciculatum and *Lepidospartum squamatum* were common both as colonizers of the pioneer zone and as species of the mature shrubland. In the latter zone, however, these species were reduced mostly to isolated, senescing individuals.

Substrate

Substrate in all three age zones consisted of flood deposits. There was no significant difference between the mean volume of small size classes in the three age zones, but distribution of boulders varied significantly among zones. The pioneer zone was unique for its boulder and debris-strewn nature (25 percent cover), a result of torrential 1969 storm runoff. Substrate of the intermediate-aged zone was indicative of its artificially disturbed character. Boulders were conspicuously absent. Ground surface of the mature zone was quite heterogeneous. Large expanses consisted only of small pebbles and deep soil, but such areas were interrupted by rocky drainages containing scattered boulders and large rocks.

Floodplain soils were high in sand (86–98 percent) and low in organic matter (0.25–0.38 percent). Wash soil was nearly pure sand (98–99 percent), whereas soils in the intermediate-aged zone had measur-

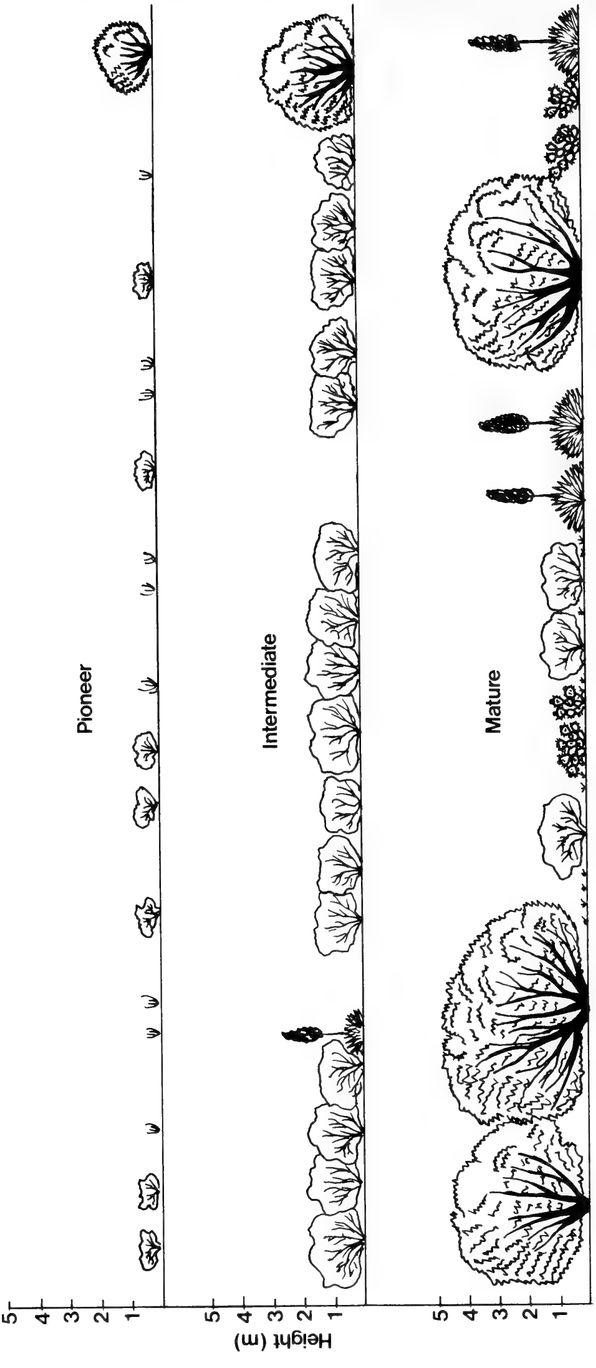

FIG. 3. Diagrammatic profile of floodplain vegetation.

able amounts of silt and clay. Soils of the mature zone were deeper and finer than those of the younger zones and contained 13 percent silt. Soil organic content increased with age of substrate.

DISCUSSION

The floodplain vegetation has strong floristic affinities with the coastal sage scrub type, as documented by Kirkpatrick and Hutchinson (1977), and should be considered a part of it. Coastal sage scrub is typically dominated by subligneous, drought-deciduous plants, but dominance of evergreen, woody shrubs in the tallest synusia gives the floodplain association a quality unlike typical coastal sage scrub. I propose the term "alluvial scrub" for the association, a name that depicts both its physiographic position and its physiognomy as a shrubland dominated by woody shrubs and small trees (Mueller-Dombois and Ellenberg, 1974).

Mooney (1977) found a trend toward increasing evergreenness with decreasing aridity in coastal sage scrub. He related this to physiological differences between evergreen shrubs and drought-deciduous shrubs, the former being favored in habitats of short drought duration because of their long period of low gas exchange. *Platanus racemosa,* a winter-deciduous, riparian tree, occurs occasionally on the floodplain, also indicating that the physical conditions of the floodplain are more mesic than those prevailing in other, more typical, coastal scrub stands where *Platanus* is absent. Both the high percentage of evergreens and the occurrence of *Platanus* place the alluvial scrub association toward the mesic end of the aridity gradient in coastal sage scrub.

Unique floodplain species. Alluvial scrub of the San Gabriel River floodplain is distinctive because it is structurally and floristically diverse. In addition, the area supports species that should be recognized as unusual because of their distribution. *Lepidospartum squamatum* is the one species occurring on the floodplain that is faithful to alluvial substrates. Perhaps *Lepidospartum* requires mechanical scarification and therefore is confined to drainages. This species is considered indicative of the alluvial scrub association. Occurrence of *Juniperus californica* on the floodplain is unusual because it is typically a species occupying desert slopes (Munz, 1974). Perhaps major drainages, such as the San Gabriel River, act as corridors for dispersal of juniper seeds from dry, interior mountain slopes. Dominance of *Rhus integrifolia,* primarily a coastal species, is also noteworthy this far inland.

Coocurrence of species and lifeforms of both desert and coastal affinities contributes to the diversity of the alluvial scrub association. It appears that the floodplain, with its sandy substrate yet mild Mediterranean climate, provides the unusual combination of physical factors that facilitates coocurrence of these types.

Succession. Cooper (1922) assumed pioneer vegetation of washes was successionally related to the climax community of older terraces. If this assumption is valid, the youngest zone of the San Gabriel River floodplain, if not flooded for a long period of time, should eventually support vegetation like that of the oldest terrace. Results of this analysis support such an inference. Many species dominant in the older zone also occur in the youngest one, indicating the two habitats are sufficiently comparable to support the same general vegetation, given adequate time for species enrichment. This can be substantiated only by long-term observation of the area.

Inferring that different vegetation types represent a chronological sequence of community development is justifiable only if all other ecological factors, especially climate and substrate, are nearly constant. Substrates of the wash and mature terrace are equivalent in origin, both formed by similar processes of erosion and deposition. The different soil textures found, however, are not necessarily related to different ages of the two zones. Debris basins and flood control channels built since 1939 have altered patterns of sediment deposition and probably are responsible for the textural differences. Old terraces are no longer being flushed of their finer material since floods have been confined to narrow channels. Relatively slight differences in soil texture are probably not sufficient to promote different types of vegetation, however. The coarser soil of the wash will probably eventually support a dry expression of the mature community, as soil moisture stress is gradually alleviated through time by wind deposition of fine-grained particles, shading by established shrubs, and incorporation of organic material into the soil.

Succession after flooding begins with the invasion of the pioneer shrubs *Eriogonum fasciculatum* and *Lepidospartum squamatum* and numerous herbaceous perennials including *Lotus scoparius* and *Chrysopsis villosa.* Occasional individuals of *Baccharis glutinosa,* typical of mesic, riparian habitats, contribute to plant cover. Cover and height increase as the community is enriched by colonizing species, including *Yucca whipplei, Opuntia occidentalis, Haplopappus pinifolius, Eriodictyon trichocalyx,* and *Salvia mellifera.* If flooding is not violent enough to excavate deep root systems of mature shrubs such as *Rhus laurina* and *Rhamnus crocea,* they may resprout and assume dominance early in succession. Eventually, the vegetation is dominated by scattered, tall, resprouting shrubs surrounded by low-growing subligneous shrubs, cacti, and *Yucca.*

The absence of seedlings of climax shrub species, even after the record rainfall of 1978, suggests that establishment by seed of these species is a rare event in the alluvial habitat. Conditions promoting establishment of existing *Rhus laurina* individuals are not known, nor is the explanation for uniformity of ages of the largest specimens. Apparently, individuals resprouted since some event approximately

40–50 years ago. A major flood (1939?) with force to destroy aboveground plant material is the most likely explanation. In contrast to the dominant evergreens, reproduction by seed of shrubs of the lower stratum occurs frequently.

Regeneration of evergreen shrubs may be stimulated by floods of sufficient power to inundate the higher terraces, as flood waters may saturate the normally well-drained soils and import inorganic nutrients and sources of organic matter. If such is the case, composition of mature vegetation may gradually shift toward a more typical coastal sage scrub with a smaller proportion of evergreen species, because flood control measures have isolated the upper terraces from most floods. However, it is likely that a major flood need inundate the upper terrace on the order of only once or twice per century to stimulate establishment and growth of evergreen seedlings and the upper terrace is still within the range of such infrequent flood waters. Several consecutive years of above-average rainfall and mild temperatures may also provide the conditions necessary to insure perpetuation of climax species. Germination studies of *Rhus laurina* and similar species could elucidate the ecological requirements for regeneration.

Low diversity of both species and lifeforms in the intermediate zone indicates the effect of unnatural disturbance on alluvial scrub vegetation. Bulldozing approximately 30 years ago apparently favored establishment of *Eriogonum fasciculatum* at the expense of other colonizing species and has led to the development of a structurally and floristically simple vegetation. The occurrence of emergent shrubs suggests the zone will eventually succeed to a more complex assemblage.

Differences in species and lifeform diversity among the three stages of alluvial scrub support general features of succession suggested by Drury and Nisbet (1973). Community development on the floodplain seems to combine two processes that result in increased species and lifeform diversity: 1) emergence into prominence of species and lifeforms present at the start, and 2) enrichment by continual colonization of the site.

Alluvial scrub is a pulse-stable climax vegetation (Odum, 1971) adapted to occasional, destructive flooding. Species either recolonize flooded areas by seed or resprout from underground tissues. Alluvial scrub is physiognomically distinct from chaparral and typical coastal sage scrub communities and should be recognized as a diverse expression of the latter, rich in both species and lifeforms.

Because urban and industrial developments are destroying this unique type of coastal sage scrub, support should be given to preservation of existing stands.

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NOTEWORTHY COLLECTIONS

CUCURBITA FOETIDISSIMA H.B.K. (CUCURBITACEAE).—USA, WY, Laramie Co., w. edge of Granite, 2225 m, 5 Aug 1979, *Dorn 3344,* RM. Along a railroad embankment where observed for 3 years.

Previous knowledge. CO and NE, s. to TX, CA, and Mex. (Herbarium consulted: RM; published sources: Bailey, Gentes Herb. 6:267–322, 1943; Barkley, Atlas fl. Gt. Plains, 1977; Harrington, Man. pls. Colorado, 1954). *Diagnostic characters.* Keys to *Echinocystis lobata* in Dorn (Man. vasc. pls. Wyoming, 1977, p. 581) but is a perennial herb; lvs truncate to cordate at base, 10–30 cm long, scabrous; corolla 6–15 cm long; calyx campanulate, 5-lobed; fr globose to ovoid-globose, striped or mottled green, 5–10 cm long.

Significance. First report for WY. About 96 km from nearest known population in Banner Co., NE.

ELYMUS INNOVATUS Beal (GRAMINEAE).—USA, WY, Crook Co., Cold Springs Creek (T48N R60W S9 NE¼), 1875 m, 16 Sep 1979, *Lichvar 2491,* RM. Frequent in partially open meadow near n.-facing slope. Associates included *Calamagrostis inexpansa, Picea glauca,* and *Pyrola elliptica.*

Previous knowledge. AK to B. C., e. to Alta. and s. to MT, SD, and WY. (Herbaria consulted: NY, RM, SDU, UC; published sources: Bowden, Canad. J. Bot. 37:1148, 1959; Hitchcock, A. S., Man. grasses U. S., 1950; Hitchcock, C. L., et al., Man. vasc. pls. Pac. Northw. II., 1964). *Diagnostic characters.* Culms tufted, to 1 m high from rhizomes; lvs mostly 1–5 mm wide; glumes 4–10 mm long, villous, somewhat bristle-like; lemmas mostly 7–9 mm long, mostly villous, awn 1–10 mm long.

Significance. Earlier report of species for WY based upon collection of *x Agroelymus hirtiflorus* (*Shear 284,* Green River, WY: RM). Alan Smith (UC) has located another collection: *Williams 2676,* Welcome, WY (NY, UC). Not collected in Crook Co. since William's collection in 1897. About 40 km from nearest known population in Butte Co., SD.

LESQUERELLA FREMONTII Rollins & Shaw (CRUCIFERAE).—USA, WY, Fremont Co., 1947, *Ripley and Barneby 8931,* CAS, NY, US. "5 miles E of Atlantic City, 2500 m, calcareous gravel ridge."

Previous knowledge. Narrow endemic to Fremont Co., WY. (Herbaria consulted: NY, RM; published sources: Dorn, op. cit.; Rollins and Shaw, The Genus *Lesquerella* N. Am., 1973). *Diagnostic characters.* Prostrate or decumbent; basal lvs elliptic to rhombic, 0.5–4 cm long, 2–6 mm wide; cauline lvs obovate to elliptic; fr pedicels recurved; sepals 3–5 mm long; petals 5–8 mm long, fr subglobose to ellipsoid, slightly flattened contrary to partition.

Significance. The locality on the label for the type, *Ripley and Barneby 8931,* is in error. Barneby writes, "No. *8931* is not 5 miles E, as given on the label, and not 5 miles W, as you surmise, but actually 3 miles N of Atlantic City at 8,200 ft . . . . I have vague memories of the spot, a vivid one of the plant itself . . . but I feel sure that the limestone substrate and elevation must be correct, even though the mileage and direction got garbled."

LYTHRUM SALICARIA L. (LYTHRACEAE).—USA, WY, Park Co., s.w. of Powell ca. 6.4 km (T55N R99W S32), 1340 m, 13 Aug 1979: *Lichvar 2275,* RM; *Dorn 3357,* RM. Abundant in marshy area along roadside. Associates included *Typha latifolia, Scirpus acutus,* and *Carex.*

Previous knowledge. Introduced from Europe; Newf. and Que. s. to VA and WV, w. to WA, ID, SD, CO. (Herbaria consulted: ID, IDS, MONT, RM; published sources: Heywood, Fl. Eur., 1968; Hitchcock et al., Man. vasc. pls. Pac. Northw. III. 1961; Shinners, Field and Lab 21:80–89, 1953). *Diagnostic characters.* Keys to *L. alatum* in Dorn (op. cit., p. 970) but has longer petals; perennial to 15 dm high; lvs sometimes whorled in threes, 5–8 cm long, lanceolate; infl spike-like, 1–5 dm long; petals red-purple or pinkish, to 1 cm long; stamens twice as many as petals.

Significance. First report for WY. About 720 km from nearest known population in Idaho Co., ID.

MIMULUS BREWERI (Greene) Cov. (SCROPHULARIACEAE).—USA, WY, Albany Co., Laramie Peak area (T28N R71W S27), 1920 m, 2 Jun 1979, *Dorn 3214,* RM. In mossy crevices of granite rocks. Associates were *Mimulus suksdorfii* and *Mimulus floribundus.*

Previous knowledge. B. C. s. to CA, e. to ID and WY. (Herbarium consulted: RM; published sources: Dorn, op. cit.; Grant, Ann. Mo. Bot. Gard. 11:99–388, 1924; Shaw, Field guide vasc. pls. Grand Teton N. P. and Teton Co., Wyoming, 1976). *Diagnostic characters.* Ann to 15 cm high; lvs linear to oblanceolate or elliptic, 0.3–2 cm long, entire or nearly so; calyx 3–6 cm long, lobes with gland-tipped hairs; corolla purple to reddish, 5–10 mm long.

Significance. 528 km from nearest known population in Teton Mts., Teton Co., WY. Easternmost locality in western U.S. Extremely unusual for a species with Pacific affinities to occur so far east.

PELLAEA ATROPURPUREA (L). Link (POLYPODIACEAE).—USA, WY, Crook Co.: Boundary Gulch (T52N R60W S16 NE¼), 1220 m, 30 Aug 1979, *Dorn 3410,* GH, RM. Sandstone cliff crevices in birch-ironwood forest associated with *Cheilanthes feei* and *Cystopteris fragilis*; Sand Creek near Fish Genetics Lab (T52N R60W S18 SW¼), 1220 m, 15 Sept 1979, *Lichvar 2484,* RM. Rare on sandstone boulder along stream. Associated with *Polygonatum biflorum, Quercus macrocarpa,* and *Phryma leptostachya.*

Previous knowledge. Guatemala and Mex., n. to SD, Sask., Alta., and B. C., e.

to FL, NC, and VT. (Herbaria consulted: RM, SDU; published sources: Dorn and Dorn, Ferns of Montana, Wyoming, and Black Hills of South Dakota, 1972; Petrik-Ott, Pteridophytes of Kansas, Nebraska, South Dakota, and North Dakota, 1979; Tryon, Ann. Mo. Bot. Gard. 44:125–193, 1957). *Diagnostic characters.* Keys to *P. glabella* in Dorn (op. cit., p. 87) but has broadly diverging petiolules; perennial to 35 cm high; petioles hairy, 2–20 cm long; lf bls 5–30 cm long, 2–16 cm wide, hairy, twice compound below; sori marginal and appearing elongate, spores 32 per sporangium.

Significance. First report for WY. About 32 km from nearest known population in Butte Co., SD.

RANUNCULUS VERECUNDUS Robins. ex Piper (RANUNCULACEAE).—USA, WY, Park Co., Absaroka Range, Galena Creek (T54N R107W S19 E½), 3050 m, 14 Aug 1979: *Lichvar 2280,* RM; *Dorn 3359,* RM; head of Hughes Creek, North Fork Shoshone River, 3000 m, 14 Aug 1979, *Evert 1610,* RM. Scattered on n.-facing talus slope. Associates included *Geum rossii, Draba nivalis, Senecio, Epilobium,* and *Carex nova.*

Previous knowledge. AK to Alta., s. to Mts. of OR, ID, and MT. (Herbaria consulted: ID, IDS, MONT, RM; published sources: Benson, Am. Midl. Nat. 40:1–264, 1948; Hitchcock et al., op. cit. 1964; Scoggan, Fl. Canada, 1978). *Diagnostic characters.* Keys to *R. abortivus* in Dorn (op. cit., p. 1139) but has longer petals; glabrous to slightly crisped-puberulent, spreading to ascending perennial to 20 cm high; basal lvs 1–2 cm long, mostly reniform to cordate, crenate to deeply lobed with 3–5 segments; cauline lvs 1–3, alternate, bract-like, 3–5 lobed or parted; sepals 3.5–5 mm long; petals yellow, 3.5–6 mm long; achenes 1–2 mm long, beak about 0.5 mm long and curved, glabrous.

Significance. First report for WY. 322 km from nearest known population in Deer Lodge Co., MT.

RHAMNUS CATHARTICA L. (RHAMNACEAE).—USA, WY, Crook Co.: Sand Creek near Fish Genetics Lab (T52N R60W S18 SW¼), 1220 m, 31 Jul 1979, *Lichvar 2171,* RM. About 4 small trees on rocky slope on streambank. Associates include *Philadelphus pubescens, Lysimachia ciliata,* and *Quercus macrocarpa*; Dugout Gulch (T52N R61W S24 SE¼), 1220 m, 16 Oct 1979, *Dorn 3415,* RM. Streambank, associated with *Quercus macrocarpa* and *Symphoricarpos.*

Previous knowledge. Introduced and naturalized from Europe; Que. to MN, s. to VA, w. to SD, MT, and CO. (Herbaria consulted: RM, SDU; published sources: Fernald, Gray's Man. Bot., 1950; Heywood, op. cit.; Wolf, Rancho Santa Ana Bot. Gard., Bot. Ser., 1, 1938). *Diagnostic characters.* Keys to *R. alnifolia* in Dorn (op. cit., p. 1153) but is a shrub or small tree to 8 m high; branches mostly opposite and ending with sharp thorns; lvs 2–6 cm long, oval to ovate or broadly elliptic, glabrous to minutely pubescent; fls unisexual; sepals 4, 2.5–3 mm long; petals 4, 1–1.5 mm long; fr a drupe with 3–4 seeds.

Significance. First report for WY. Found along about 1.5 km of Sand Creek and into Dugout Gulch. Very conspicuous in October because it is the last shrub or tree to retain green leaves. About 504 km from nearest known naturalized population in Charles Co., SD.

SCIRPUS ATROCINCTUS Fern. (CYPERACEAE).—USA, WY, Crook Co., Lucky Gulch n.e. of Alva (T54N R63W S13 NW¼), 1340 m, 1 Aug 1979, *Lichvar 2205,* RM. Common in open marshy bottom. Associates included *Scirpus pallidus, Spartina pectinata,* and *Carex praegracilis.*

Previous knowledge. Newf. s. to FL, w. to B. C., SD, and TX. (Herbaria consulted: RM, SDU; published sources: Beetle, N. Am. fl. 18(8):479–504, 1947; Hitchcock et al., Man. vasc. pls. Pac. Northw. 1969; Schuyler, Proc. Acad. Nat. Sci. Philadelphia. 119:295–323, 1967). *Diagnostic characters.* Keys to *S. pallidus* in Dorn (op. cit., p. 647) but has long bristles exceeding scales and fr; perennial to 1.5 m high; lvs narrowly linear and rigid; bracts leaf-like, spreading, dark pigmented at base; infl of spikelets in loose cluster, spikelets 3–7 mm long, scales about 2 mm long; achenes 0.7–1 mm long, usually twice exceeded by flexuous bristles.

Significance. First report for WY. About 99 km from nearest known population in Lawrence Co., SD.—ROBERT W. LICHVAR, The Nature Conservancy, Wyoming Natural Heritage Program, 1603 Capitol Ave., #325, Cheyenne 82001 and ROBERT D. DORN, Box 1471, Cheyenne, WY 82001. (Received 5 Jan 1980; accepted 10 Jan 1980; final version received 29 Feb 1980.)

ASCLEPIAS STENOPHYLLA A. Gray (ASCLEPIADACEAE).—USA, WY, Crook Co., Devils Tower Natl. Mon., ca. 90 m e. of Joyner Ridge Parking Lot, T53N R66W S12 NE¼, ca. 1300 m, 27 Jul 1979, *Marriott 541* (RM). Occasional on sandy soil of open prairie with *Andropogon gerardii* and *Artemisia ludoviciana.*

Previous knowledge. Dry prairies, plains, and rocky glades, often on limestone, w.-central IL, central MO, n. NE, s.w. SD, s.e. MT, s. to w. AR, e. and n. TX, and e. CO. (Herbaria consulted: COLO, KANU, RM; published sources: Barkley, Atlas fl. Great Plains. 1977; Correll and Johnston, Man. vasc. pls. Texas. 1970; Dorn, Man. vasc. pls. Wyoming. 1977; Mohlenbrock, Guide vasc. fl. Illinois. 1975; Woodson, Ann. Missouri Bot. Gard. 41:1–211. 1954.) *Diagnostic characters.* Keys to *A. subverticillata* in Dorn (op cit., p. 118), but leaves alternate to subopposite (vs. mostly whorled); calyx lobes 2–3 (vs. 1.5–2) mm long; hoods 3–4 (vs. ca. 1.5) mm long, 3-lobed (vs. entire), with the median, reduced lobe representing the adnate horn (vs. horn free, acicular, incurved, and much exceeding the hood in length).

Significance. First record for WY, representing a range extension from adjacent Carter Co., MT. To be expected elsewhere in extreme e. WY as it occurs in adjacent SD and NE.—RONALD L. HARTMAN, Department of Botany, University of Wyoming, Laramie 82071 and HOLLIS MARRIOTT, Chiricahua National Monument, Willcox, AZ 85643. (Received 15 Nov 1979; accepted 6 Feb 1980.)

ERIOGONUM DARROVII Kearney (POLYGONACEAE).—USA, NV, Nye Co., White River Valley, n. flank of hill in valley, T6N R61E S20, 1700 m, 5 Jun 1979, *Thorne and Harrison 575* (BRY, MARY); White Pine Co., 19 km s. of Major's Place, 1830 m, 17 Jun 1944, *Ripley and Barneby 6316* (CAS, cited as *E. divaricatum* Hook. by Barneby, Leafl. W. Bot. 5:61–66. 1947); 18.5 km s. of Major's Place, 9 Aug 1975, *Reveal 3921* (BRY, CAS, NY, OKL, RSA, US, UTC); Lake Valley Summit, 1875 m, 14 Aug 1978, *Reveal 4842* (NY, US); Spring Valley, 0.6 km e. of hwy 93 on rd to Atlanta, ne. of Lake Valley Summit, 1800 m, 14 Aug 1978, *Reveal 4844* (US).

Previous knowledge. nw. AR (type locality in Coconino Co.) and indirectly NV. (Herbaria consulted: ASU, BRY, CAS, MARY, NY, OKL, RENO, RSA, US, UTC; published sources: Kearney, Leafl. W. Bot. 4:267–268. 1946; Kearney and Peebles, Ariz. fl. 1951; McDougall, Seed pls. n. Ariz. 1973; Reveal, Phytologia 34:409–484. 1976; Reveal, *In*: Ayensu and DeFilipps, Endang. thr. pls. U.S. 1978; Parfitt et al., Madroño 26:144. 1979.)

Significance. Documentation of NV records for White Pine Co. and new county record for Nye Co., extending range 320 km from the AR stations reported by Parfitt et al.

ERIOGONUM HOOKERI S. Wats. (POLYGONACEAE).—USA, ID, Bannock Co., se. of Pocatello near Portneuf R., T7S R35E, ca. 1400 m, Aug 1973, *Burrup DEB73-36* (IFGH).

Previous knowledge. Known from CA, NV, AR, UT, CO, and WY. (Herbaria consulted: ID, IDS, NY, RM, US, UTC; published sources: Davis, Fl. Idaho. 1952; Reveal, Brittonia 20:13–33. 1968.)

Significance. New to Idaho. Northward disjunction of 175 km.

ERIOGONUM INERME (S. Wats.) Jepson (POLYGONACEAE).—USA, ID, Boise Co., 0.8 km s. of Centerville, 13 Jun 1947, *Christ and Christ 16842* (NY, filed under *Chorizanthe*).

Previous knowledge. Known only from CA where infrequent in Sierra Nevada and Coast Ranges. (Herbaria consulted: ID, IDS, NY, US; published sources: Reveal and Munz, Suppl. Calif. fl. 1968; Reveal, *In*: Hitchcock and Cronquist, Fl. Pacific N.W. 1973.) *Diagnostic characters.* Annual with glandular stems and branches; tepals white, with hooked hairs on the outer surface; achenes barely exceeding the tepals.

Significance. First record from ID; possibly introduced by miners or on mining equipment as the plant occurs in an area mined for gold.

ERIOGONUM NUTANS Torr. & Gray var. NUTANS (POLYGONACEAE).—USA, CA, Mono Co., Rough Cr. between Potato and Bodie mts., 2 Jul 1967, *Hardham 15110* (CAS).

Previous knowledge. Intermountain Region of w. NV and se. OR, e. to e. UT. Once thought to occur in CA based on misidentification of *E. collinum* Stokes ex Jones. (Herbaria consulted: BRY, CAS, DS, GH, JEPS, K, MARY, MO, NTS, NY, OKL, ORE, OSC, POM, RENO, RM, RSA, UC, US, UT, UTC; published sources: Jepson, Calif. fl. 1:376–428. 1913; Abrams, Illus. fl. Pacific states. 1944; Munz, Calif. fl. 1959; Reveal and Munz, op cit.; Reveal, Madroño 18:167–173. 1966; Reveal, Phytologia 25:169–217. 1973.) *Diagnostic characters.* Annual with deflexed glandular peduncles bearing campanulate involucres; tepals white, the outer ones oblong or oval with emarginate apices, the inner ones narrower; leaves tomentose, especially below.

Significance. First authentic CA record. Range extension of 75 km westward.

ERIOGONUM NUTANS Torr. & Gray var. GLABRUM Reveal (POLYGONACEAE).—USA, CA, Nevada Co., 0.8 km ne. of Hirschdale, 1740 m, 14 Sep 1965, *True 2588A* (CAS); 8 km n. of Truckee, just n. of Hobart Mills jct, 16 Sep 1965, *True 2646* (CAS); Hirschdale, Truckee River Canyon, 26 Aug 1970, *True 6415* (CAS).

Previous knowledge. Known only from Elko Co., NV, where locally common, especially along hwys 40 and I-80. Not relocated in search by J. T. Howell in 1978. (Herbaria consulted: BRY, CAS, DS, GH, JEPS, NY, POM, RENO, RSA, UC, UTC; published sources: Reveal, op. cit., 1966.) *Diagnostic characters.* Similar to var. *nutans* but peduncles glabrous and tepals entire-margined.

Significance. New to CA; 350 km disjunction. Apparently disseminated by motor vehicles, most likely trucks, probably carrying seeds in mud or snow from NV to CA.

ERIOGONUM VISCIDULUM J. T. Howell (POLYGONACEAE).—USA, NV, Clark Co., Lake Mead Natl. Rec. Area, 2 km w. of Overton Beach, locally common, T17S R68E S21 and S22, 430 m, 11 May 1979, *Holland 2241* (MARY); 1.6 km n. of turnoff to Steward Pt. along hwy 12, infrequent, T17S R68E S33, 410 m, 11 May 1979, *Holland 2248* (MARY).

Previous knowledge. Restricted to a single population sw. of Riverside on n. side of Virgin R., Clark Co., NV, where exceedingly rare. (Herbaria consulted: BRY, CAS, DS, GH, JEPS, MARY, MO, NY, OKL, POM, RENO, RSA, UC, US, UTC; published sources: Howell, Leafl. W. Bot. 3:138–142. 1942; Reveal, Rev. Eriogonum. 1969; Reveal, op. cit., 1976.)

Significance. New location of this rare species some 20 km s. of Riverside, where more common.

ERIOGONUM ZIONIS J. T. Howell var. ZIONIS (POLYGONACEAE).—USA, AR, Mohave

Co., Paria Plateau, locally abundant in deep sandy soil on n.-facing slope in open woodland, T39N R4E S21, 2140 m, 3 Oct 1979, *Gierisch 4690* (MARY).

Previous knowledge. sw. UT, Kane and Washington cos., in and near Zion Natl. Park. Only *E. zionis* var. *coccineum* J. T. Howell previously known from AR, this restricted to both sides of Grand Canyon. (Herbaria consulted: ARIZ, ASC, ASU, BRY, CAS, DS, GCNP, GH, MARY, MNA, MO, NY, OKL, POM, RENO, RSA, UC, US, UT, UTC, ZION; published sources: Kearney and Peebles, op. cit.; McDougall, op. cit.; Reveal, op. cit., 1976.) *Diagnostic characters.* Erect perennial herb with fistulose, glabrous stems and branches; involucres racemosely disposed along the upper branches; tepals white, glabrous; leaves basal and occasionally highly reduced and at the first node.

Significance. New to AR; range extension of 35 km.—James L. Reveal, Department of Botany, University of Maryland, College Park 20742 and Barbara J. Ertter, New York Botanical Garden, Bronx 10458. (Received 16 Nov 1979; accepted 2 Jan 1980; final version received 18 Feb 1980.)

Avicennia marina var. resinifera (Forst.f.) Bakh. (Verbenaceae or Avicenniaceae).—USA, CA, San Diego Co., San Diego, Mission Bay, Kendall/Frost Marsh (near 32°47.5′N, 117°13.8′W): 26 Aug 1979, *Bunch 35*; 9 Sep 1979, *Moran 28024* (SD and to go). Perhaps 100 or more flowering-size shrubs (to 2.3 m high; trunk to 10 cm) and many seedlings; salt marsh with *Batis* sp., *Jaumea carnosa, Limonium californicum, Salicornia virginica, Spartina foliosa,* and *Suaeda californica.* Starting to flower Aug and to fruit Nov. Verified by H. N. Moldenke, Sep 1979.

Previous knowledge. Native to Indonesia, Melanesia, Australia, New Zealand (Moldenke, 5th summ. Verbenaceae, Avicenniaceae . . . 1971). In New Zealand to 38°S (Allan, Fl. New Zeal. 1961). Andrew A. Benson planted various mangroves here ca. 1966–69, this one from Auckland, New Zealand (36°52′S). A single plant of *Aegiceras corniculatum* (L.) Blanco (Myrsinaceae) also survived, flowering 9 Sep 1979 (*Moran 28025,* SD); it came from Cairns, Australia (16°55′S), but the species reaches 34°S.

Significance. First record of *A. marina* var. *resinifera* for W. Hem. and probably for N. Hem. Also, first record of mangrove in California. Approximate northern limits (based on material in SD) for native mangroves on Pacific coast of N. Amer. (excluding Gulf of California) are as follows: *Avicennia germinans* (L.) L., 25°41′N; *Conocarpus erecta* L., 23°24′N; *Laguncularia racemosa* (L.) Gaertn.f., 26°47′N; *Rhizophora mangle* L., 26°58′N.

Kendall/Frost Marsh, the only salt marsh left in Mission Bay, is a wildlife reserve. An endangered Clapper Rail (*Rallus longirostris* subsp. *levipes*) nests in the native marsh vegetation and the avicennia is, or was, thought an undesirable weed. This note is not only a first report but also an obituary. Mangrove Lovers & Protective Association, where were you? But then, possibly some seedlings drifted off, to be heard from later.—Reid Moran, Natural History Museum, San Diego, CA 92112. (Received 12 Nov 1979; accepted 7 Dec 1979; final version received 27 Mar 1980.)

Draba stenoloba Ledeb. var. ramosa Hitchcock (Brassicaceae).—USA, CA, Modoc Co., Warner Mts., vicinity of Benton Meadow, ca. 2200 m, with *Abies, Pinus contorta* subsp. *murrayana, Stellaria, Osmorhiza,* and *Veratrum*: T44N R15E S20, 3 Aug 1979, *Schoolcraft 166*; T44N R15E S8, 8 Aug 1979, *Schoolcraft 168*; and T44N R14E S1, 8 Aug 1979, *Schoolcraft 169* (all in UC). Verified by Reed Rollins, GH, Jan 1980.

Previous knowledge. "Nevada and California, from the Lake Tahoe region" (Hitchcock, Univ. Wash. Publ. Biol. 11:102. 1941). Long cited as endemic to the Tahoe region. California Native Plant Society files show collections from El Dorado and Nevada cos. Northern Nevada Native Plant Society files show collections from Douglas and Washoe cos. (Herbaria consulted: AHUC, BOIS, BRY, CAS, CHCS, DAV, DS, HSU, IDS, IRVC, JEPS, LA, NCC, NESH, OBI, OGDF, POM, PRI, RENO, ROPA, RSA, SBBG, SBM, SD, SDSU, UC, UCR, UCSB, UNLV, UTC, WSCO, WTU; published sources: Hitchcock, op. cit.; Munz, A. Calif. fl. 1959; NNNPS, Nevada T/E plant map bk. 1978; Smith, Wasmann J. Biol. 31:121. 1973; True, Ferns seed pls. Nevada Co., CA. 1973.)

Significance. Range extension northward of ca. 240 km. Hitchcock cited *Mrs. C. C. Bruce 2248,* collected in 1898 (UC, reportedly also NY) from a place identified only as "Lake City Canon," CA. The need to map this cryptic locality for CNPS's rare plant studies led Howard to search historical files at UC, establishing that Mrs. Bruce had sent her specimen from her home in Davis Creek, Modoc Co. An 1892 topographic map showed a road even then across the Warner Mts. east from Davis Creek passing down a canyon to Lake City on the shores of Upper Alkali Lake. Modern Forest Service maps referred to this canyon as "Lake City Canyon." Therefore, Schoolcraft traversed this route and collected the three specimens cited above. This *Draba* can no longer be considered endemic to the Tahoe region and should be sought elsewhere between there and Modoc Co. It is considered a rare plant by CNPS (Spec. Publ. No. 1, 1974), NNNPS (loc. cit.), and the U.S. Fish & Wildlife Service (Fed. Reg. 40:27839. 1975).—GARY SCHOOLCRAFT, U.S. Bureau of Land Management, Susanville District, Box 1090, Susanville, CA 96130 and ALICE Q. HOWARD, University of California Herbarium, Department of Botany, Berkeley 94720. (Received 29 Jan 1980; accepted 29 Jan 1980.)

URTICA DIOICA L. subsp. DIOICA (URTICACEAE).

Previous knowledge. Europe; introduced mostly into ne. N.A., but listed by Booth and Wright (Fl. Montana II. 1966) as occurring in MT (Herbaria consulted: DS, GH, MONT, NY, RM, WTU; published sources: Bassett et al., Canad. J. Bot. 52:503–516. 1974). *Diagnostic characters.* Predominantly dioecious; stems weak, sprawling; both leaf surfaces and stem hispid with stinging hairs; tetraploid.

Significance. The 1st Fl. Montana voucher specimens at MONT and MONTU are in fact *U. dioica* L. subsp. *gracilis* (Ait.) Seland. (predominantly monoecious; upright; lower leaf surface with stinging hairs; diploid). Subspecies *dioica* should be deleted from list of plants found in MT.

URTICA DIOICA L. subsp. HOLOSERICEA (Nutt.) Thorne (URTICACEAE).—USA, MT: Beaverhead Co., Foot of Dutchman Mt., *Leithead 63* (DAO); Ravalli Co.: 6 km s. of Hamilton and ½ km n. of Bitterroot R., *Woodland 1262, 1274*; 2 km s. of Hamilton along hwy 93, along stream in field, *Woodland 1275*; 1 km s. of Corvallis jct along hwy 93, edge of marsh, *Woodland 1276.*

Previous knowledge. Great Basin and California. (Herbaria consulted: DAO, DS, GH, MONT, MONTU, MTMG, NY, RM, WTU, US; published sources: Abrams, Illus. flora Pac. States. 1940; Davis, Fl. Idaho. 1952; Hitchcock et al., Vasc. pls. Pac. Northw. II. 1964; Jepson, Man. fl. pls. California. 1953; Munz, A California fl. 1959; Peck, Man. higher pls. Oregon. 1961; Porter, Fl. Wyoming. 1967. Synonyms: *U. breweri* S. Wats.; *U. holosericea* Nutt. *Diagnostic characters.* Predominantly monoecious; stems erect; stems and lvs villous to woolly.

Significance. First report for MT. Nearest known populations in s. ID. This taxon has gone unrecognized because the older herbarium record (6 Jul 1938, *Leithead 63*) was misidentified as *U. dioica* subsp. *gracilis.*

URTICA URENS L. (URTICACEAE).

Previous knowledge. Eurasia; introduced into N.A., and mentioned by Booth and Wright (op. cit.) as only annual nettle in MT; "waste ground". (Herbaria consulted: DAO, DS, GH, IDS, MONT, MONTU, MTMG, NY, RM, WS, WTU, UC, US: published sources: Bassett et al. (op. cit.); Mason, Madroño 19:164. 1968; Woodland et al., Canad. J. Bot. 54:374–383. 1976).

Significance. Lack of herbarium or field records suggests that this species is not found in MT.—DENNIS W. WOODLAND, Biology Department, Andrews University, Berrien Springs, MI 49104. (Received 10 Aug 1978; returned 8 Sep 1978; revision received and accepted 23 Jan 1980; final version received 20 Mar 1980.)

CYTISUS SCOPARIUS (L.) Link f. ANDREANUS (Puissant) Zabel (FABACEAE).—USA, CA, Marin Co., Deer Park, 1.7 km s. of Fairfax (near 37°58′N, 112°35′W), 30 Mar 1974, *Wright 22b*; 29 Apr 1975, *Wright 560* (author's herbarium). With f. *scoparius* in a few places in annual grassland in the valley at 60 m and on ridges to the e. and ne. at 180 m; Canada, B. C., Moresby Island, 18 Jun 1964, *Calder and Taylor 35153* (UC).

Previous knowledge. Native to c. and s. Europe. In w. N.A., naturalized in San Mateo (probably this taxon), Santa Clara, and Sonoma cos., CA, as well as in B. C., in apparently low frequency with f. *scoparius*. (Herbaria consulted: UC, JEPS; published sources: Munz, A Calif. fl. 1959; Munz, Suppl. Calif. fl. 1968; Baker, Partial list seed pls. N. Coast Ranges Calif. 1972; McClintock and Knight, Proc. Calif. Acad. Sci. 32:587–677. 1968.) *Diagnostic characters.* Differs from f. *scoparius* by the red or sometimes red-brown color of the wings and calyx; banner also tinged red.

Significance. New to Marin Co. Best name (Rehder, Bibl. cult. trees shrubs. 1949; Dr. P. Hiepko, pers. comm., 1976) for the red-winged Scotch Broom referred to by Munz (Suppl. Calif. fl., p. 116. 1968) as "*Cytisus scoparius* var. *andreanus* (Puissant)". Munz's material, taken from Santa Clara Co., was distributed as *C.* × *dallimorei* Rolfe [*C. scoparius* f. *andreanus* × *C. multiflorus* (Ait.) Sweet], a hybrid made at Kew ca. 1900 that has rose-purple and white fls. and relatively small fls. and frs. (Bean, Bot. Mag. 139:tab. 8482. 1913). If the *C. multiflorus* genome were present in Munz's material, some expression in flower color and size would be expected and none is apparent. However, *C.* × *dallimorei* is cultivated locally and may escape [Marin Co., Inverness, one individual possibly escaped from a nearby garden, near Perth Way on fire road to Mt. Vision, 7 Apr 1977, *Wright 846* (author's herbarium)], leaving open the question of backcrosses with forms of *C. scoparius*.—DARRELL M. WRIGHT, 2337 Prince St., Berkeley, CA 94705. (Originally received 4 Oct 1976; resubmitted 25 Jan 1980; returned 26 Jan 1980; revision received and accepted 17 Mar 1980; final version received 28 Mar 1980.)

NOTES AND NEWS

A NEW COMBINATION IN *Epilobium* (ONAGRACEAE).—Recent work toward a comprehensive revision of the genus *Epilobium* in North America has revealed the need for a nomenclatural change in *E. obcordatum* A. Gray subsp. *siskiyouense* Munz, a rare plant of northern California and southern Oregon. Although apparently related and similar to *E. rigidum* Hausskn. and *E. obcordatum* A. Gray (Raven, Ann. Missouri Bot. Gard. 63:326–340. 1976), this entity is entirely allopatric to both species and is amply distinct in habit, leaves, and floral characteristics. We make the following new combination in advance of the publication of our more complete revision in order to make the name available.

Epilobium siskiyouense (Munz) Hoch & Raven, comb. nov.—*Epilobium obcordatum* A. Gray subsp. *siskiyouense* Munz, N. Amer. Fl. II. 5:205. 1965.—TYPE: USA, CA, Siskiyou Co., Siskiyou Mts. (T47N R11WS1), about rocks, dry open n. slope, n. side White Mt., 1800 m, 14 Aug 1934, *L. C. Wheeler 3135* (Holotype: RSA!; isotype CAS!).

Epilobium obcordatum A. Gray var. *laxum* ("*laxa*") Dempster in Jepson, Fl. Calif. 2:566. 1936; non *Epilobium laxum* Royle, Illus. Bot. Himal. 211. 1835.—LECTOTYPE here designated: USA, CA, Siskiyou Co., summit above Cold Spring, Woolly Creek, 5 Aug 1908, *G. D. Butler 46* (JEPS!; isolectotypes: JEPS!, POM!). Two of the five specimens cited in protologue (those from Placer Co., *Sonne*) are *E. obcordatum* var. *obcordatum*. The remaining three specimens are *E. siskiyouense*. The epithet is based on the informal category "*laxa*" (no rank assigned nor specimens cited) of Haussknecht (Monogr. *Epilobium* 251. 1884).

Epilobium siskiyouense differs from *E. obcordatum* in having a more distinctly suffrutescent habit, not sprawling and mat-like as in the latter; leaves larger and more broadly ovate; a floral tube 0.6–0.9 times longer than wide (vs. 1–1.8 in *E. obcordatum*); and a ring-shaped flap of tissue inside the floral tube near the base, which is unique in the genus. *Epilobium rigidum* differs from both by its distinctive seed morphology and size (Seavey et al., Ann. Missouri Bot. Gard. 64:18–47. 1977), its petiolate leaves, and shallower floral tube (0.3–0.6 times longer than wide). *Epilobium siskiyouense* occurs on scree slopes and serpentine ridges in Siskiyou and Trinity cos., CA and Jackson Co., OR, from 1500–2500 m. In contrast, *E. rigidum* is restricted to Del Norte Co., CA and Josephine Co., OR, whereas *E. obcordatum* extends from Shasta and Modoc cos., CA, s. throughout the Sierra Nevada and scattered eastward in the mountains of NV, e. OR, and ID. The presence of an endemic species of this widespread and generally weedy genus in the Klamath-Siskiyou region is not surprising in view of the high endemism prevalent in the flora of the area (Whittaker, Ecol. Monogr. 30:279–338. 1960; Raven and Axelrod, Univ. California Publ. Bot. 72:1–134. 1978), and in view of the presence of four other endemic *Epilobium* species in the region.

Although *E. siskiyouense* is remarkably intermediate in many morphological characters and in distribution between *E. obcordatum* and *E. rigidum,* we have no direct evidence suggesting that it is of hybrid origin. We are currently investigating the crossing relationships within this very interesting group of species as part of our continuing biosystematic study of the genus.

S. R. Seavey added valuable observations to this note.—PETER C. HOCH and PETER H. RAVEN, Missouri Botanical Garden, P.O. Box 299, St. Louis 63166. (Received 31 Mar 1980; accepted 1 Apr 1980.)

REEVALUATION OF *Phlox grahamii* (POLEMONIACEAE).—Edgar T. Wherry (Brittonia 6:60–63. 1943) described *Phlox grahamii* as an intermediate between *Phlox* and *Microsteris* and therein challenged Mason's view (Madroño 6:122–127. 1941) that these two genera are indistinguishable. The type specimen, the only collection referable to *P. grahamii,* is a rather tall perennial with well-spaced leaves and a distinct, relatively long corolla tube, as in *Phlox*. Yet the leaves are small and few with some lobed near the base, the corolla tube is strongly flared at the base, and the inflorescence is sparse—all features of *Microsteris*.

The holotype (USA, UT, Uintah Co., talus slopes at the mouth of Sand Wash near the Green River, 1933, *Graham 7884,* CM) is copiously infested with a rust, *Puccinia plumbaria* Peck. The base of the corolla tube is filled with hyphae that caused it to flare and one of the few upper leaves bears a number of aecia embedded in the epidermis that apparently caused the blade to lobe as it elongated. The type is best interpreted as a teratological specimen of the common *Phlox longifolia* Nutt. Accordingly, *Phlox grahamii* Wherry should be considered a synonym of *P. longifolia* Nutt. and should be dropped from consideration as a threatened species (Ripley, House Document 94–51:1–200. 1975; Welsh et al., Great Basin Naturalist 35:327–376. 1976).—FREDERICK J. PEABODY, Department of Botany, Iowa State University, Ames 50011. (Received 15 Nov 1979; accepted 6 Mar 1980; revision received 17 Mar 1980.)

EDWARD LEE

Edward Lee (12 Jul 1914–29 Dec 1979). In the early 1930's as an undergraduate and graduate student at the University of California, Berkeley, Ed made many fieldtrips, mostly in the Coast Ranges of central California, but principally in the San Francisco Bay area. He collected on the Antioch Sand Dunes while they were still almost intact, and in 1935–36 he assisted Professor Herbert L. Mason, Director of the Herbarium of the University of California, in a botanical survey of Point Lobos Reserve State Park. He was well acquainted with the flora of his native city, San Francisco, and most of his collecting there was done alone. On trips farther afield he was often in the company of Joseph and Nesta Ewan, Annetta Carter, Ethel Crum, and Charles Belshaw (with the latter mostly in the Sierra Nevada foothills). His beautifuly prepared and carefully documented collections, which numbered 2616 in 1936, are housed in the Jepson and University herbaria, University of California, Berkeley, and duplicates are widely distributed. More recent collections with numbers in the 5000 series are being processed. He was a brilliant student, but instead of continuing in academic life, he chose to work with his hands and became a machinist. However, he kept Botany as an avocation—something that he achieved very successfully, as may be attested by his many friends who shared fieldtrips with him and benefited from his extensive knowledge. In recent years, he concentrated on bryophytes, lichens, and ferns, but these represented only a fraction of his myriad interests which included socio-economic problems, music, and oriental art and language.—ANNETTA CARTER, Herbarium, Department of Botany, University of California, Berkeley 94720.

BOOKS RECEIVED AND LITERATURE OF INTEREST

The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. By HENRY A. GLEASON. 3 vols., lxxxiii + 1727 p., illus. Hafner Press, 200D Brown St., Riverside, NJ 08370. 1952. ISBN 0-02-845300-7. $99.95 per set. Recently reprinted without change.

NEWS OF CALIFORNIA HERBARIA

This new but irregular feature is one result of the formation of a consortium of California herbaria and reference collections. The first issue of the consortium's annual newsletter, CALOCHORTUS, has been mailed to all herbaria and reference collections in California. It outlines faculty, staff, and student research using those collections. Each issue of CALOCHORTUS will emphasize some aspect of herbarium activities.

The purpose of this news feature is to provide a more rapid mechanism for the dissemination of information about the consortium and the collections it comprises to a broader botanical community. Announcements, requests for material, or articles intended for either CALOCHORTUS or NEWS OF CALIFORNIA HERBARIA may be submitted at any time to: DR. THOMAS DUNCAN, Department of Botany, University of California, Berkeley 94720.

ANNOUNCEMENT

XIII INTERNATIONAL BOTANICAL CONGRESS

The XIII Botanical Congress will take place at the University of Sydney, Australia, 21–28 Aug 1981. The program is divided into 12 sections corresponding with major subdisciplines of botany: molecular, metabolic, cellular and structural, developmental, environmental, community, genetic, systematic and evolutionary, bryological, fungal, marine and freshwater, historical, and applied. Registration and accommodations (less travel and meals) should cost about $350–700 U.S. More than 35 pre- and post-Congress fieldtrips are planned. Rates for these range from $55 to $1320.

For more information, contact Dr. W. J. Cram, Executive Secretary, XIII International Botanical Congress, University of Sydney, N.S.W. 2006, Australia.

ERRATUM

vol. 24, p. 24, text line 3. For "Torr. (1865)" read "Torr. (1856)." This change is important to understand typification because a synonym is dated 1863.

Membership in the California Botanical Society is open to individuals ($16 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Institutional subscriptions to MADROÑO are available ($22 per year). The membership or subscription year begins on January 1.

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Line copy illustrations should be clean and legible, proportioned (including their captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in Figures, as should explanation of symbols. In addition, 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 board and mailed flat.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren and Keuken's list (*Index herbariorum, Part 1. The herbaria of the world.* Sixth edition. 1974. Regnum Veg. vol. 92). Abbreviations of names of journals should be those in *Botanico-Periodicum-Huntianum* (Lawrence, G. H. M. et al. 1968. Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full title of the journal should be used. Titles of books should be given in full, together with the place and date of publication, name of publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted eight pages in the journal over a two-year period. Beyond that number of pages, a required editorial fee of $40.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. 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

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Officers for 1980

SYSTEMATICS OF THE ANNUAL CALIFORNIA CAMPANULAS (CAMPANULACEAE)

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Department of Botany,
University of California, Berkeley 94720

ABSTRACT

Four of the ten species of *Campanula* that are found in the California Floristic Province are annuals: *Campanula angustiflora* has wide leaves, small flowers, equatorially-porate pollen, $n = 15$, and grows in the North Coast Ranges and in the Santa Cruz Mts; *Campanula exigua* has narrow leaves, large flowers, pantoporate pollen, $n = 17$, and grows in the inner South Coast Ranges; *Campanula sharsmithiae*, described here, also has a large corolla, pantoporate pollen, and $n = 17$, but has fleshy leaves and opposite bracts that are wider than those of *C. exigua* and is restricted to steep serpentine talus slopes in the Mt. Hamilton Range; and *Campanula griffinii*, originally described as *C. angustiflora* var. *exilis* but here recognized at the specific level, which has narrow leaves, small flowers, pantoporate pollen and $n = 17$, and grows in the inner North Coast Ranges and the South Coast Ranges. It is suggested that *C. griffinii* is closely related to *C. exigua*. *Campanula angustiflora* and *C. griffinii* are predominantly autogamous, an unusual character state for the genus. These are the first annual campanulas reported to have chromosome numbers $n = 15$ or $n = 17$. Only one other *Campanula*, *C. americana*, which is a virgate annual or biennial found in eastern North America, is known to have pantoporate pollen. Morphological similarities of these taxa to other North American Campanuloideae may be due to convergence; consequently, the relationships of these four species are obscure.

Campanula comprises about 300 species (Willis, 1973) and is the largest genus in Campanuloideae. Most campanulas are perennial, have $n = 17$, and are found in Eurasia. About 10 percent of the species are annual, and chromosome numbers reported for these are mostly $n = 10, 12, 14,$ or 16; $n = 15$ or 17 had not been reported for any annual *Campanula* (Gadella, 1964; Fedorov and Kovanda, 1976). Only 22 species of *Campanula* are native to North America. Ten species are found in the California Floristic Province, and eight are endemic to it. Four of the eight are annuals and are found only in the west central part of California.

In most campanulas allogamy predominates (Gadella, 1964) and is mediated by a pollen presentation mechanism that is unique to Campanulaceae (Shetler, 1979). In this syndrome, the stamens have introrse anthers and dilated, bearded, filaments that arch over the nectariferous style base. Before anthesis, pollen is shed onto the densely papillate style, which sweeps up the pollen as it elongates. Several hours to several days after anthesis, the papillae invaginate, any remaining pollen drops off, and the style lobes, previously tightly pressed together, reflex, exposing the receptive stigmatic surface.

MADROÑO, Vol. 27, No. 4, pp. 149–163, 30 October 1980

The character states associated with this pollen-presentation mechanism seem to be rigorously fixed and any departure from this pattern has been treated as taxonomically important. Consequently, species having undilated or unciliated filaments or incompletely papillated styles have been grouped together (Gadella, 1964, 1966; Damboldt, 1976). Two of the annual California campanulas have small corollas, narrow filaments, and styles only partially papillate.

All of the California annuals have been a source of confusion since their discovery, judging from the misidentifications found in herbaria, and they are not known to be closely related to any other campanulas. Treatment of small-flowered and annual Old World campanulas has been controversial (Boissier, 1874; de Candolle, 1830; Gadella, 1964, 1966; Fedorov, 1957), and knowledge of New World campanulas is very limited (Shetler, 1963). Here I give detailed descriptions of the Californian annual campanulas in order to facilitate eventual comparison between them and their North American relatives and between them and their Mediterranean counterparts.

TAXONOMIC HISTORY

W. H. Brewer (1867) made the earliest known collection of this group in 1862 on Mt. Hamilton (Santa Clara Co.) just a few days after he had found its striking associate, *Clarkia breweri* (A. Gray) Greene. Gray never assigned a species name to the specimen, and this campanula was not collected again until Rattan found it on Mt. Diablo (Contra Costa Co.) and described it as *Campanula exigua* (Rattan, 1886). In his description, Rattan referred to a plant taken that same year by Mrs. Curran on Mt. Tamalpais (Marin Co.). Alice Eastwood (1898) included the Mt. Tamalpais plant in *C. angustiflora* Eastwood. In her discussion of the new species, Eastwood referred to "very young specimens of an annual *Campanula*" collected in Priest Valley (Monterey Co.) that shared some characteristics with both named taxa, but that she chose to retain in *C. angustiflora*. Howell (1938) eventually described this last plant as *C. angustiflora* var. *exilis,* herein named *Campanula griffinii*.

METHODS

Seeds of field-collected plants were grown at the University of California Botanical Garden in pots of "UC Mix, formula C" soil (Matkin and Chandler, 1957), in insect exclosures, for studies of morphology, cytology, and pollination system. Seed sources are indicated in the Taxonomic Treatment and included at least one northern and one southern population of each species except *C. sharsmithiae,* seeds of which were not available. Voucher specimens are in UC.

Buds from field-collected and garden-grown plants were preserved in Carnoy's 6:3:1 solution; microsporocytes were stained in acetocarmine for chromosome preparations. Pollen was mounted in lactophenol and cotton blue for study of general morphology and was prepared following the method of Lynch and Webster (1975) for study of exine ultrastructure, except that material was CO_2-critical-point-dried directly from 100 percent ethanol. After initial preparation the pollen was coated with 30 nm of gold palladium and viewed on a Coates and Welter Model 50 Emission Scanning Electron Microscope.

Measurements of vegetative and floral parts were made on pressed, garden-grown plants and on herbarium specimens from BR, CAS, CU, DAV, DS, GH, JEPS, K, MICH, MO, ND, NO, NY, ORE, OSC, PH, POM, RSA, SBBG, UC, UCSB, US, UTC, WS, and WTU. Corollas of living plants were photographed in direct sunlight with a Tiffin 18A Photar filter with high speed Ektachrome and Tri-X films to document ultraviolet (UV) absorption patterns.

Flowers of carpellate parents in artificial crosses were emasculated before anthesis and later pollinated by transferring pollen from the styles of the staminate parent, on sterile forceps, to the stigmatic surface of the carpellate parent. Except when they were being manipulated, the flowers were covered with Kimwipe bags. Self-pollination was tested by bagging flowers with Kimwipe bags before anthesis with no further treatment. Self-compatibility of *C. exigua* was tested by transferring pollen from the style to the stigma of the same flower. Pollen is deposited on the stigmatic area of *C. angustiflora* and *C. griffinii* before anthesis and therefore was not artificially transferred. Presence of apomixis was tested by leaving emasculated flowers unpollinated.

RESULTS

The two most obvious characters that separate these annual species are leaf width and corolla size (Figs. 1 and 2). *Campanula exigua* and *C. sharsmithiae* have large flowers. The former has thin, narrow leaves and the latter has fleshy, broader leaves. *C. griffinii* has narrow leaves and small flowers, and *C. angustiflora* has broad leaves and small flowers. These species also differ in ovary shape, filament shape, and position of upper bracts. These characters, along with flower size and leaf shape, are more constant under garden conditions than most other characters. For this reason, they were chosen as major, differentiating characters.

Campanula exigua, C. sharsmithiae, and *C. griffinii* have $n = 17$, whereas *C. angustiflora* has $n = 15$; they are the first annual campanulas reported to have these numbers. At least two populations of each species (only one for *C. sharsmithiae*) were counted; vouchers are deposited in UC and indicated in the Taxonomic Treatment.

Campanula exigua has 12-pantoporate pollen, *C. sharsmithiae* has 14–20 pantoporate pollen, and *C. griffinii* has 8-pantoporate pollen

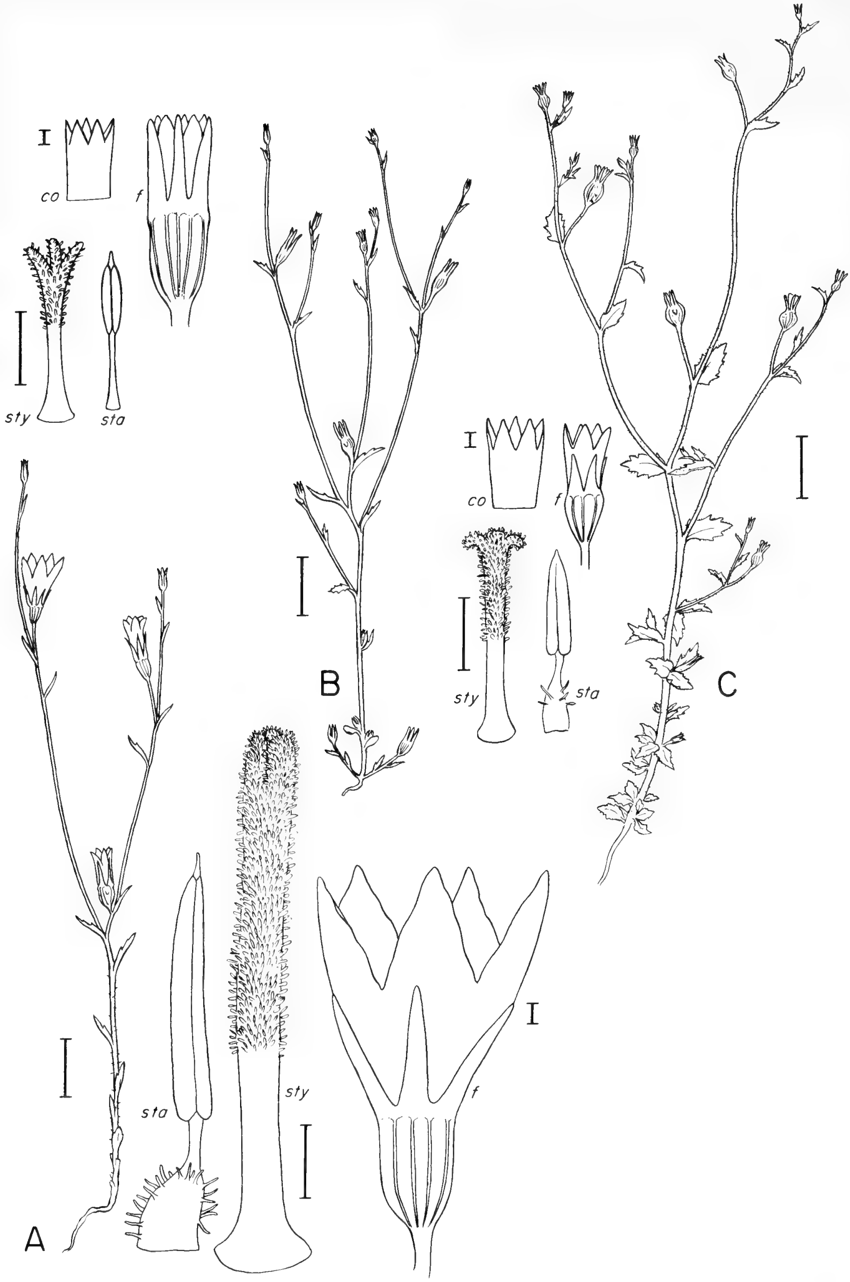

FIG. 1. A. *Campanula exigua* Rattan (after *Griffin 4141,* UC). B. *Campanula griffinii* Morin (after *Griffin 4120,* UC). C. *Campanula angustiflora* Eastwood (after *Morin 249,* UC). Habits: scale bar = 1 cm. Details (sty = style, sta = stamen, co = corolla, f = flower): scale bar = 1 mm.

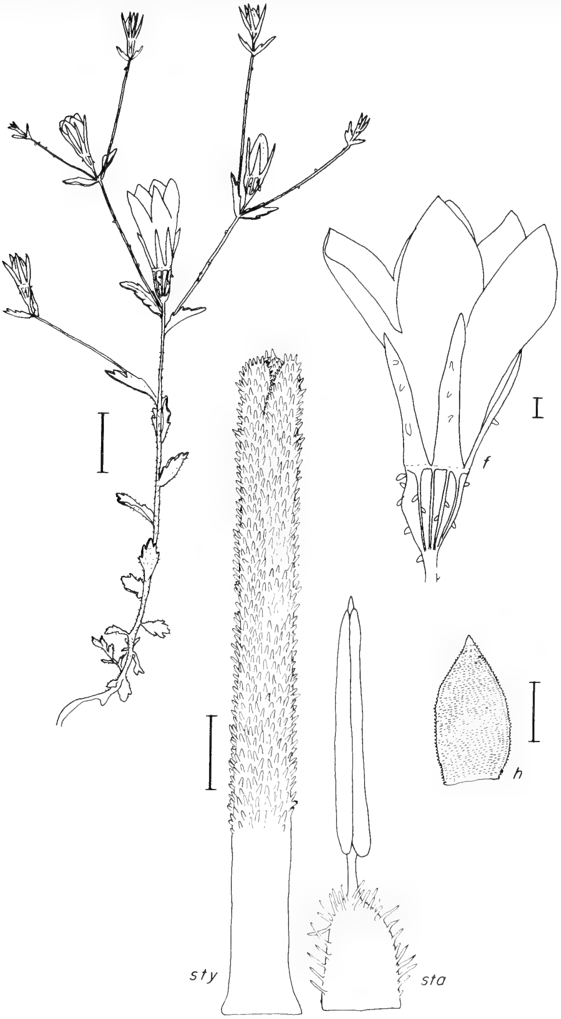

FIG. 2. *Campanula sharsmithiae* Morin (After *Morin 299,* UC). Habit: scale bar = 1 cm. Details (sty = style, sta = stamen, f = flower): scale bar = 1 mm; (h = hair): scale bar = 0.1 mm.

(Fig. 3). Pantoporate pollen in Campanulaceae has previously been known only from *C. americana* (Dunbar, 1975). *Campanula angustiflora* has 6-porate pollen, the pores equatorial (Fig. 3). Following the terminology used by Dunbar (1975), pollen sexine fine structure for the species studied can be described as short ridges, tip end bent upwards, with basally divided spinules (Fig. 3).

Reciprocal crosses among all species were unsuccessful. Unemas-

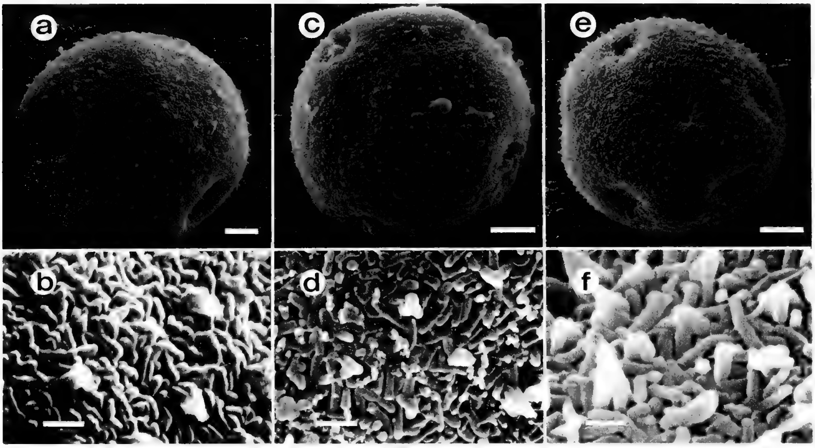

FIG. 3. a, b. *Campanula angustiflora*. c, d. *Campanula griffinii*. e, f. *Campanula exigua*. a, c, e. Pollen grains, scale bars = 5 μm. b, d, f. Detail of exine, scale bars = 0.5 μm.

culated, bagged flowers and unbagged flowers of *C. angustiflora* and *C. griffinii* set seed (50–80 seeds per capsule), but emasculated, unpollinated flowers did not produce seed. These two species are self-pollinating and self-compatible; they do not appear to be apomictic, but pseudogamy cannot be ruled out. No flowers of *C. exigua* produced seed. Since even control, intrapopulational crosses were unsuccessful even though flowers in the field produce up to 100 seeds each, failure may have been due to technical problems such as mechanical damage to the stigma. *Campanula exigua* is not self-pollinating and seems to be self self-incompatible.

TAXONOMIC TREATMENT

Key to annual California campanulas

Leaves 2–3 times as long as broad, oblong-ovate .. *C. angustiflora*.
Leaves more than 3 times as long as broad, never oblong ovate.
  Corolla equal to or shorter than ovary .... *C. griffinii*.
  Corolla 2–5 times as long as ovary.
    Upper leaves and bracts linear to linear subulate, bracts widely (ca. 8 mm) separated .... *C. exigua*.
    Upper leaves and bracts broadly lanceolate, bracts opposite or nearly so .... *C. sharsmithiae*.

CAMPANULA ANGUSTIFLORA Eastwood, Proc. Calif. Acad. Sci. 3rd Ser. 1:132–133. 1898.–TYPE: California, Marin Co., Mt. Tamalpais, 5 Jul 1886, *M. K. Curran s.n.* (Holotype CAS!). PARA-

> TYPES: same locality as holotype: June 1890 and July 1898, *Mrs. Brandegee s.n.*, ND! US!; *Eastwood s.n.* (CAS but lost in 1906?); 14 Jul 1894 (?) *Congdon s.n.* GH!; Sonoma, Mt. St. Helena, *Mrs. Brandegee s.n.* CAS!.

Erect annuals, 5–25 cm high; stems 4-angled, hispid; cauline leaves sessile, alternate, 4.5–9 mm long, oblong-ovate, acute, coarsely serrate, abaxial side hispid, longest leaf 3–4 nodes below first flower; bracts 1.5–3.5 times as long as broad, 3.5–5.5 mm long, oblong-ovate to lanceolate, few toothed, evenly distributed on branch; flowers terminal, pedicel (3–)10(–20) mm long; corollas pale blue to white, all parts equally UV-absorbing, 2.5–5 mm long, cylindrical, with five acute, spreading lobes 1.1–1.7 mm long, no inner papillae; style white, 2.1–3.0 mm long, papillate distally half its length; style lobes 0.15 to 0.3 times the length of the style, loosely appressed at anthesis; stamens 2.0–2.6 mm long, anthers as long as filaments, filaments gradually broadened to base, with few cilia; pollen 0.03 mm dia., 6-porate, the pores equatorial; ovary 2–3 mm long, obovoid, broadest at middle and narrowed apically, finely ribbed; calyx lobes slightly unequal, 2–6 mm long, erect, subulate; calyx lobes connivent in fruit forming a kind of beak; capsule spheroid, strongly ribbed, pore inter-rib area strongly infolded and tuberculate; pore about midway between base and apex of capsule; ovules 50–100, seeds light brown, 0.7 mm long, twice as long as broad, fusiform, finely striate, 3-sided or keeled (Fig. 1); $n = 15$; flowers Apr–Jul; locally abundant in serpentine soil, chaparral, or burned over areas in the Inner North Coast Ranges, central Lake Co. south to Marin Co., and central Santa Cruz Co., 30–600 m (Fig. 4).

Representative specimens: CA: Lake Co., Lakeport, 18 Jun 1925, *Munz 9868*; Marin Co., Mt. Tamalpais, 25 May 1941, *Howell 16199*; Napa Co., se. slope of Mt. St. Helena, near the old inn, 18 May 1946, *Constance et al. 3045*; Santa Cruz Co.: Boulder Creek, 10 May 1943, *Hesse 309*; n. side of Jamison Creek, 22 Apr 1978, *Morin 170* (seed source and chromosome voucher); Sonoma Co.: burned chaparral, w. slope of Hood Mt., 22 Apr 1947, *Baker 11687*; summit of Spring Mt. Rd., 4 Jun 1978, *Morin 249* (seed source and chromosome voucher).

Flowers of *C. angustiflora* depart from the pattern typical for *Campanula* as described by Shetler (1979): the corollas are small, cylindrical, and inconspicuous; the filaments are not dilated; the style is incompletely papillate. However, the corolla is usually exserted from the calyx lobes and the filaments are ciliate. Because the style lobes are not completely appressed to each other during style elongation, pollen is deposited on and trapped in the stigmatic area before anthesis. Cross-pollination is not necessarily excluded, but, considering the reduction in characters usually associated with allogamy and the presence of self-compatibility, it seems likely that autogamy is the primary breeding system in this species.

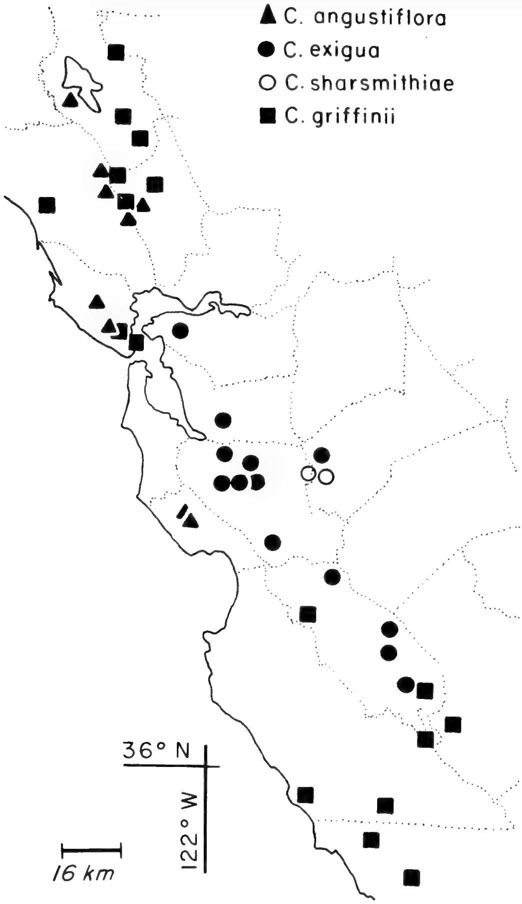

FIG. 4. Distribution of annual California campanulas.

In her description of *C. angustiflora,* Eastwood (1898) stated that the sides of the style were entirely smooth and illustrated it that way in an accompanying figure. The pictured style has fully recurved lobes: at that point in development the stylar papillae would all be invaginated (Shetler, 1979).

Campanula angustiflora can be distinguished from other small-flowered campanulas by its sessile, oblong-ovate, coarsely serrate leaves. It is vegetatively similar to *Heterocodon* and *Triodanis,* both of which have at least some cleistogamous flowers. Many of the lower cauline leaves of *C. angustiflora* subtend very short flowering stems, and this strengthens the resemblance to *Triodanis,* the leaves of which subtend seemingly axillary but actually terminal, sessile, flowers (McVaugh, 1945). The possible relationship of these three taxa through some very early ancestor should be kept in mind.

CAMPANULA EXIGUA Rattan, Bot. Gaz. (Crawfordsville) 11:339. 1886. non Formanek, 1894.—TYPE: California, Contra Costa Co., summit of Mt. Diablo, 14 June 1886, *V. Rattan s.n.* (Holotype: JEPS!; Isotypes: GH! JEPS!). The Rattan collection at GH contains a holograph description of the new species with a postcard sent to Coulter that mentions Mrs. Curran's Mt. Tamalpais collection. There is no indication on that specimen that it is the holotype. The sheets at JEPS were deposited there after Rattan's death by his daughter, according to Jepson's notes, and had been part of Rattan's personal herbarium. In the pocket of one, marked "type" in Jepson's hand, is a loose label with imprinted locality information and "*Campanula githopsidea*" handwritten. On the reverse of the label is a note in Rattan's handwriting to the effect that Gray had suggested *C. exigua* instead because he considered the former name confusing. It seems reasonable to treat this JEPS sheet as the holotype.

Erect annuals, 5–25 cm high; stems 4-angled, glabrous or hispid below the first flower, or all parts hispid; lower cauline leaves sessile, alternate, 4–7 mm long, broadly spatulate, obtuse, few-toothed, abaxial side glabrous or hispid; upper cauline leaves (5–)7–11 mm long, linear-subulate, 6–14 times as long as broad, acute, with 4 pairs of narrow, shallow, gland-tipped teeth, abaxial side glabrous or hispid; longest leaf subtends first flower; bracts sessile, 4–5.7 mm long, linear-subulate, 6.5–15 times as long as broad, acute, few-toothed, lower bract closer to flower than to leaf subtending branch but the two bracts of each branch (4–)7–10(–21) mm apart; pedicel (2–)7–15 mm long, usually curved; corollas 7.4–11(–18) mm long, 3–4.5 times as long as ovary, funnelform-campanulate, pale blue to white with fine, blue, longitudinal lines, throat more UV absorbing than lobes; lobes 5, about half the length of the corolla, twice as long as broad, acute, reflexed; corolla papillate internally at base and along sides beneath sinuses; style blue, 6–8 mm long, papillate distally two-thirds its length; style lobes 0.8–1.2 mm long, tightly appressed at anthesis; stamens 4.3–5.5 mm long, anthers twice the length of filaments, filaments abruptly dilated to a wide, ciliate base; pollen 12-pantoporate, 0.035 mm dia.; ovary 1.7–2.9 mm long, about as long as broad, conical at base, the sides cylindrical, strongly ribbed, the inter-rib area not infolded or tuberculate; calyx lobes slightly unequal, 4–5.5 mm long, erect, subulate, 2–3 times as long as ovary, twice to nearly equal capsule, erect in fruit; capsule 2.8–5.4 mm long, about as long as broad, strongly ribbed; pore midway between base and apex; ovules 60–100, seeds 0.65–0.73 mm long, oblong, elliptical in cross-section, about twice as long as wide, flat on chalazal end, light brown, shiny, finely striate (Fig. 1); $n = 17$; flowers May–Jun; scattered individuals on talus slopes, 300–1250 m in the inner South Coast Ranges from Mt. Diablo to southern San Benito Co. (Fig. 4).

Representative specimens: CA: Alameda Co., Sunol, Jun 1973, *W. Knight s.n.*; Contra Costa Co.: Summit of Mt. Diablo, 14 Jun 1924, *Bacigalupi s.n.*; Juniper Camp, Mt. Diablo, 30 May 1945, *Bacigalupi 2781*; Mt. Diablo, Mitchell Canyon, 2 Jul 1978, *Hannan 235* (seed source and chromosome voucher); San Benito Co.: Clear Creek Rd., T18S R11E S11 sw.¼, 25 May 1978, *Griffin 4123*; S11 se.¼, 15 Jun 1978, *Griffin 4141* (seed source and chromosome voucher); 32 km e. of Paicine, 13 Apr 1978, *Morin 163*; Laveaga Peak, 1160 m, T12S R7E S14, San Carlos Range, 2 Jun 1940, *Lyon 1442*; Santa Clara Co.: between San Antonio Valley and Arroyo Bayo, 760 m, 8 Jun 1935, *Carter 900*; 0.8 km above Gilroy Hot Springs, Coyote Creek, 31 May 1895, *Dudley 4117*; summit, Mt. Hamilton, 1 Jul 1862, *Brewer 1301*; on Kinkaid Rd. at crossing of Bonita Cr., 23 Apr 1978, *Morin 173*; summit, Mt. Day, 1200 m, 13 Jun 1935, *C. W. and H. K. Sharsmith 3358*; Stanislaus Co., Red Mountains, head of Arroyo del Puerto, 320 m, 18 May 1935, *C. W. and H. K. Sharsmith 3132*; same loc., 11 May 1980, *Morin 298*.

The flower structure of *C. exigua* is typical of campanulas and in terms of flower morphology *C. exigua* and *C. sharsmithae* retain the most primitive characteristics of the annual species discussed here. Rattan (1886) pointed out the morphological resemblance of *C. exigua* to *Githopsis,* another annual member of western North American Campanuloideae. *Githopsis pulchella* Vatke, the only obligately outcrossed species in that genus, and *C. exigua* are vegetatively almost identical and have very similar flowers. They differ in capsule structure, which is long, narrow, deeply ridged, and apically dehiscent in *Githopsis*. *Githopsis pulchella* has $n = 10$, 6-porate pollen, and striate, fusiform seeds. These differences suggest that these two species are similar because of convergence rather than direct relationship.

Campanula exigua is also vegetatively similar to *C. reverchonii,* an annual that is endemic to granitic outcrops in central Texas (Shetler, 1963); however, its capsule and seed morphology differ strikingly from those of *C. reverchonii*. Again, convergence rather than close relationship is suggested.

Most European *Campanula* pollen studied to date is 3- to 4-porate (Dunbar, 1975). Most North American campanulas (and other North American genera in Campanuloideae) have pollen that is 5- to 6-porate, the pores equatorial (Chapman, 1966; Chuang, pers. comm., 1978; Morin, unpubl. data). Only *C. americana* L., *C. exigua,* and *C. griffinii* are known to have pantoporate pollen, although pores of *C. reverchonii* are not strictly equatorial. Small (1903) placed *C. americana* in the monotypic genus *Campanulastrum,* and Gadella

(1964) supported this decision. There is little morphological similarity between *C. americana* (which is a tall, broadleaved annual or biennial with spicate inflorescences and rotate corollas) and the annual California campanulas. Therefore it seems likely that pantoporate pollen evolved independently in these two groups.

Campanula sharsmithiae Morin, sp. nov.

Species haec ab *C. exigua* differt foliis crassiusculis lanceolato-ovatis, bracteis oppositis; supernum dimidium pilis rigidis, verrucosis, 0.1–0.2 mm× 0.2–0.4 mm; pollen 14–20 pantoporatum (Fig. 2).

Erect annuals, 5–25 cm high; stems 4-angled, glabrous or hispid below first flower, the upper part usually with few to many broad, verrucose hairs that are 0.1–0.2 mm wide, 0.2–0.4 mm long; lower cauline leaves sessile, alternate, 5–11 mm long, broadly spatulate, obtuse, few-toothed, abaxial side glabrous or hispid; upper cauline leaves fleshy, (5–)7–11 mm long, broadly lanceolate, 3–5.5 times as long as broad, acute, with four pairs of long (0.9 mm) teeth, abaxial side glabrous or hispid; longest leaf subtends first flower; upper bracts sessile, opposite to 3 mm apart, 4–6 mm long, broadly lanceolate (3–)4–5.5 times as long as broad, flowers terminal, pedicel short, straight, 1–3 mm long; corolla (6.5–)8–16 mm long, 2–3(–4) times as long as ovary, funnelform-campanulate, deep lavender; lobes 5, about ½ to ⅓ the length of the corolla, twice as long as wide, acute; corolla papillate internally at base and along sides beneath sinuses; style blue, 9–9.5 mm long, papillate distally about ¾ its length; style lobes 1.2 mm long, tightly appressed at anthesis; stamens 4.5–5.3 mm long, anthers nearly twice as long as filaments, filament abruptly dilated to a wide ciliate base, pollen 14–20 pantoporate, 0.035 mm dia.; ovary 2–4.4 mm long, 1.5–2(–2.5) times as long as wide, long-conical at base, cylindrical sides short, strongly ribbed, the inter-rib area not infolded or tuberculate; capsule 4–6 mm long, the pore about midway between base and apex; calyx lobes erect, subulate, 1–2 times as long as ovary and capsule; ovules 60–100, seeds 0.65–0.73 mm long, oblong, elliptical in cross-section, about twice as long as broad, flat on chalazal end, light brown, shiny, finely striate; $n = 17$; flowers May–Jun; local populations on steep serpentine talus slopes on and adjacent to Red Mountain, Mt. Hamilton Range, 400–800 m (Fig. 4).

TYPE: CA: Stanislaus Co., Red Mountains, 27 km (17 mi) above mouth of Arroyo del Puerto, Mt. Hamilton Range, 420 m, rocky, almost barren talus slope, associated with *Clarkia breweri,* 19 May 1935, *C. W. and H. K. Sharsmith 3144* (Holotype: UC!; Isotypes: DS!, GH!, WS!).

PARATYPES: CA: Santa Clara Co.: near headwaters of Colorado Creek, Red Mountains, Mt. Hamilton Range, 25 May 1935, *C. W. and H. K. Sharsmith 3165*; Blackbird Valley, s. of Mt. Mocho, with

Streptanthus breweri, Eriogonum covillianum, and *Clarkia breweri,* 800 m, 12 May 1980, *Morin 301*; Stanislaus Co., confluence of Arroyo del Puerto and Hideout Canyon, with *Quercus durata, Streptanthus breweri, Eriogonum covillianum,* 400 m, 11 May 1980, *Morin 299* (chromosome voucher). These are the only known collections of *C. sharsmithiae.*

Both *C. exigua* and *C. griffinii* have narrow, somewhat sclerophyllous leaves and bracts. The bracts in both species are arranged near the apex of each branch but at least 4 mm and more often 7–8 mm apart. Consequently, subsequent branches are arranged alternately. Because the flowers of *C. exigua* have long pedicels and the branches are widely spaced, the plants appear very open and delicate. In contrast, the bracts of *C. sharsmithiae* are opposite or nearly so and the branches, both of which usually develop, seem superficially to be truly dichotomous. The fleshy leaves are wider than those of *C. exigua* and the plants of *C. sharsmithiae* accordingly appear to be leafier and generally denser.

The indumentum of most California Campanuloideae is variable in its presence or absence and in its distribution on a plant. The hairs are usually of several lengths, all fairly long and narrow. To my knowledge, short, broad, verrucose hairs are not found in any other North American Campanuloideae. The combination of unique indumentum, fleshy leaves, broadly lanceolate, opposite, upper bracts, and many-pantoporate pollen seems sufficient for the recognition of this very restricted endemic. The slopes on which *C. sharsmithiae* is found are nearly devoid of soil or grass cover and are very unstable. *Campanula exigua* grows on more gradual slopes that have a sparse covering of grass and other small herbs.

The species is named for Helen K. Sharsmith in recognition of her extensive work in the Mt. Hamilton Range and of her many careful collections and observations of Campanulaceae in California.

Campanula griffinii Morin, nom. et stat. nov.—*Campanula angustiflora* Eastwood var. *exilis* J. T. Howell, Leafl. W. Bot. 2:101. 1938. Non *Campanula exilis* (A. DC.) D. Dietrich, 1839.—TYPE: CA: San Benito Co., the Pinnacles, 19 May 1937, *Howell 12938.* (Holotype: CAS!; isotypes: GH!, POM!).

Erect annuals, 2–20 cm high, stems 4-angled, glabrous or hispid below first flower, or all parts hispid; lower cauline leaves sessile, alternate, 2–4.5 mm long, broadly spatulate, obtuse, few-toothed; upper cauline leaves (3.5–)7–9 mm long, linear-subulate, 4–6(–11) times as long as broad, with 4 pairs of gland-tipped teeth, abaxial sides glabrous or hispid; longest leaf subtends first flower; bracts 2.8–3.7(–5.9) mm long, lanceolate to linear, few-toothed, acute, glabrous to sparsely hirsute; lower bract closer to flower than to leaf subtending branch; flowers terminal, pedicel 1–4.5(–6) mm long; corollas white, all parts equally UV-absorbing, 2.2–3.7 mm long, cylindrical, lobes 1.2–1.4 mm long, acute, erect or spreading; corolla without internal papillae; style white, 2.5 mm long, papillate distally about ⅓ its length; style lobes 0.5–0.6 mm long, loosely appressed at anthesis; stamens 2 mm long, the anthers equal to the linear, glabrous filaments; pollen 0.035 mm dia., 8-pantoporate; ovary 1.7–3.6 mm long, conical at base, the sides cylindrical, strongly ribbed; calyx lobes slightly unequal, 2.5–4.2 mm long, subulate, 0.5 to 1.5 times the length of the ovary, erect in fruit; capsule nearly cylindrical, slightly constricted near the middle at a point corresponding with the pore position, conspicuously ribbed, the inter-rib area not infolded or tuberculate; ovules 50–100, seeds 0.6 mm long, twice as long as wide, oblong, elliptical in cross-section, flat on the chalazal end, light brown, shiny, finely striate (Fig. 1); $n = 17$; flowers Apr–Jul; extensive populations on serpentine soil under chaparral shrubs, North Coast Ranges from east-central Lake Co. south to Tiburon Peninsula and Mt. Tamalpais in Marin Co.; South Coast Ranges from northern San Benito Co. to northern San Luis Obispo Co. (Fig. 4).

Representative specimens: CA: Lake Co.: Mirabel Mine, 15 May 1938, *Eastwood and Howell 5530*; 9.5 km e. of Hough Springs, 20 May 1963, *Raven 18403*; Marin Co.: Tiburon Peninsula, 15 May 1943, *Howell 18095*; Carson country, 12 May 1946, *Howell 21813*; Monterey Co.: Biervelt Sargent cypress forests, 1 Jun 1960, *Hardham 5973*; Alder Creek *Cupressus sargentii* grove, 23 Jun 1963, *Hardham 10864*; Napa Co.: intersection of lower Chiles Valley Rd. and Pope Valley Rd., 11 May 1978, *Morin 217a* (seed source and chromosome voucher); Cappell Valley, 26 Jun 1951, *Raven s.n.*; head of Moore's Creek, Howell Mt., 15 May 1902, *Tracy 1463.5*; Fresno Co., below Atlas asbestos mine, T19S R13E S32 sw.¼, 24 May 1978, *Griffin 4110*; San Benito Co.: the Pinnacles, 23 Apr 1933, *Howell 11127*; Clear Creek, T18S R11E S1 sw.¼ 25 May 1978, *Griffin 4117* (seed source and chromosome voucher); S14 ne.¼, 25 May 1978, *Griffin 4120* (seed source and chromosome voucher); San Luis Obispo Co.: Sargent cypress forest, Burnett Peak, 1 Jun 1960, *Hardham 5972*; Cypress Mt., serpentine, 18 Jun 1963, *Hardham 10851*; Sonoma Co., 3.2 km se. of Monte Rio, 7 Jun 1941, *Hoover 5310*.

In *Campanula griffinii* the trend to autogamy is one step more advanced than in *C. angustiflora* in that the corolla is usually included in the calyx lobes and the filaments are narrow and lack cilia.

The combination of character states shared by *C. griffinii* and *C. exigua* seems to support the hypothesis that *C. griffinii* arose from a *C. exigua*-like ancestor. These character states are: narrow leaves, upper bracts closer to the flower than to the subtending leaf, longest leaf subtending first flower, capsules cylindrical with inter-rib area not infolded or tuberculate, seeds not fusiform, flattened at chalazal end, pollen pantoporate, $n = 17$. Because *C. griffinii* differs quantitatively in most characters from *C. exigua,* has a different breeding system, and has an independent geographical range, I consider them distinct.

The species is named in honor of James R. Griffin. His work with the pines and oaks of California is internationally recognized; less well known are his careful and insightful observations of the "belly plants" of California, particularly those found in the central Coast Ranges, and his continuous and generous help to other botanists working in the central Coast Range area.

CONCLUSION

The four campanulas discussed here are remarkable members of Campanulaceae in several ways. They are annuals in a family that contains predominantly perennials; they are the only annual campanulas reported to have $n = 15$ or 17; three of them have pantoporate pollen, a condition previously reported for only *C. americana.* In addition, autogamous species seem to have evolved twice, once from a *C. exigua*-like ancestor and once from an unknown ancestor. Ornduff (1969) pointed out that taxonomic emphasis on floral characters may result in closely related species being treated as taxonomically distant. This appears to have been the case with *C. griffinii,* whose association with *C. angustiflora* was based mainly on floral characters (Howell, 1938). Classification of Old World species that have floral character states associated with autogamy perhaps should be re-evaluated in this light.

Finally, all four species have very restricted distributions that coincide with certain areas of high endemism listed by Stebbins and Major (1965) as "endemic areas of the Central Coast Ranges." The disjunct range of *C. angustiflora* is limited to three of the northern Central Coast Range endemic areas (inner North Coast Ranges, Mt. Tamalpais, and central Santa Cruz Mts.); *C. exigua* is found in three of the southern Central Coast Range endemic areas (Diablo, Hamilton, and San Carlos) and also at several stations in the southern part of the Diablo Range that were not listed by Stebbins and Major; *C. sharsmithiae* is narrowly restricted to serpentine in the Hamilton endemic area; and *C. griffinii* has a disjunct distribution that coincides with five of the six Central Coast Range endemic areas occupied by the other three species plus one other: the Monterey area. It is curious that these four species, which may or may not all be closely related, are found mainly in areas that are also occupied by other species with restricted distributions. Furthermore, there is a remarkable association of these taxa with each other and with other Campanulaceae. *Campanula griffinii* grows with *C. angustiflora* and with *C. exigua.* All three species may be found growing with or near *Githopsis diffusa* or *G. specularioides, Heterocodon,* or *Triodanis biflora.* More needs to be known about the other campanulas of North America before the problem of relationships among these taxa can be solved.

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HETEROMERICARPY AND DUAL SEED GERMINATION MODES IN PLATYSTEMON CALIFORNICUS (PAPAVERACEAE)

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ABSTRACT

Platystemon californicus Benth. (Papaveraceae) is unique among Papaveraceae in producing a multicarpellate, semiapocarpous gynoecium. Seeds are most often dispersed singly, enclosed within a persistent pericarp that forms single-seeded joints. However, all plants in occasional populations are heteromericarpous: they also produce some seeds within the central chamber of the fruit that are dispersed as naked seeds. Naked seeds germinate after a dormant period of approximately four months while enclosed seeds remain dormant much longer under germination conditions used in this study. Differences in germination behavior are controlled by the presence or absence of the persistent pericarp. The diaspores and germination characteristics of *P. californicus* most closely resemble those of heteromericarpous Cruciferae.

Heterocarpy and heterospermy (production of different fruit and seed types, respectively, on one plant) are most frequently found in annual species of open, arid habitats. These phenomena, often associated with heterodiaspory, are particularly well-developed in plants of African deserts and the Near East, but much less common elsewhere (van der Pijl, 1972). Heterocarpy and heterospermy often are associated with differences in dormancy characteristics or germination requirements (Zohary, 1962). A number of workers have studied species in which different fruit types produced on a single plant exhibit different germination behavior (e.g., Crocker, 1906; Koller, 1957; Williams, 1960; Negbi and Tamari, 1963; Esashi and Leopold, 1968; Ungar, 1971, 1979; Baskin and Baskin, 1976). In addition, some species, particularly among Cruciferae, produce fruits in which seeds in different parts differ in germination characteristics (Zohary, 1937; Voytenko, 1968; Bermejo and Muñoz, 1977).

Platystemon californicus Benth. is a winter annual of southwestern Oregon, much of California at low- to mid-elevations, northern Baja California, and Arizona. It occupies habitats in vegetation types as diverse as coastal strand, valley grassland, chaparral, and Arizona succulent desert.

Seeds of *Platystemon californicus* germinate within several days after the first cool autumn rains, usually in October. Plants grow slowly during winter, forming a rosette of leaves. The first flowers usually open in late March and flowering continues through April or May. By June, plants have died and dispersed their seeds. Experience

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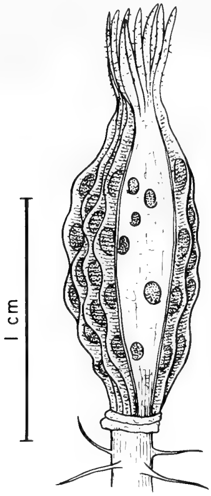

FIG. 1. Drawing of *Platystemon californicus* fruit with three carpels removed to show enclosed seeds within carpels and naked seeds in central chamber of fruit.

in cultivating this species has shown that very few seeds germinate outdoors in summer, even with daily watering.

Platystemon californicus disperses seeds in two distinct forms. Most seeds develop within the enfolding carpels and are dispersed in single-seeded joints of the carpels. The seeds are approximately 1.2 × 0.7 mm, surrounded by a leathery pericarp approximately 0.25 mm thick. In three of the 37 populations examined, all individuals produce additional seeds inside the central chamber formed by the surrounding carpels and are released as naked seeds (Fig. 1). This heteromericarpous condition is unique among Papaveraceae and uncommon among other plant groups. This paper reports germination experiments conducted to verify the existence of a dormant period following dispersal and to determine whether relative germination rates of enclosed and naked seeds differ, as suggested by studies of other heteromericarpous, heterocarpous, and heterospermous species.

METHODS

Seeds were collected on 21 May 1978 from a population of *Platystemon californicus* growing at the Hastings Natural History Reservation in Carmel Valley, Monterey County, California. Seeds collected from 40–50 plants throughout the population were pooled and stored in envelopes at room temperature.

The experiments consisted of four germination trials started at approximately monthly intervals between 7 Jul 1978 and 17 Oct 1978 and one starting on 8 Jan 1979. For each trial 25 mature, plump,

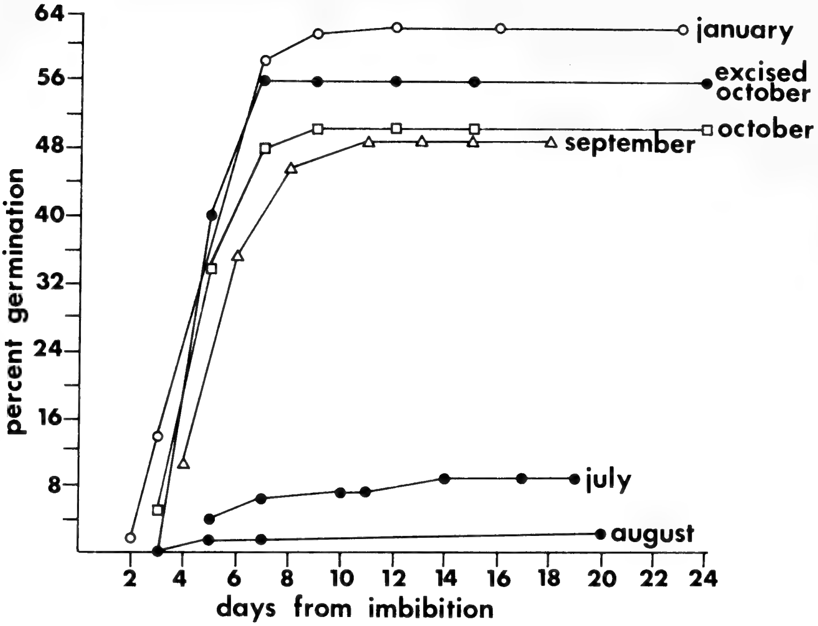

FIG. 2. Mean cumulative percent germinated seeds per day for germination trials of naked seeds of *Platystemon californicus* from Hastings Natural History Reservation, Monterey Co., California.

naked seeds were placed in each of five 6-cm Petri dishes containing two sheets of Whatman #1 filter paper moistened with distilled water. An identical set of dishes was prepared with enclosed seeds. The October trial included one Petri dish containing 25 excised seeds prepared by soaking seeds overnight at room temperature and removing their pericarps.

The dishes were placed in a dark box in a growth chamber set for alternating periods of 10 hours at 21°C and 14 hours at 13°C. These temperatures simulate alternating temperatures occurring when seeds of *Platystemon californicus* germinate in the field. The dark treatment was included because good seed germination had been obtained in cultivation by planting seeds in soil at a depth of approximately 1 cm. Four days after beginning the August trial, the temperature regime was inadvertently changed to 8 hours at 21°C and 12 hours at 13°C. Subsequent trials used the original 10 hour/14 hour regime. Seeds were examined periodically for germination, which was marked by the splitting of the seed coat by the emerging radicle. Distilled water was added as needed to keep the filter paper moist.

Because variances for numbers of germinating seeds per trial were heterogeneous even after log-transformation, an approximate analysis

TABLE 1. MEAN GERMINATION OF FIVE REPLICATES OF 25 NAKED AND 25 ENCLOSED SEEDS, AND ONE SAMPLE OF 25 EXCISED SEEDS OF *Platystemon californicus* FROM HASTINGS NATURAL HISTORY RESERVATION, MONTEREY CO., CALIFORNIA. All germination occurred within 12 days. Approximate analysis of variance was applied: $F_s' \approx F$ (d.f.$_1$, d.f.$_2$); $F_s' = 52.67$, d.f.$_1 = 4$, d.f.$_2 = 9$, $\alpha < 0.001$. Groups of homogeneous means (indicated by vertical lines by means) were determinated using the Wilcoxon-Mann-Whitney statistic.

	Naked seeds		Enclosed seeds		Excised seeds
Date of imbibition	Number germinated	Variance	Number germinated	Variance	Number germinated
7 Jul 78	2.2	0.71	0.0		
9 Aug 78	0.6	0.79	0.0	0	
14 Sep 78	12.4	9.80	0.0	0	
17 Oct 78	12.6	5.81	0.2	0.20	14
8 Jan 79	15.6	8.82	0.4	0.30	

of variance was applied to nontransformed data. The nonparametric, aposteriori, Wilcoxon-Mann-Whitney test for significant differences among means was applied to determine which groups of means were homogeneous (Sokal and Rohlf, 1969, p. 396–397).

RESULTS

Many naked seeds had a dormant period of approximately four months. Seeds in July and August trials showed little germination while those in later trials showed a 6-fold increase to approximately 50 percent germination. July and August trials had homogeneous means, as did subsequent trials (Table 1). Germination responses for September, October, and January trials were similar in both total germination after 15 days and in their germination response curves (Fig. 2).

Naked and enclosed seeds exhibited striking differences in germination response under the conditions used. Very few enclosed seeds germinated, even in October and January trials (Table 1). As many excised seeds as naked seeds germinated in the October trial and, although no replicates were used, excised seeds clearly germinated better than enclosed seeds (Table 1). All seeds that germinated in each trial did so by the twelfth day of the trial.

A survey of 37 natural populations of *Platystemon californicus* revealed that 24 populations from 15 counties in California and Arizona produced only enclosed seeds. Ten populations in Colusa, Kern, Lake, Marin, Mariposa, Monterey, Santa Clara, and Tuolumne counties, California, contained plants averaging fewer than 3.5 percent naked seeds per fruit. Three California populations (listed below) consisted of plants exhibiting striking heteromericarpy. In the following list are given the author's collection number, locality, and (in parentheses) percent naked ovules and percent naked seeds. Monterey Co.: *228*: Hastings Natural History Reservation, jct of Jamesburg-Arroyo Seco Rd. and Martin Rd. (0.282; 0.348); Santa Barbara Co.: *121*: Santa Cruz Is., Upper Eagle Canyon, e. of Prisoner's Harbor (0.550; —); *229*: Figueroa Mt. Rd., 12.6 km e. of Los Olivos (0.182; 0.177). Complete locality data are available upon request.

Discussion

Heterospermy, heterocarpy, and heteromericarpy are all mechanisms that can insure asynchronous seed germination. Germination of the two types of diaspores produced in some populations of *Platystemon californicus* differs drastically. Naked seeds are dormant for approximately four months but enclosed seeds remain dormant for at least eight months under conditions used in this study. The increased dormancy of enclosed seeds was due to effects of the persistent pericarp, as shown by the greatly increased germination of excised seeds over enclosed seeds.

A dormant period of approximately four months coincides with warm, dry conditions prevailing throughout the range of *Platystemon californicus* in Oregon and California during summer when conditions are unfavorable for seedling establishment and survival. At Hastings Reservation each of the four months following *P. californicus* seed dispersal receive less than 0.5 cm of precipitation, based on records from 1939–1978 (J. Griffin, pers. comm., 1979). Seeds capable of remaining dormant through this period avoid probable failure of seedling establishment, an advantage if they are released from dormancy when autumn rains begin. Because weather patterns are far from reliable and drought or freezing temperatures may follow periods of favorable weather, release from dormancy of all seeds is disadvantageous.

A number of heterocarpous species display dimorphic germination characteristics similar to *Platystemon californicus*. In most cases, however, one type of diaspore is nondormant while the other is dormant. *Heterotheca subaxillaris* var. *subaxillaris* produces disc achenes that are nondormant upon dispersal and ray achenes that must after-ripen at high temperatures before germination (Baskin and Baskin, 1976). The heterocarpic species *Aellenia autranii, Atriplex dimorphostegia, A. patula* subsp. *hastata,* and *Salsola volkensii* produce one fruit type containing a seed that germinates readily upon dispersal and a second fruit type with a seed that germinates only after a dormant period (Koller, 1957; Negbi and Tamari, 1963; Ungar, 1971). In *Halogeton glomeratus* black seeds germinate rapidly but brown seeds germinate poorly under all conditions and remain dormant indefinitely (Williams, 1960). The capacity for germination of one fruit or seed type immediately following dispersal in these species contrasts with the dormant period found for both diaspore types of *P. californicus*.

Heteromericarpy displayed by *Platystemon californicus* and germination of its two diaspore types most closely resemble the situation in many Cruciferae in which some seeds are produced in the dehiscent valvular part of the fruit and one or more seeds are contained in an indehiscent rostrum. Seeds released from the valvular part of the fruit of *Sinapsis alba, Erucaria boveana,* and *Herschfeldia incana* germinate readily but seeds retained within the rostrum germinate very poorly (Zohary, 1937). In *Fezia pterocarpa* seeds excised from the rostrum germinate much better than seeds enclosed by the rostrum or released from the valvular portion of the fruit (Bermejo and Muñoz, 1977). *F. pterocarpa* differs from *P. californicus,* however, in exhibiting differences in germination characteristics between excised seeds and those dispersed as naked disseminules.

Ernst (1967) considered the gynoecium of *Platystemon californicus* to be a specialized type derived from a *Hesperomecon*-like ancestor with a syncarpous gynoecium and capsular fruit containing only naked seeds. Accordingly, heteromericarpy in *P. californicus* should be considered transitional between the ancestral capsular fruit with naked seeds and the derived mericarpous fruit containing only enclosed seeds.

The rarity of heteromericarpous populations of *Platystemon californicus* makes it difficult to analyze patterns of morphological or ecological similarity among populations. Plants from the three strongly heteromericarpous populations are neither morphologically very similar to one another nor are they distinct from non-heteromericarpous populations. Heteromericarpous populations do not occupy unique habitats. All populations on Santa Cruz Island exhibited heteromericarpy, although this condition was quantified for only one population. The significance of heteromericarpy in dispersal or the possibly relictual status of the island populations is provocative, but it does not explain the occurrence of heteromericarpy in the other two populations. Studies of seedling establishment and seed dispersal of naked and enclosed seeds are required before the distribution of heteromericarpy in *P. californicus* can be explained more fully.

ACKNOWLEDGMENTS

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ANNOUNCEMENT

Workshop on Theory and Application of Cladistic Methods

A workshop to introduce botanical systematists to cladistic analysis, sponsored by the National Science Foundation, will be held on the UC Berkeley campus, 22–28 March 1981. The historical development, basic assumptions, methodological features, and application of cladistic analysis will be presented. Hennigian methods, the Groundplan-Divergence Method of Wagner, the Wagner Tree Method of Farris, Character Compatibility Analysis of Estabrook, and the Fitch-Margoliash Method will be covered by guest lectures and through analysis of their own data sets by participants. The number of participants is limited to 25. Applicants must be engaged in botanical systematic work as a graduate student or as faculty or staff of a university or research institution. A data set must be provided by each participant four weeks in advance of the workshop so that analyses can be conducted during the workshop. Support for expenses while in Berkeley is available. Applications must be received by 15 January 1981 and participants will be notified of acceptance by 1 February 1981. For further information, contact Dr. Thomas Duncan, Department of Botany, University of California, Berkeley 94720.

JOSEPH BURTT DAVY: A DECADE IN CALIFORNIA

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ABSTRACT

The British-born Joseph Burtt Davy spent 1892–1902 at the University of California, Berkeley, where he was affiliated with the Department of Botany and the State Agricultural Experiment Station. During this time he published about 80 articles on diverse aspects of botany, most of them in the journal *Erythea* for which he apparently had substantial editorial responsibility. Burtt Davy's activities in California are partially reconstructed through his correspondence with botanists at Berkeley and at Kew. The circumstances surrounding his departure from California are unclear, but in 1902 he moved to Washington, D.C., for a brief period and then went to Pretoria, South Africa, where he established a herbarium in a unit that eventually became the Botanical Research Unit.

Many western American botanists are familiar with the name of Joseph Burtt Davy through its commemoration in such binomials as *Clarkia davyi* (Jeps.) Lewis and Lewis, *Carex davyi* Mackenzie, *Gilia davyi* Milliken, and *Agrostis davyi* Scribner. Yet one encounters rather little reference to this botanist in articles concerned with the history of California botany. Indeed, Constance (1978) devotes only one sentence to the man's decade in California, and Thomas (1979) does not mention him at all. One day in 1971 while I was browsing through a miscellany of uncatalogued pamphlets in the library of the Bolus Herbarium at the University of Cape Town I came across a privately printed bibliography of Burtt Davy, examined the entries for the 10 years that he spent at the University of California, Berkeley, and concluded that in this short time period he engaged in a remarkable diversity of botanical activities. This led me to search for further details of Burtt Davy's activities while in California, the results of which I report here.

Joseph Burtt Davy was born in Derbyshire in March, 1870, and died in Birmingham (Desmond, 1977; Barnhart, 1965) or Oxford (Gunn, 1940), England, in August 1940. (Burtt Davy was himself inconsistent in hyphenating his surname, but seemed not to favor the hyphen.) He was educated "privately" (Hutchinson, 1940) and received two Ph.D. degrees, one from Cambridge in 1924 and an honorary one from Oxford in 1936 (Ramsbottom, 1940–1941). During 1891–1892, he was assistant to the director of the Royal Botanic Gardens, Kew, but resigned that position because of ill health. The illness was vaguely specified in a letter of December, 1906, to David Prain, director of the Royal Botanic Gardens, Kew, as a "threatening of the lungs which made it desirable to seek a drier climate." Burtt Davy

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FIG. 1. Joseph Burtt Davy in December, 1899.

made plans to leave England, apparently intending initially to seek employment in Canada (letter from Thistelton-Dyer, 1892). Instead, he went to the University of California, Berkeley, where he "obtained temporary employment in the Herbarium" of the Department of Botany (letter to W. T. Thistelton-Dyer, May 6, 1893). From 1893 to

1896 he termed himself "assistant in botany"; from 1896 to 1901 Lecturer in Botany and Assistant Botanist, California State Agricultural Experiment Station; and in 1901 and 1902 Instructor in Botany (Burtt Davy, n.d.). Dates of these various posts provided by Lee Bonar (pers. comm., 1971) and University Archivist J. R. K. Kantor (pers. comm., 1980) differ somewhat from those given by Burtt Davy and from each other as well.

Burtt Davy's published bibliography reflects a diversity of interests while in California; in his decade in the state he published 80 articles. These range from miscellaneous minor notes to translations, reviews, accounts of introduced species, nomenclature, horticulture, ethnobotany, and agriculture. Most of these were published in Jepson's journal *Erythea.* Burtt Davy contributed the treatments for a number of genera in L. H. Bailey's *Cyclopedia of American Horticulture* and was responsible for the Gramineae, Cyperaceae, and Juncaceae in Jepson's *Flora of Western Middle California.* As a consequence of his appointment in the experiment station, he also published articles on range plants and on alkali lands, the latter a particular interest of the influential soil chemist, Dean of Agriculture E. W. Hilgard. Burtt Davy's first "new" species was *Diplacus speciosus,* based on a plant cultivated in the university botanical garden and called to his attention by E. L. Greene; later novelties grew out of extensive general collecting trips in various parts of the state. Apparently in connection with his survey of the vegetation of alkali soils, Burtt Davy collected and described the "remarkable" grass genus *Neostapfia* (as *Stapfia*). Also, midway during his stay in California, Burtt Davy met and married Alice Bolton of Berkeley, who illustrated numerous of his papers.

In going through his correspondence with W. L. Jepson, one gets an insight into certain attitudes and events of the day. A letter of June, 1895 to Jepson mentions indecision concerning the administrative housing the Department of Botany, and refers to a rumored change that would allow Hilgard "to absorb control of this Department and work his own sweet havoc". There are pressures to publish: "Hilgard wants me to get out a Bulletin on my alkaline soils and their flora within a few weeks" (September, 1896). At this time Jepson was indicated as editor for the journal *Erythea,* and was "assisted" by Alice Eastwood and Burtt Davy. But there is evidence that Burtt Davy had primary responsibility for editing this journal for at least part of his time in Berkeley. In October, 1896, he wrote Jepson from Los Angeles that he had "just heard that I have got into hot water with Dr. [H. H.] Behr for my treatment of his article". In a letter to W. A. Setchell written at the same time, he commented that "Miss Eastwood says the good old Dr. is really angry." A week later, he wrote Jepson that "Dr. [Anstruther] Davidson . . . does not intend to send any more to *Erythea,* as he does not like the way in which Hasse's Lichen-paper has been treated . . . . He says that Hasse is very sore about the matter". Finally, exasperation overtook Burtt Davy and two days before Christmas, 1896, he wrote Jepson that "I have had a terrible time over *Erythea,* and you must not ask me to do a thing for it next term. I had to give up all my Chemistry on account of it, and have put off my grass work and Bulletin work from time to time on the same account". The January, 1897 number of *Erythea* no longer carried Burtt Davy's name, nor that of Miss Eastwood.

Burtt Davy engaged in various other botanical activities while in Berkeley. In addition to his herbarium work, he wrote that his duties included "direction of the University Botanic Garden" (Burtt Davy, n.d.). In 1894 he wrote to Thistelton-Dyer that "I am trying to form the nucleus of a Museum of Economic Botany for the University". If he succeeded in this, the collection has subsequently been dispersed. In general, Burtt Davy's letters were business-like, though on occasion he commented pointedly on some of his contemporaries. In June, 1897, he wrote Setchell from Reno that "Marcus Jones is here . . . he is a droll bird and is hunting for rare Astragali to fill his botanical gizzard, which, however, seems inclined to the omnivorous, snapping up anything in sight from a grass or Equisetum to a root. I take good care not to commit myself to the expression of a botanical opinion in his presence, but find him wonderful good company nevertheless".

The circumstances surrounding Burtt Davy's departure from California are not clear. Apparently during a visit to Washington, D.C., in 1901 he was offered a herbarium curatorial position at the USDA by Frederick V. Coville, and in 1902 he moved to Washington to fill one of the vacancies left by the departures of C. L. Scribner and E. D. Merrill for the Philippines. In October, 1902, he wrote Setchell from Washington that "I am safely here and settled down". Possibly a cause of his departure from Berkeley was that his relationships with various of his colleagues were not satisfactory. Nearly 25 years later in a letter written to Jepson (who at the time was in Britain and had visited with Burtt Davy) in July, 1926, he reflects that "I think I did suggest to W.A.S. [Setchell] that the U.C. might see its way to grant me the B.A. or B.Sc. (not *Honorary* B.A.). I feel sore about it for had I used my job at Berkeley as a means to a degree I should have shirked my work but should have had the degree . . . I do feel sore that the head of the Department could not see his way to grant my request . . . you can imagine how my California friends smile at a Faculty which considers its B.A. worth more than a Cambridge Ph.D. or an Oxford M.A.!" He continued that ". . . I feel strongly that the training and experience of the last 30 years ought to be made use of to further the cause of botanical science, and to assist in training the men who are to follow us. I had hoped I might be allowed to do this at the U.C., but the door was slammed in my face". Nevertheless, he goes on to say that "I am none the less indebted to California for what she has done for me, and in spite of all that has happened, I hope to do something to show my gratitude. If you can consider further the point we discussed about a fund to encourage post-graduate work in Systematic Botany, I shall be glad to consider the possibility of leaving $5,000 in my will, to start such a fund. I have already mentioned to President [W. W.] Campbell the desire to do *something*". In the letters written by Jepson to Burtt Davy later the same year, there is no mention of this proposal, and when Burtt Davy died in 1940 he left £7,000 to the Imperial Forestry Institute at Oxford University to establish the Burtt Davy Research Scholarship for research in taxonomic botany and/or tropical plant ecology.

Burtt Davy remained in Washington for only six months. "This post I resigned on receiving a call from the Transvaal" (letter to Prain, 1906). He left the United States for the post of Government Agrostologist and Botanist in Pretoria. He later became the Chief of the Division of Botany of the Department of Agriculture there. In 1907 he wrote to Prain that "news from the Transvaal is very disturbing as regards the future of British-born civil servants and I am advised confidentially to seek another post". In the same year, he returned to the United States and spent several months studying plant breeding with the noted cytologist-geneticist H. J. Webber at Cornell University. Despite his advice to leave government service, Burtt Davy wrote Prain in the same year that "I do not intend to resign or give notice" and returned to South Africa late in 1907.

In 1913 Burtt Davy resigned his government post and began breeding corn on his own farm at Vereeniging, Transvaal. In 1920, he went to Kew, where he published the first two volumes of *The Flora of the Transvaal and Swaziland*. In 1925, he was appointed Lecturer in Tropical Forest Botany at the Imperial Forestry Institute, Oxford, a post he held at the time of his death. In the same year, he returned again to California, where "while collecting material for a flora of the Redwood belt . . . [he] had an accident which necessitated a return home for special treatment" (Ramsbottom, 1940–1941). Ramsbottom (1940–1941) characterized Burtt Davy as enthusiastic, a perfectionist, indefatigable, humane (he was a Quaker), and a man who served to inspire many students.

In his government post in South Africa, Burtt Davy's duties included extensive travelling throughout the Transvaal to meet farmers, to observe and discuss agricultural practices, to collect and identify weeds or toxic plants, and to collect and preserve native species as well. He is credited with establishing the herbarium in a unit that eventually became the Botanical Research Institute in Pretoria; the herbarium is now the largest in Africa, with approximately 600,000 specimens. The Institute celebrated its 75th anniversary on 1 May 1978, the 75th anniversary of Burtt Davy's appointment in 1903. The birthday celebrations commenced with a "symbolic re-collection" of *Aloe davyana* Schoenl., a species first collected by Burtt Davy and named for him very shortly after his arrival in South Africa. Later in the day, the plants were placed in a small commemorative garden outside the Institute's building.

ACKNOWLEDGMENTS

Letters to Prain and to and from Thistelton-Dyer are in the archives at Kew, those to Jepson in the Jepson Herbarium, and those to Setchell in the University Herbarium, Berkeley. Obituaries of Burtt Davy include those by M. D. Gunn (S. African J. Science 37:xvii–xix, 1940; Bothalia 4:45–46, 1941); J. Hutchinson (Nature 146:424, 1940); A. D. Cotton (J. Kew Guild 6:84–85, 1941 [1942]); A. J. H. Goodwin (Trans. Royal Soc. S. Africa 29:lxii, 1942); and J. Ramsbottom (Proc. Linn. Soc. Lond. 153:291–293, 1940–1941 [1942]). There is also an anonymous but informative biographical note inspired by the award of his Cambridge Ph.D. (Gard. Chron. 75:266, 1924). I am indebted to D. E. Johnson for scouring the files at the Hunt Institute for Botanical Documentation, L. Constance for reading the first draft of this sketch, and J. R. K. Kantor for archival assistance.

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NOTEWORTHY COLLECTIONS

HEMIZONIA MINTHORNII Jeps. (ASTERACEAE: MADIINAE).—USA, CA, Ventura Co., Simi Hills, Sage Ranch (34°30′N, 118°40′W), 0.8 km nw. of Rocketdyne Laboratory on Black Canyon Rd, scattered on open, rocky, sandstone outcrops in crevices with *Eriogonum fasciculatum, Ribes indecorum, Prunus ilicifolia,* and *Eriodictyon* sp., 670 m, 28 Nov 1979, *Tanowitz 1803 and Whitmore* (UCSB); Los Angeles Co., Santa Monica Mts. (34°05′N, 118°44′W), Corral Canyon, at end of county-maintained Corral Canyon Rd, ca. 8.2 km (5.1 mi) e. of hwy 1, scattered on steep, sandstone outcrops in crevices with *Rhus laurina, Adenostoma fasciculatum,* and *Quercus dumosa,* 600 m, 11 Apr 1980, *Tanowitz 1848 and Gordon* (UCSB).

Previous knowledge. Known only from the type locality (34°16′N, 118°38′W)—a small population in chaparral on e. side of Santa Susanna Pass summit (480 m) on either side of Ventura-Los Angeles co. line. (Herbaria consulted: CAS, DS, JEPS, LA, MO, NY, POM, RSA, UC, UCSB, US; published sources: Munz, A Calif. fl. 1959; Munz, A fl. S. Calif. 1974; Abrams and Ferris, Illus. fl. Pac. States. 1960; Smith et al., Inv. rare endang. vasc. pls. Calif. CNPS Spec. Publ. 1, ed. 2. 1980; Raven and Thompson, Fl. Santa Monica Mts., Calif. 1966.)

Significance. Second and third sites for this narrow endemic. Considered "Rare and Endangered" by Smith et al. (op. cit.); the cited specimens were included in that determination. More widely distributed in the Transverse Ranges than previously thought. Perhaps 500 individuals now have been seen, scattered in more or less contiguous populations on suitable substrates of arkosic, Upper Cretaceous sandstone. Many peaks between the three known localities have similar stratigraphy and may support yet other populations, but collecting is difficult due to steep terrain. There is little current endangerment but these populations should continue to be monitored.—BARRY D. TANOWITZ and PATRICIA J. GORDON, Department of Biological Sciences, University of California, Santa Barbara 93106. (Received 5 Dec 1979; returned 7 Dec 1979; revision received 25 Apr 1980; final version accepted 8 Jul 1980.)

OTTELIA ALISMOIDES (L.) Pers. (HYDROCHARITACEAE).—USA, CA, Butte Co., between Biggs and Richvale, Lattemore portion of California Rice Experiment Station, T19N R2E, ditch dividing S33 and S34: 8 Sep 1977, *Turner 541* (UC); 10 Sep 1977, *Seaman s.n.* (DA); 20 Sep 1977, *Barbe 2334 and Fuller* (CDA, UC). About 350 plants in flower and fruit in an 80-m interval of silt-bottomed, shallow drainage ditch. First observed by Bill W. Brandon, verified by Donald E. Seaman, California Rice Experiment Station.

Previous knowledge. Native to ne. Africa, Asia, Malay Archipelago, Australia. A weed apparently requiring control in Thailand, Indonesia, Japan, Taiwan. Naturalized in rice fields of n. Italy. Known previously in N.A. from Calcasieu and Cameron parishes, LA. Unconfirmed report of presence in Canada (Holm et. al., Geog. atlas world weeds. 1979). (Herbaria consulted: AHUC, CAS, CDA, CHSC, CPH, DA, HAY, HSC, JEPS, LA, RSA, SACT, SD, UC; published sources: Koch, Ber. Schweiz. Bot. Ges. 62:628–663. 1952; Ernst-Schwarzenbach, Phytomorphology 6:296–311. 1956; Van Steenis, Fl. Malesiana 5. 1958; Sculthorpe, Biol. aq. vasc. pls. 1967; Kaul, Phytomorphology 18:13–35. 1968; Dike, Contrib. biol. *Ottelia alismoides,* M.S. thesis, Univ. sw. Louisiana. 1969; Kaul, Amer. J. Bot. 56:951–959. 1969; Aston, Aq. pls. Australia. 1973; Cook, Waterpls. of world. 1974; USDA, Econ. imp. foreign weeds. 1977; Pancho and Soerjani, Aq. weeds se. Asia. 1978; Godfrey and Wooten, Aq. wetl. pls. se. U.S. 1979; Holm et. al., op. cit.) *Diagnostic characters.* Submersed or partly emersed, rooted aquatic with rosette growth habit; lvs variable, often broadly ovate, blade very thin; hermaphroditic fls with 3 white to pink epigynous petals, fls borne singly inside spathe; spathe with 2–10 longitudinal, crisped wings, 2 wings often larger, all sometimes reduced to ribs; fruit initially enclosed by spathe; seeds oblong to fusiform, 1.5–2 mm long, 0.5 mm wide.

Significance. New to w. N.A. A potentially serious weed of rice culture and slow-moving or still bodies of water. Population exterminated with sterilant (diuron) shortly after discovery, but many viable seeds had already been produced. (In two separate trials, 53 and 15 percent of scarified seeds germinated within two weeks at 20°C. No unscarified seeds germinated.) No plants seen since 1977. Plants observed should be reported to Donald E. Seaman, (916)868-5481, California Rice Experiment Station, P.O. Box 306, Biggs, CA 95917, or to Thomas C. Fuller, (916)445-4521, California Dept. Food and Agriculture, 1220 N. Street, Sacramento, CA 95814.—CHARLES E. TURNER, Department of Botany, University of California, Berkeley 94720. (Received 21 Feb 1980; accepted 3 Mar 1980; final version received 25 Jun 1980.)

ELEUSINE TRISTACHYA (Lam.) Lam. (POACEAE).—USA, CA, Imperial Co., Imperial Valley, Westmorland vegetable-growing area, 1979, *W. Isom s.n.* (UCR). A weed in the vegetable fields found in lighter textured soils.

Previous knowledge. Native to Argentina, Brazil, Paraguay, and Uruguay; adventive in various parts of the Old World, Australia, and USA. Known from NY, NJ, VA,

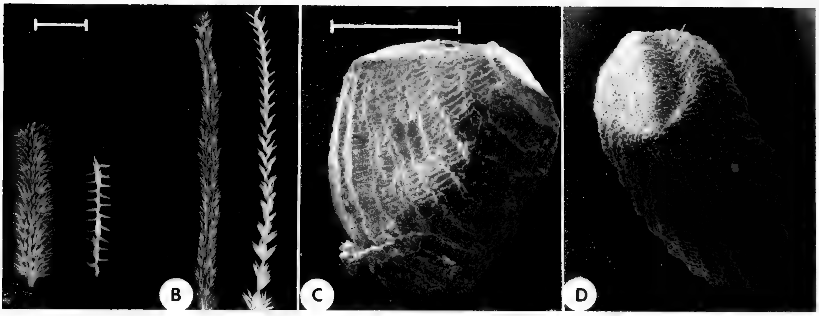

Fig. 1. Photographs of inflorescences and grains of *Eleusine tristachya* (A and C) and *E. indica* (B and D). Bar in A and B is 1 cm long. Bar in C (for C and D) is 0.5 mm long.

and 60 years ago collected several times in OR. The only New World taxon of a predominantly African genus. Poorly known because not included in Phillips's survey of African species of *Eleusine* Gaertn. (Phillips, Kew Bull. 27:251–270. 1972). (Herbaria consulted: K, MO, UC; published sources: Burbidge, Austral. grasses. 1. 1966; Hitchcock, Man. grasses U.S. 1950; Hitchcock and Cronquist, Fl. Pac. Northw. 1973). Hitchcock (1950, op. cit.) maintained that *E. tristachya* is native to tropical Africa and that it was introduced into tropical South America. Phillips (op. cit.), however, indicated that this species is not found in Africa except as a rare adventive. The presence of wild forms of *E. tristachya* in South America and their absence from Africa is indicative of the New World origin of this species. *Diagnostic characters.* Infl. of 2–3 terminal, digitately arranged, spicate branches; branches oblong or occasionally oblanceolate, compact, (1.5–)3–6(–8.2) cm long, 5–14 mm wide (Fig. 1A). Spikelets 5–9(–11) flowered, very closely overlapping on the rachis and perpendicular to it; lower glume 3.0–3.5 mm long; upper glume 4.2–5.0 mm long; lemma 4.0–5.1 mm long. Seed broadly oblong-globose, 1.0–1.2 mm long, obliquely ridged (Fig. 1C); pericarp membranous.

Significance. First record for CA. The occurrence of the species in CA and South America suggests that it could be present in Central America or Mexico but it has not been collected yet, or has been confused with *E. indica.* The latter is readily distinguished from *E. tristachya* by its slender 4–10(–17) terminal and subterminal spicate branches 3.5–15.5 cm long and 3.0–5.5 mm wide; spikelets less compact and obliquely arranged on the rachis (Fig. 1B); lower glume 1.1–2.3 mm long; upper glume 1.8–2.9 mm long; lemma 2.4–4.0 mm long; seeds oblong-ovate in outline, 1.0–1.3 mm long, obliquely striated (Fig. 1D); pericarp membranous. *E. tristachya* (Lam.) Lam. (Lamarck, Tabl. encycl. 1:203. 1791) is based on *Cynosurus tristachyus* Lam. (Lamarck, Tabl. encycl. 2:188. 1786). Kunth's combination was also based on *C. tristachyus* Lam. but was made at a later date (Kunth, Rev. Gram. 1:92. 1829) and is therefore invalid.—Khidir W. Hilu, Department of Agronomy, University of Illinois, Urbana 61801. (Received 1 Aug 1979; returned 16 Aug 1979; revision accepted 26 Dec 1979; final version received 9 May 1980.)

Sisyrinchium montanum E. L. Greene (Iridaceae).—USA, ID, Bonner Co., Round Prairie, 10.4 km s. of Canadian border at Kingsgate on hwy 95 (T65N R2E S29 ne.¼ ne.¼), 17 Jun 1979, *Cholewa and Cholewa 230* (ID). Abundant. Population covering ca. 110 m^2 on a moist, narrow floodplain adjacent to Douglas-fir forest, 810 m. Associated with *Carex aurea, C. xerantica, Poa pratensis,* and *Festuca pratensis.* Flowers Jun–Jul. Verified by D. M. Henderson, Sep 1979.

Previous knowledge. Known in Rocky Mt. states and Canada e. of Continental Divide (w. of Divide only in Powell Co., MT). (Herbaria consulted: CAN, ID, MO, NY, UC, UTC, WIS, WS, WTU; published sources: Henderson, Brittonia 28:149. 1976.) Prior to Henderson's study this taxon was little understood and consequently was not recognized by Hitchcock et al. (Vasc. pls. Pac. Northw. 1. 1969), Hitchcock and Cronquist (Fl. Pac. Northw. 1973); nor Mosquin (Madroño 20:269. 1970). *Diagnostic characters.* Tepals with retuse to emarginate and aristulate apex, oblanceolate to elliptic; outer bract at least twice the length of the inner; densely caespitose.

Significance. First report for ID, a range extension of 800 km w. from Continental Divide.—ANITA F. CHOLEWA, Department of Biological Sciences, University of Idaho, Moscow 83843. (Received 14 Apr 1980; accepted 15 Apr 1980; final version received 24 Apr 1980.)

ORYZOPSIS SWALLENII Hitchc. & Spellenberg (POACEAE).—USA, WY, Sublette Co., dry plains bordering Cottonwood Cr. along e. side of hwy 189, 25 km n. of Big Piney, 2100 m, 18 Jul 1977, *Reveal 2079,* SD, UTC. Identified by A. H. Holmgren, UTC, 1979.

Previous knowledge. Known only from c. ID in se. Lemhi, w. Clark, and se. Custer cos. (Herbaria consulted: SD, UTC; published sources: Hitchcock and Spellenberg, Brittonia 20:162–165. 1968; Hitchcock, Univ. Wash. Publ. Biol. 17(1):629–635. 1969; Holmgren and Holmgren, Intermt. fl. 1:354. 1977). *Diagnostic characters.* Keys to *Oryzopsis* with some difficulty in Dorn (Man. vasc. pl. Wyo. 1977, p. 763–766), tending to be similar to *Stipa* as well. Will key nearest to *O. hymenoides* (Roem. & Schult.) Ricker ex Piper and *O. contracta* (Johnson) Shechter, but has cespitose culms to 4 dm tall; leaf blades 0.5 mm wide; glumes 5–6 mm long; lemma about 1.5 mm long, long-pilose, the awn 5–6 mm long.

Significance. First record for WY, a se. range extension of 250 km.—JACK L. REVEAL, San Diego Museum of Natural History, San Diego, CA 92112. (Received 9 Jun 1980; accepted 10 Jun 1980.)

CAMPANULA SCABRELLA Engelmann (CAMPANULACEAE).—USA, CA: Shasta Co., Lassen Volcanic National Park: Ski Heil Peak, T30N R4E S10 nw.¼, 100 m e. of summit, locally common in a 30 × 60-m population on s. slope of volcanic scree, 2660 m, 21 Jul 1979, *Heckard 5146* (JEPS) [plants first discovered on same peak, 26 Jul 1975 (*T. and S. Harris s.n.,* CAS) and independently by Dale E. Johnson and students in 1976]; summit of Loomis Peak, alpine fell-fields, 1 Aug 1978, *Showers 4218* (CAS); Siskiyou Co., Scott Mts.: n. side China Mt. 41°22′40.1″N, 122°34′28.2″W, 2604 m, on granodiorite, 3 Aug 1978, *Muth 7403* (PUA); e. ridge S. China Mt., 41°21′35″N, 122°34′58.1″W, 2438 m, on serpentine, 2 Aug 1978, *Muth 6762* (PUA); Cory Peak, on serpentine: w. ridge, 41°19′45″N, 122°36′30.1″W, 2219 m, 1 Aug 1978, *Muth 6901* (PUA); n. side, 41°19′59.3″N, 122°36′13.9″W, 1 Aug 1978, *Muth 6957* (HSU).

Previous knowledge. Cascade Mts. of c. WA and the Rocky Mts. of ID and MT, rare in OR and CA where its distribution as given in the literature is poorly documented and apparently erroneous. The species occurs in the Wallowa Mts. of OR (Mason, Guide pls. Wallowa Mts. ne. Oreg. 1975) but no specimens have been found to document its occurrence on the high peaks of the Cascade Mts. of either OR or CA as given by Peck (Man. higher pls. Ore. 1961) and Abrams and Ferris (Illust. fl. Pac. States. 1960) nor have any been re-collected on Scott Mt., which Engelmann cited as the type locality. In CA the species was known heretofore only on Mt. Eddy. (Herbaria consulted: CAS, DS, GH, HSU, JEPS, NY, ORE, OSC, POM, PUA, RSA, SOC, UTW, WTU, UC, US; other published sources: Shetler, Rhodora 65:319–337. 1963).

Significance. The Lassen National Park localities extend the range of the species 120 km se. and are the first records in the Cascade Mts. of CA. The collections in the Scott Mts., although only 10 km nw. of Mt. Eddy of the Trinity Mts., are the first documentation in that range since Engelmann's type collection in 1880. A question remains as to the precise locality of Engelmann's collection but the area can be limited to the China Mt.-Mt. Eddy region. China Mt. fits Engelmann's locality description in being directly "west of Mt. Shasta." However, searches in the area by Gilbert Muth and students have not discovered another associated Engelmann species, *Eriogonum alpinum,* which is known only on Mt. Eddy to the sw. of Mt. Shasta. That Engelmann was not on Scott Mt. as known today nor Scott Mt. of the 1894 quadrangle of the U.S. Geological Survey (=Bolivar Mt. and later Craggy Peak), is confirmed by the absence on these two peaks of *Pinus albicaulis* (Griffin and Critchfield, Distr. for. trees Calif. 1972), which Engelmann cited as an associated species. *Pinus albicaulis* is known in this region only in the China Mt.-Mt. Eddy area. I acknowledge the many persons who have searched specimens and supplied information in this inquiry, especially Gilbert Muth.—L. R. HECKARD, Jepson Herbarium, Department of Botany, University of California, Berkeley 94720. (Received 31 May 1980; accepted 10 Jun 1980; final version received 30 Jun 1980.)

ESCHSCHOLZIA CALIFORNICA Chamisso subsp. MEXICANA (Greene) C. Clark (PAPAVERACEAE).—México, Sonora, 11 km s. of Tónichi, thorn woodland on hillsides, with *Bursera, Fouquieria,* and *Jatropha*, 275 m, 22 Mar 1979, *G. L. Webster 23817* (DAV).

Previous knowledge. Lowland AZ, e. to mts. around El Paso, TX, n. and w. into s. NV and adj. CA and UT, s. to just s. of Benjamin Hill, Sonora. (Herbaria consulted: CAS, DAV, DS, UC; published sources: Clark, Syst. Bot. 3:374–385. 1978; Jepson, Fl. Calif. 7. 1922; Munz, A Calif. fl. 1959.)

Significance. Nearly 150 km s. of previous s.-most locality and well out of the desert to which this subsp. was thought to be restricted. The locality is in "thorn forest" as described from the Rio Mayo area by Gentry (Publ. Carnegie Inst. Wash. 527:27–30. 1942). Brown and Lowe (USDA For. Serv. Gen. Tech. Rep. RM-41. 1977) designate the vegetation of this area as "Sinaloan thorn scrub".—CURTIS CLARK and GRADY L. WEBSTER, Department of Botany, University of California, Davis 95616. (Received and accepted 17 Oct 1979; final version received 17 Apr 1980.)

For all taxa reported below, herbaria consulted are BRY, COLO, CS, KANU, RM, USFS, UTC; published sources are: Barkley, Atlas fl. Great Plains. 1977; Booth and Wright, Fl. Mont. 1966; Cary, N. Amer. fauna. 42. 1917; Correll and Johnston, Man. vasc. pls. Tex. 1970; Cronquist et al., Intermt. fl. 1977; Davis, Fl. Idaho. 1952; Dorn, Man. vasc. pls. Wyo. 1977; Fernald, Gray's man. bot, ed. 8. 1950; Gleason and Cronquist, Man. vasc. pls. ne. U.S. adj. Can. 1963; Harrington, Man. pls. Colo. 1954; Hermann, Man. Carices Rocky Mts. and Colo. Basin. 1970; Hermann, Man. *Juncus* Rocky Mts. and Colo. Basin. 1975; Hitchcock and Chase, Man. grasses U.S. 1950; Hitchcock and Cronquist, Fl. Pac. Northw. 1973; Hitchcock et al., Vasc. pls. Pac. Northw. 1–5. 1955–1969; Kearney and Peebles, Ariz. fl. 1964; Little, Atlas U.S. trees. 1. 1971; McVaugh, N. Amer. fl. 32A:78, 79. 1943; Moore, Rhodora 40:135, 136. 1938; Munz, A Calif. fl. 1959; Munz, Aliso 7:65–71. 1969; Scoggan. Fl. Can. 1978, 1979; Wahl, Bartonia 27:1–46. 1954; Weber, Univ. Colo. studies, ser. biol. 23:1–24. 1966; Weber and Johnston, Nat. hist. inv. Colo. 1. 1976; Welsh and Moore, Utah pls. 1973; Woodson, Ann. Missouri Bot. Gard. 41:1–211. 1954. All collections are in RM unless otherwise indicated.

ASCELPIAS INCARNATA L. (ASCLEPIADACEAE).—USA, WY, Big Horn Co., hwy 32, 3.2 km sw. of Lovell (T56N R96W S28), roadside ditch with *Elaeagnus, Juncus, Populus,* and *Salix,* 1190 m, 25 Jul 1978, *Dorn 3151.*

Previous knowledge. Moist to wet soils near water in e. N.A., w. to s. Manitoba (Scoggan), c. ND (Barkley), sw. SD, w. NE, e. CO, e. NM (Woodson); and n. UT (Welsh and Moore). *Diagnostic characters.* Keys to *A. hallii* A. Gray in Dorn (p. 119). Plants to 1.5 (2) dm high; leaves opposite; calyx 1–2 mm long; corolla bright pink, 4–6 mm long; hoods paler pink, 2–3 mm long; horns surpassing the hoods, strongly incurved.

Significance. First record for WY, a range extension of 370 km from Custer and Fall River cos., SD.

HAPLOPAPPUS ANNUUS (Rydb.) Cory (ASTERACEAE).—USA, WY, Goshen Co., 9.7 air km ne. of Lingle (T26N R62W S15 se.¼), common on sandy clay in borrow pit and at end of abandoned field, 1340 m, 27 Sep 1978, *Nelson 2415.* Synonyms: *Machaeranthera annua* (Rydb.) Shinners; *M. phyllocephala* (DC.) Shinners var. *annua* (Rydb.) Shinners.

Previous knowledge. Annual of open habitats, w. NE, w. KS, e. CO, OK, and n. TX (Barkley). *Diagnostic characters.* Keys to *H. multicaulis* (Nutt.) A. Gray or *H. lanceolatus* (Hook.) T. & G. in Dorn (p. 391) but is densely glandular-pubescent (vs. eglandular) and annual (vs. perennial).

Significance. First record for WY, a range extension from Weld Co., CO (150 km) and Garden and Sheridan cos., NE (160 km) (Barkley).

MATRICARIA MARITIMA L. (ASTERACEAE).—USA, WY, Carbon Co., 3.2 km w. of Hog Park Reservoir (T12N R85W S2), several plants in disturbed area near road, 2620 m, 27 Aug 1977, *Hammel and Hartman 546.* Synonym: *M. inodora* L. var. *maritima* (L.) Wahlenb.

Previous knowledge. European weed on roadsides and in waste places; e. N.A. (Gleason and Cronquist); ND, s. NE, n. KS (Barkley), MT (Booth and Wright), CO (Weber and Johnston), ID (Davis), WA, and OR. *Diagnostic characters.* Keys to *M. chamomilla* L. in Dorn (p. 422) but differs in that plants are nearly inodorous (vs. aromatic); the receptacle is hemispheric, rounded (vs. conic, pointed); and the achenes have two marginal (vs. nearly marginal) and 1 (vs. 3) ventral, strongly callous-thickened, almost winglike (vs. simply raised) ribs, and are minutely roughened (vs. smooth) on back and between the ribs (Hitchcock and Cronquist).

Significance. First record for WY, a range extension of ca. 350 km from s. CO.

ALYSSUM MINUS (L.) Rothm. var. MICRANTHUM (C. A. Meyer) Dudley (BRASSICACEAE).—USA, WY, Campbell Co.: hwy 14-16, 9.7 km se. of Horse Creek Butte (T53N R73W S17), 1280 m, 5 Jun 1978, *Dueholm and Hartman 1852;* T56N R75W S28, 6 Jun 1978, *Hartman and Dueholm 6121*; T56N R72W S31, 7 Jun 1978, *Hartman and Dueholm 6236*; T53N R72W S31, 6 Jul 1978, *Dueholm and M. A. Sanguinetti 3392*; T55N R72W S26, 8 Jul 1978, *Dueholm and M. A. Sanguinetti 3567*; Converse Co.: 3.2 km w. of Douglas (T32N R72W S3,10), 20 May 1968, *R. L. Tresler 407* (distributed as *A. alyssoides*); T40N R71W S33, 3 Jun 1978, *Hartman and Dueholm 5840*; T40N R71W S14,23, 3 Jun 1978, *Hartman and Dueholm 5847.* Disturbed roadsides and plains.

Previous knowledge. Eurasian weed of disturbed sites, known in US from CA (Munz, 1969), CO (Weber), NM (COLO), UT (UTC), and KS (KANU). *Diagnostic characters.* Keys to *A. alyssoides* (L.) L. in Dorn (p. 516) but differs in having sepals 1.5–2 (vs. 2–3.5) mm long, soon deciduous (vs. persistent); fruits 4–5.5 (vs. 3–4) mm long, coarsely (vs. finely) stellate pubescent with trichome branches often 0.3–0.5 (vs. less than 0.2) mm long; styles 1–2 (vs. 0.2–0.5) mm long.

Significance. First records for WY, a range extension of ca. 230 km from Larimer Co., CO.

LOBELIA SIPHILITICA L. var. LUDOVICIANA A. DC. (CAMPANULACEAE).—USA, WY, Goshen Co., s. of golf course along the North Platte R., 2 air km sw. of Torrington (T24N R61W S17 ne.¼), infrequent in sandy soil in river bottom with *Scirpus,* 1250 m, 26 Sep 1978, *Nelson 2372.*

Previous knowledge. Variety *ludoviciana* found in moist, often shaded places from WI and sw. Manitoba (Scoggan), s. to e. TX, e. CO (Harrington), and Central America. *Diagnostic characters.* Keys to *Porterella* Torr. in Dorn (p. 164) but differs in that the corolla tube is split to near the base (vs. not split) and that the filament tube is 12 mm or more (vs. less than 8 mm) long.

Significance. First record of the genus for WY, a range extension of ca. 30 km from Scotts Bluff Co., NE.

ARENARIA SERPYLLIFOLIA L. (CARYOPHYLLACEAE).—USA, WY, Lincoln Co.: Strawberry Cr., 1.3 km e. of hwy 89 (T34N R119W S36), 1840 m, 10 Jun 1978, *Harrison 242*; 0.3 km e. of hwy 89 (T34N R119W S36), gravel soil of old stream flood plain in opening of *Populus* with *Antennaria microphylla, Arnica sororia, Erigeron pumilus,* and *Gilia,* 1830 m, 23 Jun 1978, *Harrison 241*; Sheridan Co., Little Bighorn R. Canyon, 27 air km w. of Parkman (T58N R90W S25), grassy slopes and limestone outcrops with *Alyssum, Astragalus, Danthonia,* and *Festuca,* 1700 m, 25 Jun 1979, *Hartman and Odasz 9369.*

Previous knowledge. Eurasian, naturalized in disturbed sites throughout much of temperate N.A. (Gleason and Cronquist); e. N.A., w. to e. NE, e. and c. KS and OK (Barkley), and c. TX (Correll and Johnston); CA (Munz, 1959) to s. B.C. (Scoggan), e. to ID (Davis) and w. MT (Booth and Wright); also CO (Harrington). *Diagnostic characters.* Keys to *A. lateriflora* in Dorn (p. 184), but differs as follows: taprooted annual (vs. rhizomatous perennial), leaves ovate (vs. elliptic-oblong to lanceolate), 3–6 (vs. 5–30) mm long, and sepals acute (vs. rounded).

Significance. First records for WY, a range extension of ca. 270 km from Gallatin Co., MT.

ATRIPLEX HETEROSPERMA Bunge (CHENOPODIACEAE).—USA: NE, Scotts Bluff Co., bank of Platte River, 0.8 km s. of Mitchell, 21 Sep 1970, *Stephens 45499* (KANU); SD: Butte Co., bank of Indian Cr., 4.8 km s. of Newell, 17 Sep 1970, *Stephens 45397* (KANU); Fall River Co., 16.1 km n. of Ardmore, 20 Sep 1970, *Stephens 45470* (KANU); Hughes Co., 0.8 km e. of Blunt, 15 Sep 1972, *Stephens 61718* (KANU); Hyde Co., 22.5 km s. of Highmore, 16 Sep 1972, *Stephens 61792* (KANU); Meade Co., 6.5 km e. and 10.5 km n. of Sturgis, 17 Sep 1970, *Stephens 45413* (KANU); WY: Albany Co., Bamforth Lake (T16N R74W S6), 2135 m, 25 Sep 1977, *Hartman and Hammel 5090*; Big Horn Co., 19 km wsw. of Basin (T50N R95W S10), 1280 m, 24 Aug 1977, *R. G. and V. Schreibeis R-1078*; Campbell Co.: Spotted Horse Cr., 6.5 km nw. of Spotted Horse (T55N R75W S16 nw.¼), 1160 m, 19 Sep 1978, *Nelson 2090*; T55N R75W S4 ne.¼, 19 Sep 1978, *Nelson 2104*; T58N R70W S32 nw.¼, 20 Sep 1978, *Nelson 2166*; Goshen Co.: near Springer Reservoir (T22N R62W S14 se.1/4), 1280 m, 28 May 1976, *Luce 13*; T19N R61W S5 sw.¼, 25 Sep 1978, *Nelson 2328*; T23N R60W S17 se.¼, 26 Sep 1978, *Nelson 2401*; T28N R62W S7 nw.¼, 27 Sep 1978, *Nelson 2443*; T22N R62W S10 ne.¼, 28 Sep 1978, *Nelson 2487*; Johnson Co.: hwy 387, 12 air km ne. of Edgerton (T41N R78W S25), 1620 m, 17 Sep 1978, *Nelson 1938*; T41N R77W S36 se.¼, 17 Sep 1978, *Nelson 1941*; Natrona Co., hwy 387, 3.5 air km ne. of Edgerton (T40N R78W S8), 1520 m, 17 Sep 1978, *Nelson 1937.* Moist, disturbed, often alkaline roadsides, ditches, lake or pond margins, and bottom lands. Associates include *Aster pauciflorus, Atriplex patula* subsp. *hastata, Chenopodium, Conyza, Kochia, Populus, Salix,* and *Suaeda.*

Previous knowledge. Weedy halophyte of s. USSR, reported in N.A. from CO and MT (Weber), MN and ND (Barkley), and WY (Dorn). Also known from Cache Co., UT and Washoe Co., NV (UTC).

Significance. First records for NE and SD. The collections by Stephens were distributed under *A. patula* L. Dorn (p. 222) gave the WY distribution of this species as Albany Co., based on a 1974 collection (*Dorn 2367*). Apparently it has been overlooked for some time, being rather widespread in the e. half of WY. Although this taxon was first reported for N.A. by Weber, it is not a recent introduction as evidenced by a much earlier CO collection (Weld Co., Windsor, near the river, 3 and 14 Oct 1924, *Osterhout 6361*) distributed as *Atriplex hastata* L.

CHENOPODIUM WATSONII A. Nels. (CHENOPODIACEAE).—USA, WY, Laramie Co., along hwy I-25, ca. 1.6 km n. of CO border (T12N R67W), disturbed area with *Chenopodium album* and *Salsola,* 1890 m, 7 Aug 1977, *Dorn 2999.* Verified by D. J. Crawford, OS, Apr 1979.

Previous knowledge. Dry, disturbed sites, w. SD, MT, CO, w. KS, n. NM, and AZ (Wahl). *Diagnostic characters.* In WY, most closely resembles *C. fremontii* S. Wats. and *C. atrovirens* Rydb., but differs in that the perianth entirely conceals (vs. spreads to expose) the mature fruit and the pericarp is adherent to the seed (vs. separating easily from the seed).

Significance. First record for WY, a range extension of ca. 10 km from adjacent Weld Co., CO.

SALSOLA COLLINA Pall. (CHENOPODIACEAE).—USA, WY, Laramie Co., hwy 85 at CO border (T12N R66W S16), disturbed area with *Kochia, Melilotus,* and *Grindelia,* 1890 m: 6 Aug 1977, *Dorn 2993*; 25 Sep 1977, *Dorn 3054.*

Previous knowledge. Eurasian weed first reported in N.A. from se. MN in 1938 (Moore), now known from w. MN, w. IA (BRY), ND, se. SD, ne. and s. NE, w. KS, MT (Booth and Wright), and e. CO (Barkley). *Diagnostic characters.* Keys to *S. kali* L. (*S. iberica* Sennen & Pau) in Dorn (p. 239) but differs in that young plants virgate (vs. diffusely branched and bushy), developing lateral branches with age; in fruit, leaves and bracts erect to somewhat spreading (vs. widely spreading), weakly (vs. strongly) spine-tipped and not markedly (vs. markedly) pungent to the touch, concealing (vs. exposing) the calyx and forming (vs. not forming) a bony, burlike disseminule, the calyx segments each with an inconspicuous (vs. conspicuous, irregularly lobed and toothed, prominently veined) transverse wing from the back, less than 0.3 (vs. 2.0–3.0) mm long.

Significance. First record for WY, a range extension of ca. 130 km from Yuma Co., CO.

CAREX RETRORSA Schwein. (CYPERACEAE).—USA, WY, Crook Co., draw on s. side of Carlson Ridge (T54N R62W S7), wet ravine with *Juncus* and *Lycopus,* 1460 m, 4 Sep 1977, *Dorn 3032.*

Previous knowledge. Wet places, Quebec to B.C., s. to NJ, OH, IA (Hermann), sw. SD (Barkley), nw. MT (Hitchcock), e. ID, and ne. OR (Cronquist); also CO (Harrington). *Diagnostic characters.* Keys to leads for *C. hystricina, C. rostrata,* and *C. vesicaria* in Dorn (p. 603). Spikes 4–10, the upper 1–4 staminate, the lower pistillate, the middle sometimes androgynous; scales lanceolate, acute to cuspidate, shorter than perigynia; perigynia inflated, the upper widely spreading, the middle and lower usually reflexed, 7–10 mm long, ca. 3 mm wide, the beak 2–3.5 mm long; achenes trigonous, 2.5 mm long.

Significance. First record for WY, a range extension of ca. 100 km from Custer and Pennington cos., SD (Barkley).

CAREX VULPINOIDEA Michx. (CYPERACEAE).—USA, WY: Campbell Co., Arco Coal Cr. Study Area, 40 km s. and 6 km e. of Gillette (T46N R70W S33), 1430 m, 23 Aug 1976, *W. R. and D. B. Keammerer CC-284*; Sheridan Co., Big Horn Coal Site, 9.7 km n. of Sheridan (T57N R84W S22 nw.¼), sandy soil adjacent to stream channel, 1130 m, 1 Jul 1977, *Brink 1380.*

Previous knowledge. Wet places, Newfoundland to B.C., s. to FL (Hermann), TX

(Correll and Johnston), AZ; apparently missing from UT, NV, and CA (Cronquist). *Diagnostic characters.* Keys to *C. diandra* Schrank in Dorn (p. 593) but leaf sheaths conspicuously cross-rugose (vs. smooth) and immaculate (vs. speckled with red) ventrally.

Significance. First records for WY, a range extension from Treasure Co., MT (160 km) and adjacent counties of SD (120 km) (Barkley).

CYPERUS ACUMINATUS Torr. & Hook. (CYPERACEAE).—USA, WY, Campbell Co., 13 air km ne. of Gillette (T51N R71W), in a playa with *Agropyron, Cirsium arvense, Eleocharis macrostachya, Hordeum,* and *Rumex,* 1340 m, 2 Sep 1978, *Schreibeis and Luther E 78-99.*

Previous knowledge. Wet places, VA to OH, IL, MN, ND, and WA, s. to n. FL, TX (Fernald), Coahuila, and CA (Correll and Johnston). *Diagnostic characters.* Keys to *C. aristatus* Rottb. in Dorn (p. 638), but differs principally in having 3-nerved (vs. 5- to 9-nerved) scales with apices that are recurved-acuminate (vs. squarrose-recurved with awns 0.3–1 mm long).

Significance. First record for WY, a range extension of ca. 150 km from Custer Co., SD (Barkley).

DIPSACUS SYLVESTRIS Huds. (DIPSACACEAE).—USA, WY, Platte Co., along Wheatland Cr., 1.6 km n. of Wheatland (T24N R68W), growing in a two-acre area along creek, 1430 m, Aug 1976, *Hohnholt s.n.*

Previous knowledge. European weed, naturalized through much of the U.S.; ME to MI, se. SD (Barkley), MT (Booth and Wright), and WA, s. to NC, TN (Fernald), AR, OK (Barkley), CO (Harrington), and CA (Munz, 1959). Keys to Compositae in Dorn (p. 56).

Significance. First record for WY, a range extension of ca. 340 km from Cheyenne Co., KS (Barkley).

DALEA ENNEANDRA Nutt. (FABACEAE).—USA, WY, Weston Co., near Clifton Canyon (T42N R60W S5 nw.¼ se.¼), open areas of *Pinus ponderosa,* 1220 m, 18 Jul 1976, *Schreibeis EW-1.* Synonym: *Dalea laxiflora* Pursh.

Previous knowledge. Dry prairies and plains from w. IA, w. to e. MT (Barkley), and s. to MS, TX, NM (Correll and Johnston). *Diagnostic characters.* Differs from *D. aurea* Nutt. ex Pursh, the other WY species of this genus, as follows: plants glabrous (vs. silky-canescent); leaflets conspicuously (vs. minutely) gland-dotted beneath; flowers white (vs. yellow), 5–6 (vs. 9–15) mm long, in a lax (vs. densely congested) spike 4–5 (vs. 14–25) mm broad.

Significance. First record for WY, a range extension of ca. 20 km from adjacent Custer and Pennington cos., SD (Barkley).

JUNCUS COMPRESSUS Jacq. (JUNCACEAE).—USA, WY: Carbon Co.: flood plain of Medicine Bow R., 0.8 km n. of Medicine Bow (T22N R78W S5), abundant in wet sandy soil around pool, 2020 m: 8 Aug 1973, *Stephens 70504* (KANU, NY: distributed as *J. gerardii* Loisel., verified by J. C. Coffey, NCSC, Mar 1979); 31 Jul 1979, *Nelson and Hartman 4215*; Seminoe Reservoir, 16 air km sse. of Seminoe Dam (T24N R84W S14,24), 1950 m, 11 Jul 1979, *Hartman 9921*; Converse Co., North Platte R., 10.4 air km e. of Glenrock (T33N R74W S9), 1520 m, 9 Aug 1979, *Dueholm 8816*; Johnson Co., 27.2 air km se. of Buffalo (T48N R81W S24), 1370 m, 29 Jun 1979, *Dueholm 7447*; Natrona Co.: North Platte R., 1.6 air km e. of Pathfinder Reservoir Dam (T29N R83W S19), 1740 m, 11 Jul 1979, *Hartman 9958, 9959*; oil field, 6.8 air km n. of Waltman (T36N R86W S6 and R87W S1), 1900 m, 12 Jul 1979, *Hartman 10037.*

Previous knowledge. Wet meadows and brackish marshes from Newfoundland and Nova Scotia, w. to w. Manitoba (Scoggan); Beaverhead Co., MT; Larimer Co., CO

(Hermann); Eurasia. *Diagnostic characters.* Keys to *J. confusus* Cov. in Dorn (p. 824), but has obtuse (vs. acuminate) perianth segments 1.5–2.5 (vs. 3.5–4) mm long.

Significance. First records for WY; the southernmost WY locality is ca. 180 km nw. of the CO site.

ABIES CONCOLOR (Gord. & Glend.) Lindl. ex Hildebr. (PINACEAE).—USA, WY, Sweetwater Co.,, Little Mt. (T13N R105W), growing with *Populus tremuloides,* 2530 m, 28 May 1977, *Dorn 2893.*

Previous knowledge. Mt. slopes, se. ID, c. CO, w. and c. NM, w. to w. OR, w. CA, and n. Baja Calif. (Little).

Significance. Included in Dorn based on a report (Cary) of its occurrence in s. Sweetwater and Uinta cos., although it was not recorded for WY by Little. This is the only WY collection known to the authors.

CRYPSIS ALOPECUROIDES (Pill. & Mitterp.) Schrad. (POACEAE).—USA, WY, Goshen Co.: Springer Reservoir, 2.4 air km s. of Yoder (T22N R62W S10 se.¼), 1310 m, 28 Sep 1978, *Nelson 2497*; Hawk Springs Reservoir, 10.5 air km se. of Hawk Springs (T20N R61W S9 se.¼), 1360 m, 28 Sep 1978, *Nelson 2523.* Common in dry sandy clay left by receding reservoirs. Associates include *Cyperus, Gnaphalium, Leptochloa, Spergularia,* and *Suckleya.*

Previous knowledge. Weedy species of Europe and n. Africa to Iraq; introduced near Philadelphia, PA, and Portland, OR, and spreading in w. U.S. in n. CA (RM), w. and ne. NV (UTC), w. UT (BRY), w. OR, sw. WA, s. ID (Cronquist), and s. MT (MONT). *Diagnostic characters.* Keys to *Alopecurus* in Dorn (p. 701), but differs in having glumes unequal (vs. subequal); lemmas exceeding (vs. equal to or shorter than) the glumes, awnless (vs. awned from middle or below); palea slightly shorter than the lemma (vs. absent).

Significance. First record of the genus for WY, a range extension of ca. 350 km from s. MT.

LEPTOCHLOA FASCICULARIS (Lam.) A. Gray (POACEAE).—USA, WY, Goshen Co.: 16 km sse. of Torrington, 1250 m, Sep 1969, *Tresler 425*; T22N R62W S10 se.¼, 28 Sep 1978, *Nelson 2498*; T20N R61W S9 se.¼, 28 Sep 1978, *Nelson 2522.* Saline fields and on dry sandy clay left by receding reservoirs. Associates include *Crypsis, Cyperus, Gnaphalium, Spergularia,* and *Suckleya.*

Previous knowledge. Growing in shallow, brackish or alkaline water of marshes, ditches, and ponds, NH to ND, CO, UT, and WA, s. to FL, TX, and CA; s. through tropical America to Argentina (Hitchcock and Chase). *Diagnostic characters.* Keys to *Eragrostis* in Dorn (p. 706), but differs by having membranous (vs. ciliate) ligules and lemmas appressed-pubescent (vs. glabrous) along the lateral nerves.

Significance. First record of the genus for WY, a range extension of ca. 120 km from Dawes Co., NE (Barkley).

POLYGONUM PENSYLVANICUM L. (POLYGONACEAE).—USA, WY: Goshen Co., NE border, 13 km se. of Torrington (T24N R60W S34 se.¼), roadside ditch with *Kochia* and *Helianthus,* 1220 m, 20 Aug 1977, *Dorn 3021*; Crook Co., 12.8 air km nne. of New Haven (T56N R66W S7, 8), eroded, loose, shaley ridge with oak and pine, 1160 m, 26 Jul 1978, *Dueholm 4992.* Synonym: *Persicaria pensylvanica* (L.) Gomez.

Previous knowledge. A highly variable weedy species ranging from Nova Scotia and Quebec to MN (Gleason and Cronquist), ND, MT (Booth and Wright), w. SD, and e. CO (Barkley), s. to FL, TX, and AZ; Mexico (Kearney and Peebles). *Diagnostic characters.* Keys to couplet for *P. lapathifolium* and *P. persicaria* in Dorn (p. 1069), but differs by having stipitate glands on upper stems and peduncles (vs. glands sessile if present).

Significance. First record for WY, a range extension of ca. 130 km from Weld Co., CO (Barkley). Erroneously reported from Albany Co., WY (Barkley) based on *Stephens 43631* (KANU), a collection of *P. lapathifolium* L. in early flower.

The Rocky Mountain Institute of Energy and Environment of the University of Wyoming provided financial support for much of the field work by Hartman, Nelson, and Dueholm.—Ronald L. Hartman, B. E. Nelson, and Keith H. Dueholm, Department of Botany, University of Wyoming, Laramie 82071 and Robert D. Dorn, Wyoming Department of Environmental Quality, Cheyenne 82002. (Received 5 Mar 1980; accepted 19 Jun 1980; final version received 7 Jul 1980.)

NOTES AND NEWS

Isozyme Variability in *Cortaderia selloana* and Isozyme Constancy in *C. jubata* (Poaceae).—*Cortaderia selloana* (Schult.) Asch. et Graebn. (pampas grass), a dioecious species, and *C. jubata* (Lem.) Stapf, an agamospermous one (Costas-Lippmann, Bot. Gaz. (Crawfordsville) 140:393–397. 1979) are the popular horticultural cortaderias in California. Both are native in South America. *Cortaderia selloana* is commonly seen in cultivation whereas *C. jubata* has escaped from ornamental plantings, becoming an aggressive weed in coastal California (Costas-Lippmann, Fremontia 4:25–27. 1977). and in New Zealand (Connor, New Zealand J. Bot. 3:17–23. 1965).

The fact that these two species are not easily distinguishable morphologically before flowering (Conert, Die Systematik und Anatomie der Arundineae. 1961; Costas-Lippmann, Ph.D. diss. Univ. Calif. Berkeley. 1976) raised the question of how much variability could be detected electrophoretically. Five enzyme systems (peroxidases, esterases, acid phosphatases, leucine-amino peptidases and amylases) were analyzed using standard techniques for starch electrophoresis.

Leaf material from the sheath close to the ligule was collected from plants of both species growing in cultivation in the research area of the University of California at Davis, and from naturally occurring populations in California. The plants at Davis were grown from seeds collected in natural populations in Argentina and Ecuador, and from naturalized populations in New Zealand.

California material of *Cortaderia selloana* was collected from Grizzly Island Road, Solano Co. (from two sites with different moisture conditions, close to the Montezuma Bridge) and Golden Gate Park, San Francisco Co. (from four plantings around Mallard Lake and two at the entrance of the Conservatory). Material of *C. jubata* came from Elk River, Humboldt Co. (cut-over land in the Redwood Forest, 8 km se. of Eureka); Redwood Road and Skyline Blvd., Oakland, Alameda Co. (serpentine soil); Oakland International Airport, Alameda Co. (filled land); Point Isabel, Contra Costa Co. (abandoned field); and Lucia, Monterey Co. (seacliff).

In *Cortaderia selloana,* amylase and leucine-aminopeptidase had only one band. The peroxidases, acid phosphatases, and esterases showed polymorphic systems. Values for the polymorphic index (PI) of Marshall and Allard (Heredity 25:373–382. 1970) suggest that variability in the first two systems is greatest in the material from Argentina (General Roca) and slightly less in the material from New Zealand. A slightly higher PI was obtained for New Zealand esterases than for Argentinian esterases. All of the Californian material showed less variation for these three systems. In particular, all the plants of the Golden Gate Park population proved to be virtually identical (one plant appeared to have an extra anodic band in the peroxidase system). This supports an early supposition that all these plants were derived from cuttings from a single plant (or very few plants) at the time of landscaping the area.

Enzyme activity, as judged by staining intensity, seemed comparable in all systems and populations with the exception of esterases in the material from Grizzly Island

Road. Here the marshland subpopulation indicated a much greater level of activity than the roadside subpopulation.

By contrast, the banding patterns in *Cortaderia jubata* for all enzymes were identical, not only in presence of bands but also in activity levels, even though habitats were diverse. Lack of electrophoretic variation here is correlated with apomixis. Our result agrees with that of Sternberg (Madroño 23:408–417. 1976), who found electrophoretic uniformity within ring-clones of *Larrea tridentata*.—MARTHA COSTAS-LIPPMANN and IRENE BAKER, Department of Botany, University of California, Berkeley 94720. (Received 30 Aug 1979; returned 11 Jan 1980; resubmitted 3 Apr 1980; accepted 9 Apr 1980; final version received 14 Apr 1980.)

BOOKS RECEIVED AND LITERATURE OF INTEREST

Diatoms of North America. By WILLIAM C. VINYARD. 120 p., illus. Mad River Press, Eureka, CA. 1979. ISBN 0-916-422-15-1. $5.25. Presents keys to and descriptions of the genera of freshwater and marine diatoms of the United States; illustrations of representative species; and discussions of ecology and distribution, cell wall structure, physiology, economics, and techniques for collection and preparation of both living and fossil forms.

Plants of Deep Canyon and the Central Coachella Valley, California. By JAN G. ZABRISKIE. 174 p., illus. Philip L. Boyd Deep Canyon Desert Research Center, Univ. California, Riverside. 1979. LCCN 79-63644. $14.95 (hardcover) or $8.95 (paper) plus tax and $1.00 for mailing. Will be reviewed in a subsequent issue.

California's Spanish Place-Names: What They Are and How They Got There. By BARBARA and RUDY MARINACCI. 267 p. Presidio Press, San Rafael, CA. 1980. ISBN 0-98141-102-X. $6.95 (paper) plus tax and shipping. Organized loosely historically, covering everything from abajeños to Pt. Zuniga. Delightful reading for those interested in the stories our place-names tell. Includes a useful 58-page dictionary-index.

Flora of Baja California. By IRA L. WIGGINS. 1025 p., illus. Stanford Univ. Press, Stanford, CA. 1980. ISBN 0-8047-1016-3. $65.00. A monumental work in preparation for 51 years. Will be reviewed in a subsequent issue.

Checklist of United States Trees (Native and Naturalized). By ELBERT L. LITTLE, JR. 375 p. U.S.D.A. Agriculture Handbook 541. 1979. USGPO stock number 001-000-03846-0. $10.00. The revised (from 1953) checklist compiles scientific names, synonyms, approved common names, and geographic ranges of U.S. trees (including Alaska but not Hawaii). Derivations of names, other common names, references, and other notes are included.

A Dictionary of Botany. By R. JOHN LITTLE and C. EUGENE JONES. 400 p. Van Nostrand Reinhold, New York. 1980. ISBN 0-442-24169-0. $18.50. If you have ever been puzzled by synaptinemal complexes, synemata, or the differences between syngameons and syngamodemes, this book offers an excellent place to begin reducing your confusion. Add succinct definitions of biological species and biosystematics and you have a book that will provide knowledge and enjoyment to botanists at all levels from introductory or amateur to research professionals. Highly recommended.

Flora Neotropica. Tremellales. By BERNARD LOWY. Monograph 6, 18 p. New York Botanical Garden, Bronx 10458. 1980. ISBN 0-89327-220-5. $4.50.

MEETING ANNOUNCEMENTS

16 October 1980:	Jean Colvin, Program Director, University Research Expeditions Program, University of California, Berkeley. *UREP—Public Support and Involvement in University Field Research.* 8 p.m., 2003 Life Sciences Bldg., UCB.
20 November 1980:	Robert Raabe, Department of Plant Pathology, University of California, Berkeley. *Some diseases of ornamental trees and approaches to control.* 8 p.m., 2003 LSB.

REVIEWS

Nevada through Rose Colored Glasses: The Fossil and Plant Collecting Percy Trains, 1928–1942. By Agnes Scott Train. vii + 177 p., frontis. + 26 figs. Western Printing & Publishing Co., Box 601, Sparks, NV 89431. 1977. $6.50, paper.

This is a charming book about the collecting experiences of two adventurous and independent people, Percy Train and his wife, Agnes Scott Train, in Nevada and adjacent states from 1928 until Percy Train's death in 1942. Percy Train was a mining engineer who for many years made his living as an assayer. About 1915 he began collecting fossils which he sold to museums in North America and Europe, gaining in the process a considerable reputation as an excellent collector. In 1928 Train married Agnes Scott, a librarian from Chicago, and the two made collecting of fossils and later plants a joint venture.

A close association was formed with the late Professor Chester A. Arnold of the University of Michigan [see C. A. Arnold, Some Recollections of Percy Train (1876–1942). Huntia 2:111–116. 1965] in the collection of plant fossils. This led to collecting extant plants and the Train's association with the late Dr. W. A. Archer and the eventual publication by Percy Train, J. R. Hendricks, and Archer of the "Medical Uses of Plants by Indian Tribes of Nevada" (Contr. Fl. Nevada. 33. 1957).

This book describes vividly the experiences, trials, joys, often documented with amusing anecdotes, of a remarkable couple engaged in a unique profession in a far-from-hospitable land. For supplementary biographical information the reader is referred to Olga Reifschneider's account of the Trains (Biographies of Nevada Botanists. 1844–1963. Univ. Nevada Press. 1964).—John H. Thomas, Department of Biological Sciences, Stanford University, Stanford, CA 94305.

Oakes Ames: Jottings of a Harvard Botanist. 1874–1950. Edited by Pauline Ames Plimpton. x + 403 p., frontis. + 41 illus. Botanical Museum of Harvard University, Cambridge, MA 02138. $12.95, cloth.

The definitive history of botany at Harvard University, and hence much of the history of botany in North America, has not yet been written, but books like the one under review will fill a part of the picture. Oakes Ames is best known for his systematic work in the Orchidaceae and his role in the development of economic botany. However, he is generally less well known for his very important position in the biological sciences at Harvard, especially from about 1925 through 1935, when he was chairman of the Division of Biology and of the Committee of Botanical Collections.

Ames was independently wealthy, perhaps giving him a more detached and objective view of biology than that of his many colleagues. Private funds allowed Ames to travel widely, hire personal research assistants, amass an excellent library and herbarium, and live in many ways the life of a "country squire". He was obviously devoted to his work and to his family. His wife, Blanche, was a gifted artist, particularly skilled in botanical illustration.

Most of this book comes from Ames' letters and diary, concentrating very heavily on his home and personal life. After reading it, I was left with the feeling that I wanted to know more about his professional life, but we should be grateful for this much information about an important and influential botanist.—JOHN H. THOMAS, Department of Biological Sciences, Stanford University, Stanford, CA 94305.

A Monograph of the Genus Lasianthaea (*Asteraceae*). By KENNETH M. BECKER. Mem. New York Bot. Gard. 31(2):1–64. 1979. ISBN 0-89327-211-6. $6.50 + postage and handling ($1 for USA, $2 for others, from Publications Dept., N.Y.B.G., Bronx, NY 10458).

Becker supports his essentially α-taxonomic treatment of the predominantly Mexican eleven species and nine non-typical varieties with synopses of history, diagnostic characteristics of and within *Lasianthaea,* preliminary results of flavonoid studies, chromosome numbers, and instances of hybridization. Keys, nomenclature, typification, and descriptions are well-done. Habitats are indicated, as are distributions (including six maps). Selected specimens are cited for each taxon and a list of specimens seen is appended.—JOHN L. STROTHER, Department of Botany, University of California, Berkeley 94720.

A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland. II. The Biota of North America. By JOHN T. KARTESZ and ROSEMARIE KARTESZ. 498 p. Univ. North Carolina Press, Chapel Hill 27514. 1980. ISBN 0-8078-1422-9. $35, cloth.

Seven years of work by the authors has produced the most extensive and comprehensive plant checklist yet compiled. It is intended to provide a complete list of currently accepted names of North American vascular plants and of currently used synonyms.

This enormous task has been mitigated by the collaboration of more than 250 specialists. Publication of this volume is an important step in understanding the North American flora. It represents the best synthesis of taxonomic knowledge currently available and will serve as an important reference as well as the basis for more detailed studies.

As with any floristic list, this one should be considered neither final nor completely accurate. However, the authors are to be commended for their dedication, the quality of their work, and the service they have performed for the taxonomic community.—THOMAS DUNCAN, Department of Botany, University of California, Berkeley 94720.

INDEX TO VOLUME 27

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. Names of authors followed by titles of articles or notes are listed alphabetically in Table of Contents, p. iv.

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All members of the California Botanical Society are allotted eight pages in the journal over a two-year period. Beyond that number of pages, a required editorial fee of $40.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. 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.

REVIEWS

CALIFORNIA BOTANICAL SOCIETY