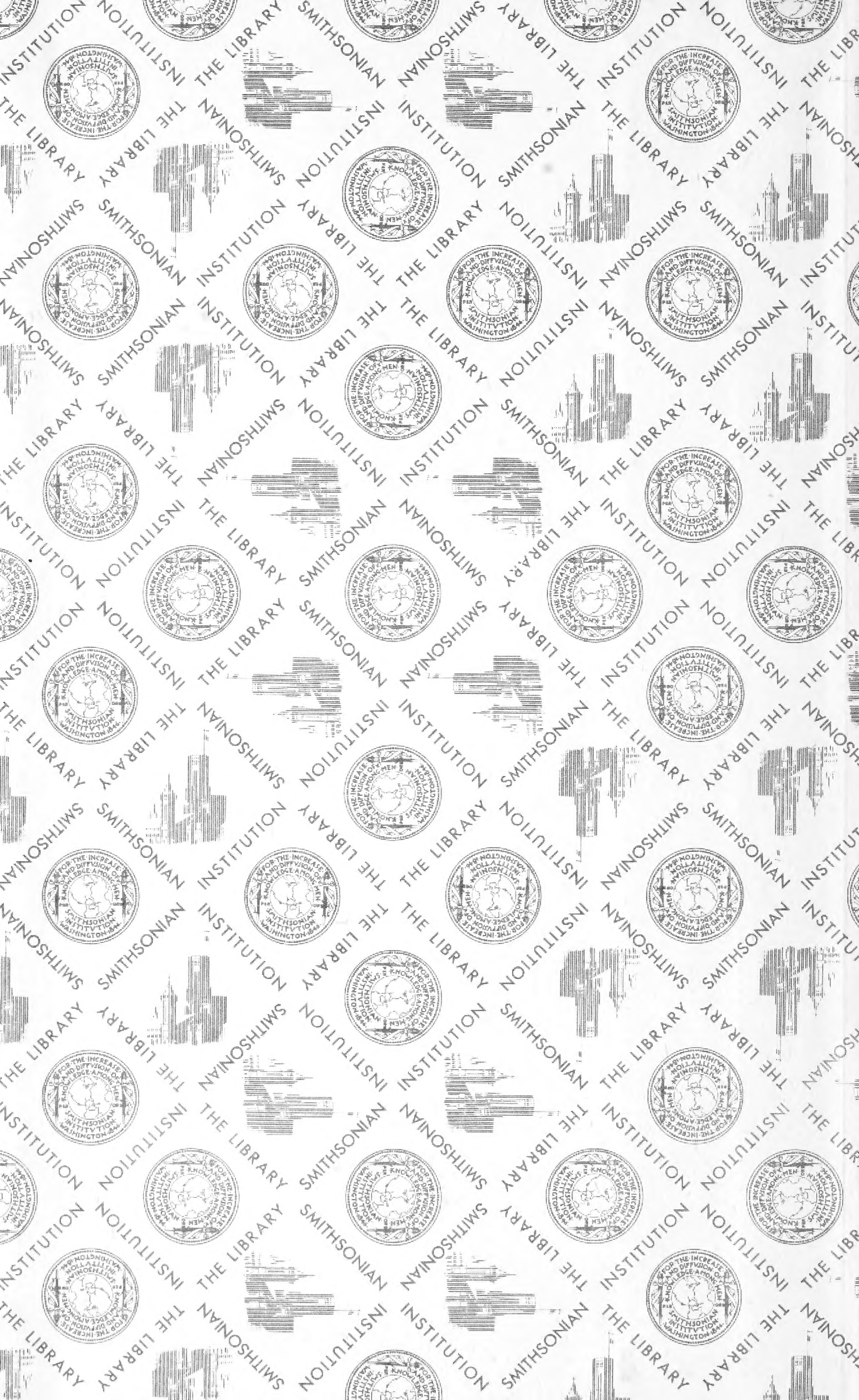
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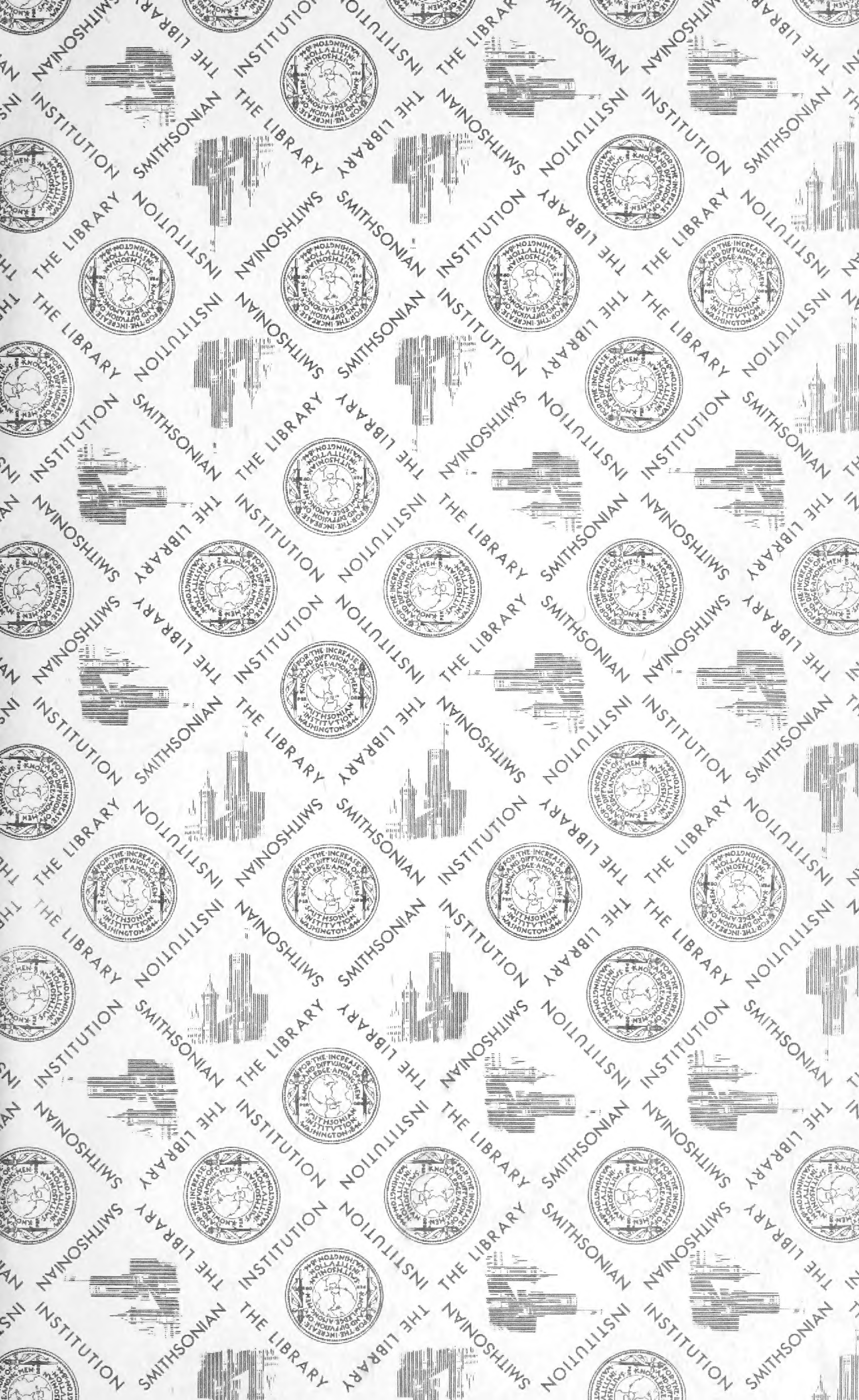
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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME XVI
1961–1962

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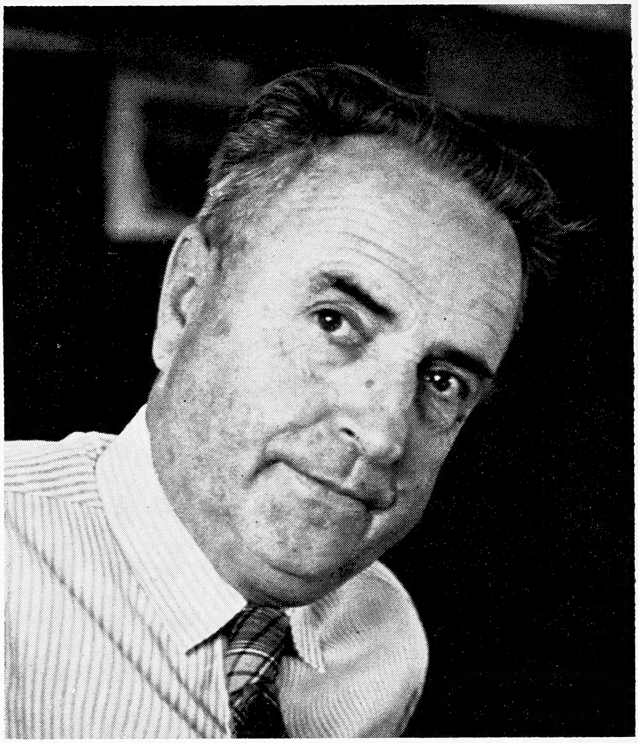

Marion Cave photograph

To Herbert Louis Mason. Upon the approaching retirement from your official duties, we, the California Botanical Society, wish to dedicate the sixteenth volume of Madroño to you. Our dedication is not only an expression of our appreciation for your wise counsel and devotion in your editorial capacity which, with the not inconsiderable help of two successive secretaries of the Editorial Board, has helped to maintain our Journal at a consistently high degree of excellence, but also in recognition of your far-reaching and often provocative contributions to Western Botany . . . notably in the fields of paleobotany, ecology, taxonomy and in the basic philosophical approaches to botanical problems.

During your nearly forty years of association with the University of California at Berkeley, an ever-widening circle of botanical students, who have since taken their places in leading universities throughout the world, has benefited by your wise and pioneering tutelage. Their number could be easily computed but the influence, through them, which you have exerted, is incalculable. On another plane, you have long been a staunch defender of our natural heritage. "A Flora of the Marshes of California" is concrete evidence of your and your students' support of the Wildlife Restoration Project. Your many other activities on behalf of conservation have furthered the preservation of our fast-disappearing natural areas. We hope you will persevere in the good work.

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ERRATA

Page 96, line 14: *for* Madroño 9 *read* Madroño 11.

Page 97: *transfer* figure to p. 99.

Page 99: *transfer* figure to p. 97.

Page 107, line 5: for *Sphenopyllum* read *Sphenphyllum.*

Page 120, line 8: *for* GALIUM ROTHROCKII Gray subsp. ROTHROCKII *read* GALIUM WRIGHTII Gray subsp. ROTHROCKII (Gray) Ehrend.

Page 121, line 38: *for* eu-ployploid *read* eu-polyploid.

Page 149, next to last line: *for* $n=25$ *read* $n=24$.

Page 167, legend: *after* Fig. 1, add *Galium hardhamae.*

Page 201, running head: *for* UREDINALIS *read* UREDINALES.

Page 203, running head: *for* UREDINALIS *read* UREDINALES.

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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 16, NUMBER 1 JANUARY, 1961

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MADROÑO

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EDWARD PALMER'S VISIT TO GUADALUPE ISLAND, MEXICO, IN 1875

S. F. BLAKE[1]

From the standpoint of the discovery of new forms of birds, one of the most important short expeditions in the history of North American ornithology (in the sense of the American Ornithologists' Union Checklist) was that made by Dr. Edward Palmer to Guadalupe Island off the coast of Baja California in the spring of 1875. In addition, his plant collections formed the first scientific botanical records known from the island and they give the best approximation of the vegetation there before introduced goats had done extensive damage.

Palmer (1831?–1911), at the time a man of about 44, had already been active off and on for a score of years, beginning in 1853, making collections in most branches of biology and ethnology in various parts of the United States, northern Mexico, and Paraguay, principally for the Smithsonian Institution. Further details of Palmer's life and work are discussed by McVaugh (1956) and in a paper read by Safford (1911) at the meeting of the Botanical Society of Washington on 10 January 1911 to celebrate Dr. Palmer's (supposed) 80th birthday, only a few months before his death.

Among the archives of the New Crops Research Branch (formerly Division of the Plant Exploration and Introduction) of the Agricultural Research Service, United States Department of Agriculture, are fourteen envelopes of manuscript material relating to Palmer's work from 1853 to 1911, twelve envelopes containing field books and copied data covering the years 1902–1910, and an unpublished manuscript in twelve envelopes by the late William E. Safford (1859–1926), a former botanist in the Department, dealing especially with Palmer's work as a plant collector. All of this material was drawn upon by Dr. McVaugh in writing the book on Palmer, but unfortunately space limitations prevented him from including many quotations. Two items relating to Palmer's first collecting trip to Guadalupe Island have so much human interest in connection with this first scientific expedition to that island that they deserve to be put on permanent record. One is an eight page manuscript by Palmer; the other a letter from Robert Ridgway to Palmer. The manuscript tells of Palmer's disagreeable experiences after his collections had been made, owing to shortness of food and the failure of the promised boat to come and take

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[1] EDITOR'S NOTE: Dr. S. F. Blake passed away on December 31, 1959. His manuscript had been prepared in the form of a note; its posthumous publication in another form necessitated transferring parenthetical citations to "Literature Cited" and making other minor alterations in the introductory material. In addition, it seemed pertinent to incorporate information about Harry Bye Stewart and the items from the San Diego *Union*, all of which were contributed by Dr. Reid Moran of the San Diego Natural History Museum.

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them off. The eight pages, written on only one side and measuring 22.3 × 14.5 cm., appear to have been copied from Palmer's notes after his return to San Diego and not entered from day to day upon the island. Safford evidently planned to use the manuscript in his projected publication (he refers to it in his published biographical sketch) and had corrected in blue crayon Palmer's frequently faulty spelling and grammar, but the journal is here printed in the original spelling, punctuation, and capitalization, with the addition in brackets of a few words that are needed for clarity, and the indication by "(sic)" of the principal misspellings.

Palmer sailed from San Diego on 30 January 1875 aboard the "San Diego" (San Diego *Union*, 30 January 1875) and may well have arrived at Guadalupe Island by the first of February. With him was his assistant for the trip, Harry Bye Stewart (1862–1922), the twelve year old son of Wm. W. Stewart, San Diego shipping agent. As related in the journal following, they were not taken from the island until nearly four months had passed. Palmer's second trip to Guadalupe Island in 1889 was briefer and less harrowing.

Palmer's journal follows.

Guadalupe Island. Lower Cal. *Dissapointment* (sic). *I miss the Alaska Expedition.* 1875. As arrangements had been made to send over a schooner after me in 6 weeks and no boat came, I became anxious & I went daily to Pt. Lookout to watch for it. All provisions had given out but goat meat & coffee & beens (sic) that had been on the island for years.

The young man [Safford's note: Harry Stewart] who had accompanied me, bore up well until the bread gave out, when he said he wanted to go home. I was kept busy carrying collections on my back a foot (*sic*), to the beach in a cave. These journeys were very tiresome, & all but one load was stored when I became sick.

April 30—it was [thought that] a schooner was [sighted] in the distance but, it was not,—a cruel dissapointment (sic) as I had expected to join a party for Alaska May 1st.—I had hurried my collections so as to [be] ready in/[p. 2] 6 weeks & now to be kept back, together with physical weakness made me so sick that for some days [I] could with difficulty move about.

May 11—with much difficulty reached the Point, but no schooner. Coffee all gone & nothing to eat but old beans & goat meat. I ate mustard leaves which toned up the stomach somewhat.

May 14—all hands sick, including myself in bed for 3 days, with violent disorder of the bowels—& the fleas nearly ate me up & the flies by day, nearly worried the life out of me. As I could no longer [go] to point disappointment, asked Mr. Sanford [Safford's note: an old sailor, who was in charge of the island], to go. he was just able to be about. he said if Jack [the burro] came up he would go, so the yard gate was opened, for this faithful old /[p. 3] Jack was very fond of bones, they where [were] always thrown in a pile for him, he could crunch them lik [like] a dog, this Jackass had carried not only myself, but several others over the Island, was a great favorite, he being worthy of a title named him Saint John, which name he went by. but he soon came along and while devouring his bones, the saddle was put on, and to [i.e., the] journey to the point made but no boat. May the 15th.—the gate left open Saint John entered [and] while at the usual bone pile was saddled by Mr. Sanford, who rode to the look out, he returned and reported seeing an object like a boat approaching shore,/[p. 4] hopes revived, and the old name of the point restored, he went to the landing riding St. John, after much effort [I] rolled out of bed, and dressed, was sitting by the bed putting the remainder of my specimens the best I could together in bundles to carry them down to the landing, when Mr. Sanford returned with a man from the boat. he said he had come for me and my companion, the agents son Mr. W. Stewart, He said seeing the bundles, but you are not going to carry all that are you, yes I must try was the reply, they are birds, and valuable. no he said you are not able, and I doubt if/[p.5] you can walk to the beach. yes I must try, for the mules must be left for tomorrow. the sick men must go also. they are no use hear (sic), no medicine or food. The man took my choicest bundles on his back, and little by little, with his help started for the beach, leaving the rest with the baggage to come next morning, nearing the beach, and the boat was by a sudden puff of wind carried out to sea, my feeling at this sight was indiscribable (sic) it was near dark before she came again to anchor. It was a hard task to make the Journey to the beach, owing to my feebleness,/[p.6] after getting on board, my first request was after bread and tea, a small slice of bread was toasted a little, butter spread over it with a cup of tea, was given me and I fell over a sleep (sic) to awaken next morning late. The party from the Island came, things and men were put on board, they opened my Cave on shore, its choice contents brought on board. The Superintendent and one of the ablest men was left on the Island, all the provisions that could be spared from the boat, was given them, with the promise that more should spedily (sic) be sent them, when we /[p.7] bid them, the Island, and the faithful St. John, farwel (sic), and pushed off, food and drink was given to us sparingly, Reached San Diego, Thursday night may 20, 1875, weighing 125 pounds, going on the Island, weighing one hundred and sixty.

The cause of the long detention on the Island, was owing to the inability of W. W. Steward [Stewart],—with whom arrangements had been made to send a boat in six weeks, to dispatch one from San Diego before, as no boat smaller than mail steamer, entered the harbor of San Diego, during that time, if a boat was kept at the/[p. 8] Island, the hands might escape, and when the want of food, was made known by Telegraph to the President of the goat company, it turned out he had unintentianally (sic) kept the memorandum of Provisions in his pocket, instead of sending them on the Island at the time of my visit,—The distressed condition of those from the Island,—awoke the simpathy (sic) of the company, A new president was elected, and six months provisions with some new men was promptly sent on the Island.

In the San Diego *Union* for May 21, 1875, is the following: "The schooner *Coso* arrived last evening from Guadalupe Island to W. W. Stewart & Co., bringing up as passengers Dr. Palmer, of the Smithsonian Institution, Master Harry Stewart, and two of the men employed on the island. Dr. Palmer has been engaged in collecting specimens of natural history for several weeks past. There has been some sickness among the men on the island, the supply of flour having given out some weeks ago, and an exclusively meat diet having proved unwholesome. The schooner left the men all the flour she could spare, and more will be forwarded immediately."

The second item of interest is a holograph letter from Robert Ridgway, then twenty-five years old, requesting Palmer to use his influence with S. F. Baird, Secretary of the Smithsonian Institution, to have Palmer's birds turned over to him rather than to Dr. Elliott Coues for identification. History shows that this was done.

Ridgway's letter to Palmer runs as follows:

Smithsonian Instn.
Washington, D.C.
Nov. 14, 1875

Dear Doctor:

I have just returned from a months absence at my old home in Illinois, and embrace my first opportunity to answer your favor of the 16th of October. On visiting the Smithsonian yesterday I found your birds in Dr. Coues' hands, but informed Professor Baird that you had requested me to work them up, and strongly urged my claim to the first right. Please write to him yourself *at the earliest moment*, regarding this matter, as I would like to work up all your collections in the bird line—will do it with pleasure, and in a manner which I am sure will meet your approval in all respects.

In looking over your collection I was astonished to find apparently *every species an entirely* new one [last two words not italicized]—most of them *very* distinct from any previously known, while Dr. C., was not aware of any difference whatever until I informed him. I will be glad to have all the information you can possibly give me regarding each species of these birds, and also full notes upon the geographical location, geological formation, natural productions of all kinds (particularly the flora and sylva, since these influence so much the distribution of the birds) so that I will have material for an elaborate paper —in which you shall have full, and entire credit.

I am now making a hobby of big trees; and if you can supply me with any newspaper scraps, or original notes, on large trees of any part of the world, I will accept them most gratefully; the smallest items will be thankfully received. During the course of your explorations and ramblings you must have come across many "monarchs of the forest"—particularly in the tropics. And you probably have stored up much information, both general and detailed, in this branch.

Let me hear from you, and believe me, in haste Yours truly Robert Ridgway

Dr. Edward Palmer
St. George, Utah

Crops Research Division,
United States Deparment of Agriculture,
Beltsville, Maryland.

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VEGETATION HISTORY OF THE PACIFIC COAST STATES AND THE "CENTRAL" SIGNIFICANCE OF THE KLAMATH REGION[1]

R. H. Whittaker

Introduction

Among the major developments in the biogeography of the eastern United States were three interrelated ideas: (1) the close floristic relation between the eastern United States and eastern Asia (Gray 1846, 1873, Li 1952), (2) the central relation of the southern Appalachians to eastern vegetation (Adams 1902), and (3) the significance of the mixed mesophytic forests in eastern forest history (Braun 1947, 1950). It is through vegetation history that these points take on their meanings in relation to one another. During the Tertiary, in Oligocene and Miocene time, Arcto-Tertiary forests occupied much of the present temperate latitudes of Eurasia and North America. Although these forests differed from one area to another, there was floristic exchange between the two continents across the Bering land bridge, and the forests showed general floristic similarity around the Northern Hemisphere. With the increasingly dry climates and glaciation of later time, these forests were increasingly fragmented, restricted, and modified, while other, more dry-adapted types of vegetation spread through the interiors of Eurasia and North America. Remnants of the Arcto-Tertiary forests exist now on opposite sides of the two continents—in the eastern United States and eastern Asia, and (with fewer surviving genera) in the western United States and western Europe. In the southern Appalachians especially, mixed mesophytic forests occur which are suggestive of the Arcto-Tertiary forests, have a "central" relation to the forest floras of other parts of the eastern United States, and have strong floristic affinities with forests of eastern Asia.

It is natural to seek a comparable center for western forests. An extensive area of old and geologically complex mountains, the Klamath Ranges, extends from the southern end of the Cascade Range and the northern end of the Great Valley of California, west to the Pacific Ocean. One may observe of these mountains that: (1) The area has, like the Southern Appalachians, one of the most highly complex vegetation patterns in North America (Whittaker 1956, 1960). Into this area extend and meet in a complexly interdigitating pattern, various types of vegetation which form the prevailing climaxes of other areas. All western plant formations dominated by trees occur in the Klamath Region, as in no other area. (2) Those forest formations which are of most highly mixed tree-stratum composition and are thought most to resemble Arcto-Tertiary forests in

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[1] A contribution from the Department of Zoology, Washington State University, and the Department of Biology, Brooklyn College. The author's studies in the Klamath Mountains were supported in part by the funds for medical and biological research of the State of Washington Initiative Measure No. 171. The author is indebted to R. W. Chaney, D. I. Axelrod, and H. D. MacGinitie for comments on the manuscript.

the West, occur in this region—the redwood forests and mixed evergreen forests. Of these the mixed evergreen forest is the link between two major fractions of western forest vegetation—the coniferous forests, and the sclerophyll and oak-pine woodland grouping. (3) The Klamath Region has also an exceedingly rich flora for its latitude; it is a center of floristic diversity and narrow endemism (Jepson 1923–25, 1935, Mason 1927, Peck 1941, Detling 1948b), and many plant genera have maximum numbers of species in the West, including endemics, occuring there. One may, with certain qualifications to be observed, regard the Klamath Region as a "center" for the western forests.

The prevailing climax at low elevations over much of the Klamath Region is the Mixed Evergreen Forest (Munz & Keck 1949, 1950, 1959, cf. Cooper 1922, Clark 1937)—mixed forests with two-level canopies of larger evergreen-needleleaf or coniferous trees (*Pseudotsuga menziesii, Pinus lambertiana, Chamaecyparis lawsoniana*, etc.) and smaller evergreen-broadleaf or sclerophyllous trees (*Lithocarpus densiflora*, *Arbutus menziesii*, *Castanopsis chrysophylla*, *Quercus chrysolepis*, *Umbellularia californica*, etc.), with deciduous trees (*Acer macrophyllum* and *A. circinatum, Cornus nuttallii, Corylus californica, Quercus kelloggii,* etc.), usually present also. In relation to moisture the canopy changes, from mesic stands in which the coniferous stratum is dense and deciduous trees may outnumber sclerophylls, through stands in which the conifers are scattered in open growth above a dense sclerophyll stratum, to more xeric stands in which both strata are open and pines (*P. lambertiana, P. ponderosa*) rather than *Pseudotsuga* are principal conifers.

The complex vegetation of the Klamath Region may be conceived in terms of these mixed evergreen forests as the central, prevailing climax or vegetational matrix for the region, giving way to other types of communities in various ways (Whittaker 1960). (1) Within the main area of the mixed evergeen forests, distinctive communities of different composition and structure occur on serpentine and other special parent materials. (2) Toward more humid environments nearer the Coast the density of the conifers increases while that of the sclerophylls decreases, and the mixed evergreen forests gradate into *Pseudotsuga* forests. These in turn gradate into coastal *Sequoia* forests in which sclerophylls are represented by small numbers of stems. (3) Toward the north and higher elevations the sclerophylls decline, and the mixed evergreen forests gradate into montane forests dominated by *Pseudotsuga*, *Abies concolor*, and *Pinus ponderosa*. Toward still higher elevations these gradate into subalpine forests dominated by *Abies procera, Tsuga mertensiana,* and (locally) *Pinus monticola* and *Picea breweriana*. (4) Toward the drier interior, *Pseudotsuga* declines and the sclerophyll strata become more open, and the mixed evergreen forests gradate into northern oak woodland (*Quercus kelloggii, Q. garryana*) in Oregon, pine-oak foothill woodland (*Pinus sabiniana, Quercus douglasii, Q. agrifolia*, etc.) in California. (5) Toward the south, the mixed evergreen forests narrow toward the coast (to become part of the "redwood border" vegetation of the California Coast Ranges), and in drier climates gradate into broad-sclerophyll forests and these into chaparral.

It will be the object of this paper to consider the vegetation history of the Pacific Coast states with special reference to the Klamath Region and two questions—the origin of this vegetation pattern and the central relation of this region to the western forests.

Vegetation History

Some aspects of vegetation history bearing on the Klamath Region have been summarized by Chaney (1936, 1938a, 1938c, 1940, 1947, 1948a) and Axelrod (1940a, 1950c, 1952, 1958, 1959). Geological history bearing on the story has been summarized by Diller (1894, 1902), Hershey (1903), Smith & Packard (1919), Clark (1921), Willis (1925), Fenneman (1931), Smith (1933), Reed (1933), Weaver (1937), and Williams (1948).

Pre-Cenozoic (Jurassic and Cretaceous) floras of the Klamath Region and Oregon Coast Ranges are described by Fontaine (1905a, 1905b, 1905c) and Chaney (1948a). Forest trees of more modern types became widespread in Cretaceous time; Cretaceous floras include almost all the families of the subtropical Eocene floras of the West, as represented by the Goshen flora (Chaney & Sanborn 1933). Much of the area of California and Oregon, inland to the Sierra Nevada and Blue Mountains, was submerged in the Cretaceous; the Klamath Region itself formed an extensive, mountainous island which later was probably reduced by erosion and subsidence to an archipelago of scattered islands (Diller 1894, Condon 1902, 1910, Smith & Packard 1919, Smith 1933, Reed 1933). Toward the close of the Cretaceous the Klamath Region was raised above the sea again.

In Eocene time the full land surface of the Klamath Region was occupied by vegetation as it has been (except for local alpine glaciation) through the whole of Cenozoic time since. With continued evolution of modern plant types, extinction of archaic ones, and probable climatic warming accompanied by migrations toward the north, subtropical forests of essentially modern types appeared in the United States in the Eocene, as the Wilcox and other floras of the East (Berry 1916, 1930, 1937), the Goshen and other floras of the West (Chaney & Sanborn 1933, Chaney 1936, 1938c, 1947). During the Eocene epoch, the Oregon coast north from the Klamath Mountains was submerged (Weaver 1937), as was the Great Valley and much of California west of the Sierra Nevada (Clark 1921, Reed 1933). The Oregon and California Coast Ranges were not yet formed, although submarine volcanic activity on an immense scale was producing the lavas later to become the core of the Coast Ranges of Oregon and Washington (Williams 1948). The Cascade Mountains were not yet elevated to intercept the moisture of maritime air masses. Most of Oregon was a broad plain, across which mesophytic forests extended from the coast to the John Day Basin area of eastern Oregon (Clarno flora, Knowlton 1902, Chaney 1938c, 1948a) and beyond. The high temperatures of the Eocene permitted subtropical floras to extend northward to about 50° north latitude on the coast (Chaney 1947), and some elements of these forests to extend as far as 56–57° in Alaska (Hollick 1936, Chaney 1949).

Mesophytic subtropical forests, representing the Neotropical-Tertiary Geoflora, appear in fossil floras from widely separated points in the Pacific Coast states—from the California Sierra Nevada (Chalk Bluff and La Porte floras, MacGinitie 1941, Potbury 1935), through western Oregon (Comstock and Goshen floras, Sanborn 1935, Chaney & Sanborn 1933, Chaney 1936, 1948a) to the Puget floras of Washington (Newberry 1898, Chaney 1947). Physiognomically, such forests were dominated by trees with leaves of subtropical types—of moderate size, thick and probably evergreen texture, mostly entire margins, and in many cases elongate tips; floristically the Lauraceae (*Cinnamomum, Persea, Ocotea, Neolitsea, Cryptocarya, Lindera, Nectandra*) predominated along with *Ficus, Anona, Meliosma, Magnolia,* and other subtropical or tropical forms. Such subtropical forests doubtless prevailed in the lowlands of the Klamath Region. There is little indication of the upland forests of that time; but it may be presumed that temperate forests, probably including such genera as *Sequoia, Pseudotsuga,* and *Abies, Alnus, Lithocarpus,* and *Ulmus* occurred there (Chaney 1936, 1938a, 1938c) and were related to the temperate forests which then existed far to the north in Alaska (Hollick 1936, Chaney 1938a, 1947).

Much of western California, Oregon, and Washington was submerged during the Oligocene, but the submergence was less extensive in the lands adjacent to the Klamath Region (Clark 1921, Reed 1933, Weaver 1937). Volcanic activity in the area of the Cascade Mountains, which had begun in the Eocene, continued in the Oligocene to form a belt of scattered mountains which were still not effective as a climatic barrier (Williams 1948). In the Klamath Region itself a major uplift believed to have occurred at the close of the Eocene (Diller 1902) initiated the long cycle of erosion which was to produce the Klamath peneplain. With lower temperatures in the Oligocene, subtropical forests were displaced to the south, while the temperate forests were shifted southward and downward. In the western states *Metasequoia* and other temperate forms which had occurred in Alaska entered lowland forests along with *Sequoia* and other forms which had occurred on the uplands of the West during the Eocene (Chaney 1936, 1947, 1951). Through a wide area of the West there occurred forests which may be broadly characterized as redwood-mixed, dominated by either evergreen or deciduous redwood (*Sequoia* or *Metasequoia,* see Chaney 1948b, 1951) mixed with a variety of deciduous and some evergreen broad-leaved trees. These temperate forests of the Eocene in the Far North and the Oligocene and Miocene in the United States, taken in the broad sense and with allowance for the regional and topographic differentiation within them, represent the Arcto-Tertiary Geoflora (Chaney 1947, 1959). The transition between the Arcto-Tertiary and subtropical forests of the West was apparently represented in moist lowlands by warm-temperate forests in which *Taxodium* was dominant rather than the redwoods, with *Nyssa* as a major broad-leaved form among a mixture of subtropical and temperate forms—forests suggestive of the swamp forests in warm-temperate eastern North America of the present.

Lowland forests of this sort, dominated by *Taxodium* and *Nyssa* and including forms of both temperate (*Metasequoia, Juglans, Salix, Quercus, Platanus, Tilia, Ulmus*) and tropical (*Ocotea, Lindera, Persea, Ficus*) affinities are represented in the Klamath Region by the Oligocene Weaverville flora (MacGinitie 1937). Although these do not represent the upland forests, they imply the prevalence of temperate forests over most of the land surface of the Klamath Region from that time on. Far east from this, the Florissant flora (MacGinitie 1953) occurred in the area of the Colorado Front Range; this flora also included forms of subtropical affinities but was predominantly temperate in character. *Sequoia, Chamaecyparis, Fagopsis,* and *Zelkova* are believed to have occurred along streams and on moist bottom-lands, broadleaf forests with many forms now represented in forest-grassland transitions of the eastern and southwestern states in sites of intermediate moisture conditions, and pine woodland with evergreen oak and chaparral forms on drier uplands. Species of *Picea, Abies,* and *Acer* in the flora are believed to represent mountain forests of higher elevations. As observed by MacGinitie (1953, p. 52), the low-elevation pattern from mesophytic streamside forest to pine-oak woodland is suggestive of vegetation patterns now existing in parts of the Klamath Region. A related complex pattern ranging from mesic forest with *Zelkova, Cercidiphyllum,* and *Fagopsis* through prevailing deciduous forest to dry-slope communities with pines, sclerophyll oaks and xeric shrubs, with coniferous mountain forests also represented, is described by Becker (1956) from the Ruby River Basin of Montana.

Temperate forests of the upper Oligocene are represented in the Bridge Creek flora of the John Day and Crooked River basins (Knowlton 1902, Chaney 1924, 1925a, 1927, 1938c), forests of redwoods (*Metasequoia*) mixed with many other species, the living relatives of which occur in the West (*Tsuga, Abies, Taxus, Lithocarpus, Quercus, Acer, Alnus, Cornus, Fraxinus, Philadelphus, Rhamnus*), and in forests of eastern North America and eastern Asia (*Carpinus, Castanea, Fagus, Liquidambar, Nyssa, Ostrya, Platanus, Tilia, Ulmus, Cercidiphyllum*). Forests of this type, but with *Sequoia* rather than *Metasequoia*, are represented in the Klamath Mountains by the Ashland flora (Chaney 1938c). Although no Oligocene fossils of upland forests are available for the Klamath Region, the Ashland, Florissant, and Bridge Creek floras together suggest a probable vegetation pattern: mesophytic forests of mixed needle-leaved evergreen (*Sequoia, Chamaecyparis,* etc.), broad-leaved evergreen (*Quercus, Litho-*

carpus, etc.), and deciduous trees, giving way toward higher elevations to cool-temperate forests including *Abies* and *Picea.* In the coastal climate the pattern would be more strongly mesophytic, with less contrast of the extremes of the moisture gradient, than the Florissant pattern. Allowing for a warmer and more humid climate than at present, and the extinction of some early-Cenozoic forms, especially among deciduous trees, this pattern would be not unlike that now occurring in the more humid Klamath Mountains near the coast.

With continued cooling of climates from Oligocene through and beyond Miocene time, the Neotropical-Tertiary flora almost wholly disappeared from most of the United States, though certain members of predominantly tropical and subtropical families became adapted to life in temperate forests and remain as remnants of the Eocene forests (Chaney 1944b, 1947). In the earlier Miocene, the belt of Oregon now occupied by the Coast Range, and additional lands to the west of it, were above sea level (Weaver 1937). Warm-temperate forests including forms of subtropical affinities extended north on this coastal plain through and beyond the Klamath Region, in a manner comparable to that of the vegetation of the coastal plain of the eastern United States today. In floras from Rujada and Cascadia, in west-central Oregon (Chaney 1938c, 1948a), forms of the redwood forests (*Sequoia, Lithocarpus, Alnus, Berberis*) and deciduous trees now extinct in the West (*Tilia, Castanea, Ulmus, Carya*) occur together with subtropical *Persea, Ocotea,* and *Sabalites.* In the Klamath Region itself, the long-continued Klamath erosion cycle (Diller 1902) reduced much of the land to a peneplain of gentle or moderate relief. Scattered, low mountain ranges, which later became the monadnock summits of the major mountain groups of the region, rose locally 1000 meters or more above the peneplain. It may be presumed that inland from the coastal plain the Klamath lowlands continued to be occupied by redwood-mixed forests, while mountain forests occurred at higher elevations.

Through later Miocene time, the widespread Arcto-Tertiary forests were affected by increasingly dry climates. Great lava flows successively destroyed existing vegetation in the interior of Oregon and Washington in Miocene and later time (Williams 1948), and formed land surfaces which were occupied by new and more dry-adapted vegetation. In the Mascall flora of the John Day Basin, and related floras widely distributed from California to Washington and Oregon (Knowlton 1902, Chaney 1925b, 1948a, 1959), mixed forests with *Taxodium* and redwoods appeared. The reduction of the redwoods and other mesophytic forms in these suggests, however, a climate drier than that of the Bridge Creek flora (Knowlton 1902, Chaney 1925b, 1938c, 1948a, Axelrod 1940a). Resemblance of these forests to the redwood-border forests was emphasized in earlier accounts (Chaney 1925b, 1938c, Oliver 1934). The redwood in question was the deciduous *Metasequoia,* however; and the oaks were predominantly species with larger, dissected leaves resembling many of those now in the deciduous forests of the eastern states, *Q. kelloggii* and other deciduous western oaks (Knowlton 1902). The Mascall flora of the John Day Basin was thus a predominantly deciduous forest adapted to still relatively humid, but increasingly continental climates, of eastern Oregon (Chaney 1948a). Forms of subtropical affinities in the Mascall flora and the Latah flora of eastern Washington (Chaney 1938c, 1938a, Knowlton 1926) suggest continued warmth of climate. Mixed forests including conifers (*Sequoia, Abies, Libocedrus, Pseudotsuga, Picea, Thuja*), sclerophylls (*Lithocarpus, Quercus*), and deciduous trees occurred at Weiser, southwestern Idaho (Dorf 1936). A vegetation pattern including mixed sclerophyllous and deciduous trees as the prevailing climax, and a montane forest with *Abies, Pinus, Pseudotsuga,* and *Chamaecyparis,* is suggested by La Motte (1936) for the upper Cedarville flora of northwestern Nevada and northeastern California. Farther south, vegetation more distinctly adapted to drier climates appeared in the sclerophyll forests of the Tehachapi and Mint Canyon floras (Axelrod 1939, 1940b).

Changing climates of the later Miocene were thus reflected in geographic and topographic shrinkage of the mesophytic, Arcto-Tertiary forests. The complement to this process was the spread of dry-adapted vegetation types and floras, many forms of which expanded northward from centers of origin probably in scattered areas of the Southwest where Neotropical-Tertiary plants became adapted to aridity in Cretaceous and Paleocene time (Axelrod 1958), other forms of which probably evolved from species of temperate forests to occupy cooler dry environments as these became increasingly available, some forms of which entered the North American flora from the dry-climate flora of eastern Asia (Babcock & Stebbins 1938). Because of the importance of the spread out of the Southwest, and of the Mexican mountains as a center, Axelrod (1940a, 1950a, 1950c, 1958) has termed the dry-adapted floras of southwestern derivation, an even broader grouping than the Arcto-Tertiary, the Madro-Tertiary Geoflora.

At the end of the Miocene, the whole Cascade belt was upheaved by folding and tilting (Williams 1948), further desiccating the interior of Oregon and Washington. Uplift occurred in the Klamath Region (Diller 1902, Williams 1948), the Olympic Mountains (Weaver 1937) and the Sierra Nevada (Diller 1894, Fenneman 1931), drying the interior farther south; and further, major uplift occurred at the end of the Pliocene. In Pliocene time most of the coastal belt of Oregon was above the sea, but lobes of the sea extended into some areas of California and Washington (Clark 1921, Reed 1933, Weaver 1937). Deformations producing the California and Oregon Coast Ranges occurred at the beginning and end of the Pliocene. Islands off the California coast, the history of which may be traced backward through earlier Cenozoic time (Reed 1933), supported and permitted the differentiation of the California closed-cone pine flora (Mason 1934, Cain 1944). The trend of increasing dryness of climate continued through the Pliocene, though with fluctuations toward more humid climates during part of the epoch. Axelrod (1944c, 1944d, 1948) suggests climates which were more humid and warmer than at present in the lower, drier and warmer than at present in the middle, and cooler and moister than at present in the upper Pliocene.

Some of the floras of lower Pliocene (or upper Miocene) age are mesophytic and warm-temperate in character. Coastal plain vegetation of warm climate and moist situations is represented in central California (San Pablo or Neroly flora, Condit 1938, Axelrod 1944d), with forests including *Taxodium, Nyssa, Persea,* and *Magnolia.* The Remington Hill flora of the Sierra Nevada (Condit 1944a) and the Troutdale flora of the Columbia River Gorge (Chaney 1944a) include *Sequoia* and *Chamaecyparis,* together with deciduous and sclerophyllous broad-leaved trees. These are the last samples of forests of Arcto-Tertiary type in which *Sequoia, Chamaecyparis,* and other conifers, *Umbellularia* and other sclerophylls, are mixed with a diverse deciduous component including many genera now restricted to the eastern United States or eastern Asia. *Metasequoia* had apparently become extinct by the end of the Miocene (Chaney 1951). At lower elevations in the area of the Remington Hill flora, the Table Mountain flora (Condit 1944b) included more xerophytic woodland and chaparral forms. Eastward from these areas, forests of the interior are represented in floras of west-central Nevada (Axelrod 1956, 1957), and the Alvord Creek flora of southeastern Oregon (Axelrod 1944e). In the Nevada floras Sierra redwoods (*Sequoiadendron*) occurred with other conifers with modern equivalents in the Sierra Nevada and Klamath Region on cooler slopes, and chaparral on exposed slopes, in vegetation patterns dominated by oak woodlands (Axelrod 1956). At Alvord Creek montane forests of *Pseudotsuga, Abies* and *Pinus* on more mesic slopes gave way to woodland and chaparral forms on drier slopes. Vegetation patterns most nearly resembling this contact of an interior, montane derivative of the Arcto-Tertiary forest with Madro-Tertiary woodland occur now in the drier, eastern portion of the Klamath Region. The Alvord Creek flora suggests the increasing importance of conifers other than redwoods (*Pseudotsuga, Abies, Picea, Pinus*) which were to dominate the later forests of the interior. These and other lower Pliocene floras represent the latest occurrence over extensive areas of the West of forest types and vegetation patterns similar to those now existing in the Klamath Region and California Coast Ranges.

With increasing dryness of middle Pliocene and later time, the more strictly mesophytic forms of these forests were eliminated from most or all of the western states. Middle Pliocene Mulholland and Petaluma floras of west-central California, and the Oakdale from the central Sierra (Axelrod 1944a, Dorf 1933, Axelrod 1944b, 1944d) represent oak-woodland communities and reflect the expansion of Madro-Tertiary vegetation. The Deschutes and Alturas floras (Chaney 1938b, Axelrod 1944f) of northeastern California and eastern Oregon, with *Populus, Salix,* and other riparian forms of semi-arid climates, indicate the elimination of the mesophytic forests from the lowland interior east of the Cascades. Woodland, chaparral, grassland, and desert were spreading over much of the area formerly occupied by forest (Axelrod 1948, 1950c, 1958). Cooler and more humid climates of later Pliocene time are indicated by extension into west-central California of more mesophytic forests—the Sonoma, Wildcat, and Santa Clara floras (Dorf 1933, Axelrod 1944c, 1944d), in which *Sequoia* was present or dominant, together with sclerophyllous and deciduous trees.

The cooler and drier climates of the Pliocene, accompanied by and in part produced by rising mountain ranges along the Pacific Coast, effected the replacement of widespread Arcto-Tertiary forests by essentially modern vegetation patterns. The mesophytic redwood-mixed forests shrank from wide occurrence into a limited area of coastal California and southern Oregon. *Sequoia sempervirens* and *Chamaecyparis lawsoniana* have become wholly restricted to this area; the evergreen-broadleaf or sclerophyll component (*Umbellularia, Lithocarpus, Castanopsis, Arbutus,* and *Quercus* spp.) has become largely restricted to this same coastal belt and somewhat less humid climates inland from it. Deciduous components were even more strongly affected by increasingly dry summer climates. *Metasequoia* and many broad-leaved deciduous forms are extinct in the West; those that have survived have done so by restriction to the same areas of humid forests or to mountain forests, by restriction to valleys and the vicinity of water-courses in more arid regions, or by such adaptations to aridity as are indicated by smaller and thicker leaves (Chaney 1944b). As the range of the mesophytic forests decreased, that of the diverse Madro-Tertiary forms increased; and woodlands and other types of the less humid West spread as regional climaxes (Axelrod 1948, 1958). Floristic differentiation separated the vegetation of southern California from that of northern California (Axelrod 1937, 1950b). Floristic differentiation also separated the forests of the North Pacific Coast, and those of the Rocky Mountains and interior ranges, from those of the California coastal belt (Axelrod 1940a, 1948, 1950c, Mason 1947), although forms now of the North Coast and Rocky Mountains lived with the redwood-mixed forests in the California Coast Ranges into middle or upper Pliocene time (Axelrod 1944a, 1944c, 1948), and many of these forms are represented in the Klamath Region and Cascade Mountains today. Climatic and topographic changes combined to convert mesophytic forest patterns, which changed slowly across great distances of the West, into complex and strongly zoned patterns of many plant communities closely juxtaposed along steep climatic gradients of the mountains and valleys of the Pacific Coast states.

It is thought that during the Pliocene epoch the vegetation of the Klamath Mountains took on essentially its present character. Forests related to the present *Sequoia* and mixed evergreen forests have probably existed in this region, with changing distributional relations to elevation and topography, through most of Cenozoic time. But it is probably in middle Pliocene time that the *Sequoia* forests, which had occurred at

Ashland in the eastern Siskiyou Mountains in Oligocene time, became restricted to the coastal belt, while Madro-Tertiary woodland forms entered the Klamath Region from the south. Thus would result the major features of the modern pattern—coastal redwood forests, mixed evergreen forest in the central portion of the region, and oak woodland and other more xeric types toward its eastern limits.

California Pleistocene floras (Chaney & Mason 1930, 1933, Potbury 1932, Mason 1934) represent essentially modern vegetation types. Climates distinctly cooler than those of the present are indicated, however, by the Willow Creek and Carpinteria floras (Chaney & Mason 1930, 1933); forests corresponding to the former now occur 600 km. or more north along the coast from Santa Cruz Island. The extent to which Pleistocene climates were cooled and vegetation displaced south of the ice sheet in the eastern United States has been debated (Braun 1947, 1950, 1955, Potzger & Tharp 1947, Deevey 1949). The combination of fossil forest types well south of their present occurrence with glacial topography in the higher Klamath Mountains (Hershey 1900, Flint 1957) suggests substantial climatic effects accompanying glaciation in this area. Displacement of the northern limit of the *Sequoia* forest southward, and expansion of the montane forests into lower elevations at the expense of the mixed evergreen forests, are likely. Cooler climates would also displace species which had previously occurred farther north, southward into the Klamath Region. In warmer, post-glacial climates, these species could persist in the area by movement upward in the mountains, as well as northward. Detling (1954) has observed that the flora of Saddle Mountain in the Oregon Coast Range includes a number of boreal relicts resulting from this kind of displacement; a number of these have the present southern limits of their distributions at higher elevations in the Klamath Mountains. Other Klamath species have distributions suggesting that they are relicts from glacial time—notably *Chamaecyparis nootkatensis,* the known southern limit of which is represented by three isolated patches at high elevations in the Siskiyou Mountains, two reported by Mason (1941) and one found by the author on Preston Peak.

Retreat of the glaciers was followed by warmer and drier climates until the xerothermic period, about 4000–8000 years ago, which was drier and warmer than the present (Hansen 1947, Flint 1957). Effects of the drier climate were less evident near the coast than in the interior (Hansen 1947); but vegetational displacements the reverse of those during the glacial periods must have occurred in the Klamath area—with movement northward of the *Sequoia* forests and expansion of the mixed evergreen forests and still more xeric types relative to forests of more mesic situations and higher elevations. Expansion of chaparral over an extensive area of California and northward into the Klamath Region probably occurred also during drier climates of Pleistocene time (Axelrod 1937). Relicts of xerothermic vegetation occur on some peaks west of the Cascades in Oregon, in areas now dominated by mesophytic forests (Detling

1953). Comparable relicts, including some of the species listed by Detling, occur in the Klamath Region, especially on serpentine and other special parent materials and on drier mountain slopes in the eastern part of the region.

THE CENTRAL RELATION OF THE KLAMATH REGION

Major points on the origin of the Klamath vegetation pattern are indicated in the preceding account; they may be summarized: (1) The history of the western forests from Miocene time to the present has been one of progressive shrinkage toward the coast and higher elevations, accompanied by progressive differentiation in the different areas of the West. Within the Klamath Region, mixed forests of Arcto-Tertiary derivation were modified by extinction of the greater share of their tree species, especially among deciduous forms, and became restricted to more humid climates near the coast. (2) From the Arcto-Tertiary forests evolved also, with even more severe depletion of tree species, montane and subalpine forests adapted to environments which were cooler, or drier, or both than those in which the redwood and mixed evergreen forests occur. Higher elevations of the Klamath Region are occupied by montane and subalpine forests which are in large part similar in derivation and character to those of other western mountains, in part distinctive in occurrence of species (*Picea breweriana, Quercus sadleriana, Ribes marshalli,* etc.) endemic to the Klamath Region. (3) An extensive transition of communities belonging neither simply to Arcto- nor Madro-Tertiary floras has probably existed at least since early Tertiary time and has, with the evolution and differentiation of its own species and evolution of Arcto- and Madro-Tertiary species into and through it, differentiated into various communities occurring between forests and more xeric non-forest communities. The mixed evergreen forests and woodlands of the Klamath Region have probably such mixed derivation from Arcto- and Madro-Tertiary and intermediate floras. Among these communities there is a range of climatic variations and probable derivation, from more mesic types of mixed evergreen forests which are primarily of Arcto-Tertiary derivation, to more xeric pine-oak woodlands primarily of Madro-Tertiary derivation. (4) In reciprocal relation to the forest history, dry-adapted communities progressively expanded and differentiated in the Southwest and interior lowlands, communities predominantly of Madro-Tertiary derivation in the south but with increasing representation of forms of Arcto-Tertiary or other cooler-climate derivation toward the north. As part of this development, woodland, chaparral, and grassland communities spread in the drier inland environments of the Klamath Region.

The thesis has been developed by Braun (1935, 1938, 1947, 1950, p. 39, 1955) that the Mixed Mesophytic Association of the Appalachian Plateaux is the central, the oldest, and the most complex association of the Deciduous Forest Formation, that from the Mixed Mesophytic, or its ancestral progenitor, the mixed Tertiary forest, all other climaxes of the deciduous forest have arisen. The corresponding relation of the coastal redwood and mixed evergreen forests of the Klamath Region to the western forests is suggested, but a number of qualifications on too literal an interpretation of this relation should be observed. The Arcto-Tertiary forests were not "a community," but a vegetation pattern with marked regional differentiation in dominance and floristic composition, with differentiation also in relation to moisture gradients and presumably other local factors. Their species were variously distributed, and widespread species probably showed marked ecotypic differentiation then, as today (Axelrod 1941). Much of the West has been occupied by vegetation at all times; and the effect of climatic change was not to segregate different forest types from a single ancestral type, but to cause increasing local differentiation of forests that were already regionally differentiated in the Oligocene and Miocene. Many tree species and species-groups have been in existence through the whole of the Cenozoic (Stebbins 1950); and many of the trees of the West have some history of association with redwoods and the Arcto-Tertiary forests (Mason 1947). But the species and ecotypic populations that have evolved into the present have been variously associated with one another and total community floras variously derived from different sources, resulting from diverse patterns of evolution and migration in different species and species-complexes. In evolutionary time species change their patterns of ecotypic differentiation and association with other species; and the evolution of communities is reticulate, not simply divaricate (Mason 1936, 1947, Whittaker 1957). If the forests of the West are in part derived by differentiation from the redwood-mixed forests, they may also be derived in part from other coniferous forest communities whose history in the West—in higher elevations and drier situations in the mountains—may go back as far as that of the redwood-mixed forests. Resemblance of the coastal redwood and mixed evergreen forests to the earlier redwood-mixed forests does not imply that the former are in any very real sense ancestral to western forests in general. It implies only that, in the progressive shrinkage, species-extinction, and regional differentiation of the western forests from the Miocene to the present, the largest fraction of Arcto-Tertiary forms, representing all three tree growth-forms, survived in the most favorable climate—that of the Klamath Region and northern California Coast Ranges.

One reason for the "central" relation of the Klamath Region thus lies in geographic and climatic circumstance. It is in this region, as in the Southern Appalachians in the East, that a combination of sufficient humidity and warmth of climate occurs to support mesophytic, mixed forests which are most like Arcto-Tertiary forests among existing vegetation types. Location and climate of the Klamath Region, and the steep climatic gradient from the coast inland, are responsible also for much of the vegetational diversity of the region, and for the meeting there of plant communities of diverse climatic and geographic relations.

The notable floristic diversity of the region is also in part a consequence of edaphic diversity. Geological history has resulted in an unusually complex mosaic of parent materials, often with striking effects on vegetation and flora (Whittaker 1954, 1960). Parent material contrasts also contribute to the meeting of community-types and species of widely different geographic relations. Thus at low elevations in the central Siskiyou Mountains, *Chamaecyparis-Pseudotsuga* forests with deciduous and sclerophyll trees and Northwestern floristic affinities, and Jeffrey pine woodlands with *Libocedrus decurrens* and *Arctostaphylos viscida* and floristic affinities with the montane forests of the Sierra Nevada, occur in close proximity—but the former on diorite, the latter on serpentine. Many of the numerous species which reach their distributional limits in the Klamath Region occur there as localized, "relict" populations on serpentine, gabbro, or other special parent materials. Greatest numbers of narrowly endemic species occur on these same parent materials; other narrow endemics appear on more "normal" parent materials at high elevations and in other special situations. Concentrations of narrowly endemic species in the area are thus related to edaphic factors (cf. Mason 1946a, 1946b) and other environmental extremes (cf. Detling 1948a).

The Klamath Region thus shares characteristics with other centers of floristic diversity and narrow endemism—topographic complexity, edaphic diversity, and age of land surfaces. The diversity of habitats has been characteristic of the area throughout its long history, although climatic gradients were probably less steep before middle Pliocene time. Even at the maximum development of the Klamath peneplain, mountains of diverse parent materials existed in the area. The region has at all times offered a complex mosaic of habitats in which species of diverse environmental requirements might survive, while submergence, glaciation, climatic desiccation, and lava flows have affected surrounding areas. From the unlimited diversity of the present geographic and probable historic relations of species represented in the area, one may recognize such major groupings as: (1) widespread western species, and Sierra-Cascade species, which extend through the region; (2) formerly more widespread species which are now relict endemics or epibiotics in the region; (3) species of diverse present distributional relations which extend, from the south, the north and the interior, into communities in appropriate climates in the region, many of these species being at or near their limits of distribution there; (4) species of diverse distributional relations represented in the region by localized, "relict" populations on special parent materials, at higher elevations, or both; (5) narrowly endemic species of diverse origin, many of which may have evolved within the region to occupy some part of its complex mosaic of habitats.

The central relation of the Klamath Region is regarded primarily not as one of a center of origin for forests of other parts of the West, but as a center toward which mesophytic forests of the past have shrunk, and as a center of accumulation of species of varied evolutionary history in the diverse habitats of ancient land surfaces. This does not mean, however, that the area has not also been a center of origin of major significance for some groups of plants—a reservoir of species populations of diverse environmental adaptations and of genetic diversity within some species and species-complexes, from which populations have evolved and migrated into other areas. The genus *Crepis* provides an example (Babcock & Stebbins 1938), with a number of diploid species now relict in the Klamath area, while genetic material from these has been used in apomictic polyploids which have spread over semi-arid environments of the interior. The cytogenetics of *Crepis* further suggest that endemic species shared by the Klamath Region and the Tehaman area of the northern Sierra Nevada (Jepson 1923–25) have reached the latter from the Klamath Mountains (Babcock and Stebbins 1938).

It may be noted that the two aspects of the central relation of the Klamath Region discussed are to some extent separate phenomena. The central vegetational relation is a consequence of location and climate, primarily because of adjacency to the Coast; the concentration of species diversity and endemism is a consequence of climatic and edaphic diversity and age, primarily because of the mountains inland from the coastal belt. A series of criteria for centers were suggested by Adams (1902, 1909); but these are each subject to limitations and are to some extent independent of one another (Cain 1944). "Centers" are conceptual products of interpretation according to chosen criteria (Whittaker 1956). The Klamath Region is by no means the only center for forest vegetation and flora in the West. The Sierra Nevada is of comparable antiquity; this and other California ranges are rich in species, including narrow endemics. A center of maximum development of conifereous forests may be located in the Puget Sound area, and the center for the sclerophyll complex is well to the south of the Klamath Region. In the complex vegetational and floristic pattern of the West there may be no single area which has the same degree of "central" significance as the Southern Appalachians in the East. Yet, when these various allowances are made, it remains true that the Klamath Region possesses a central relation to other forest areas which is one of the significant features of the biogeography of the western United States.

SUMMARY

1. The Klamath Region of northwestern California and southwestern Oregon is an area of old and geologically complex mountains, supporting a complex vegetation pattern and a diverse flora rich in narrowly endemic species. The region is a floristic and vegetational "center" for the forests of the western United States.

2. Vegetation history of the Pacific Coast states since Miocene time has involved progressive shrinkage of Arcto-Tertiary forests and progressive expansion and differentiation of Madro-Tertiary communities. Mixed forests (coastal *Sequoia* and mixed evergreen forests) most nearly related to the Arcto-Tertiary forests in the West are now limited to the Klamath

Region and northern California Coast Ranges, while woodland, chaparral, and grassland communities primarily of Madro-Tertiary derivation have entered the Klamath Region from the south to form the more xeric part of its vegetation pattern.

3. Floristic diversity of the Klamath Region has resulted from climatic and parent-material diversity, together with age of the mountains which has permitted species of diverse histories and environmental relations to survive there, often as relicts restricted to special parent materials or situations.

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GERMINATION OF CEANOTHUS SEEDS[1]

Clarence R. Quick and Alice S. Quick

The many species of ceanothus in California are ecologically diverse, but they occur most frequently and most abundantly on relatively arid sites and where repeated wildfire has been a determinant of vegetative composition. Because of prompt and abundant seedling regeneration after fire (Quick, 1959) and because many or all ceanothus species have nitrogen-fixing nodules on their roots (Quick, 1944), the genus is an important factor in development and conservation of high-quality soil profiles under wildland vegetation. In order to survive fire, seeds "stored" in duff and topsoil must lie in relatively well-insulated positions and be quite obdurate to heat (Quick, 1956).

Most ceanothus seeds will not imbibe water and "plump" in the laboratory unless they are first subjected to some type of heat treatment (Quick, 1935), or to seed-coat scarification. Unplumped seeds cannot germinate because they are dry. Seeds of montane species of ceanothus commonly will not germinate, even if thoroughly plumped, unless an embryo dormancy has been obviated by appropriate stratification treatment; i.e., by continuously-moist aerated storage for some weeks at temperatures slightly above freezing. The present paper reports data from experiments aimed

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[1] Facilities for seed storage and culture, stratification and germination were made available by the California Forest and Range Experiment Station, United States Forest Service, in cooperation with the University of California at Berkeley.

TABLE I. EFFECTS OF "STEEP" TYPE HOT-WATER TREATMENT ON GERMINATION OF DEERBRUSH (CEANOTHUS INTEGERRIMUS) SEED

Water temperature degrees C.[1]	Seed sample, weeks stratified at 2.2° C., and age of seeds (years) when cultured. Percent of 40 seeds germinating			
	Q-015 14 2	Q-018 12 ½	Q-018 15 1	Q-087 14 2
70	----	77.5	72.5	----
75	----	77.5	50.0	----
80	72.5	47.5	75.0	100.0
82.5	----	----	60.0	----
85	85.0	87.5	95.0	92.5
87.5	----	----	87.5	----
90	70.0	70.0	67.5	87.5
95	----	70.0	85.0	----
Mean	75.8	71.7	74.1	93.3

[1] Temperature of one liter of water in container at start of "steep" treatment.

at defining optimum laboratory methods for inducing germination of seeds of snowbrush (*Ceanothus cordulatus* Kell.) and deerbrush (*C. integerrimus* H. & A.)[2] Records of seed longevity of these and other ceanothus species are reported also.

The two separate requirements for germination of ceanothus seed of montane species, plumping followed by stratification, are equally important in that either treatment alone is ineffective. Stratification as a prerequisite to germination of seeds of wildland plants is much more frequently encountered than need for special treatment to obviate seed-coat impermeability. However, because seeds must be plumped before they can be conditioned for germination by stratification, methods of plumping will be considered first.

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[2] SEED SAMPLES. Seeds used in the experiments were collected from vigorous plants when fruits were fully mature. Collections were thoroughly air dried. Seeds were then extracted from pods by rubbing as gently as possible between two pieces of board. Seeds were sieved, winnowed, recleaned, desiccated over calcium chloride, placed in air tight containers, and stored at 2.2°C. (36°F.).

Collection data for seed lots of *Ceanothus cordulatus* Kell. follow: *Q–155*, August 1937, South Fork Stanislaus River, at ca. 4800 ft. altitude. *Q–156*, August 1937, southwest of Cow Creek Guard Station, Stanislaus National Forest, at ca. 5800 feet altitude. *Q–239*, September 1940, Stinchfield Place, west of Pinecrest, Stanislaus National Forest, at ca. 5500 feet altitude.

Collection data for seed lots of *Ceanothus integerrimus* H. & A. follow: *Q–015*, collected September 1934, same locality as *Q–155*. *Q–018*, July 1935, roadside, state highway 49, south of Grass Valley, Nevada County, at ca. 2500 feet altitude. *Q–026*, August 1931, same locality as *Q–155*. *Q–087*, September 1934, sub-sample of *Q–015* which passed 12-mesh sieve. *Q–113*, September 1936, same locality as *Q–239*. *Q–158*, October 1937, southeast of Cow Creek Guard Station, Stanislaus National Forest, at ca. 6300 feet altitude.

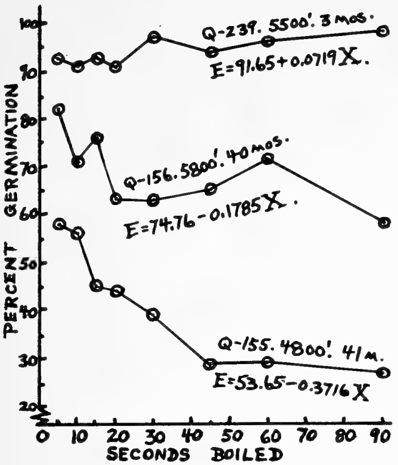

FIG. 1. Boiling water and germination of snowbrush (*Ceanothus cordulatus*) seeds. (Seed collection number, altitude of collection, and age of seed in months.)

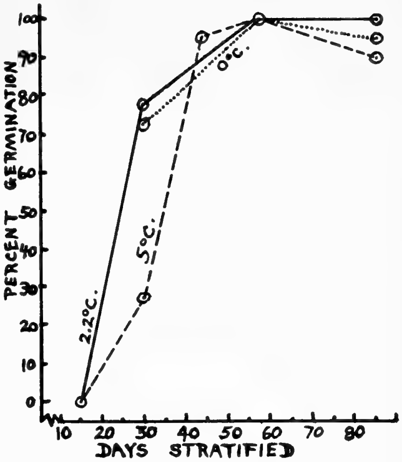

FIG. 2. Temperature of stratification and germination of deerbrush (*Ceanothus integerrimus*) seeds, sample Q–018. (Seeds were placed in 1 liter of water at 85°C. [185°F.] and allowed to cool to room temperature before culturing.)

HOT WATER TREATMENT

Two convenient methods of treating seeds with hot water to increase seed-coat permeability have frequently been used. In the "steep" method, seeds are tossed into a measured volume of water at a given temperature and left in the water until cooled to room temperature. In the boiling-water treatment, seeds are vigorously boiled in water (212°F.) for a given length of time. After the allotted period of boiling, the seeds are soused in an excess of cold water and then cultured.

Table 1 reports results of treating four lots of deerbrush seeds in hot water by the steep method. The volume of water in all tests of this series was one liter (1.06 quarts). Temperature at start of treatment varied from 70°C. (158°F.) to 95°C. (203°F.). All cultures were of 40 seeds, and all were stratified at 2.2°C. (36°F.) after the hot-water treatment. The steep treatment obviously is satisfactory for removing impermeability of deerbrush seed-coats.

Boiling water also will condition ceanothus seeds for successful stratification and germination (Quick, 1935). A treatment somewhere between a few seconds and perhaps 10 minutes might be expected to be the optimum period in boiling water. This optimum treatment could be expected to vary with different species, and with differences in maturity, age, and condition of seed of a single species.

Figure 1 presents data resulting from treatment of three samples of snowbrush seed (*C. cordulatus*) in boiling water. The objective was to determine if optimal treatment with boiling water lay between 5 and 90

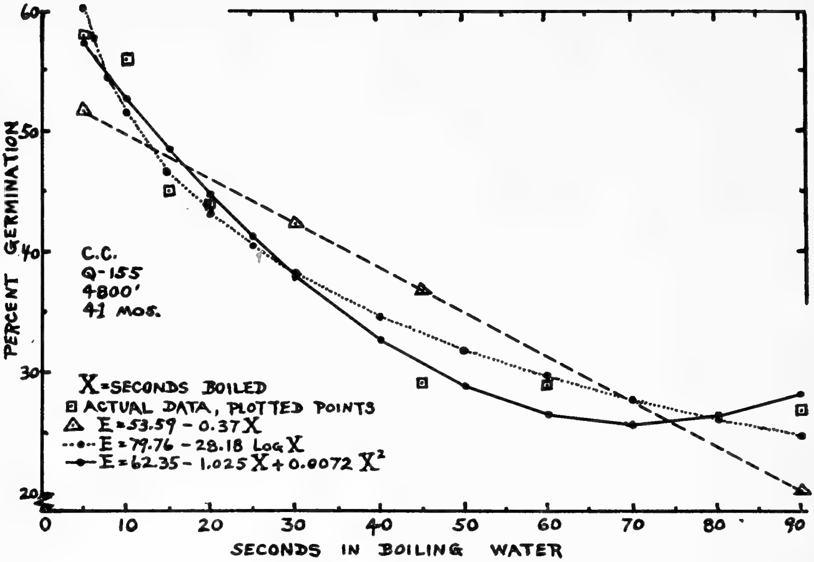

FIG. 3. Statistical generalization of germination data from snowbrush (*Ceanothus cordulatus*) seeds boiled in water, showing curves for straight-line regression, logarithmic regression, and multiple regression. (Seed collection Q–155, 4800 feet altitude, age 41 months.)

seconds. Each culture consisted of 100 seeds. Seeds were treated in Berkeley at an altitude of about 125 feet by tossing them into vigorously boiling tapwater and by pouring the boiling water and the seeds into excess cold water at the end of treatment. Seeds were planted in autoclaved river sand, left at room temperature a few days to plump, then stratified at 2.2°C. for 94 days, and finally germinated in the greenhouse for 5 weeks.

No obvious optima appear on the graphs of figure 1. The best period of treatment in boiling water for sample Q–239 at time of testing may have been more than 90 seconds. In contrast, the other two lots appeared to have very short optimal periods of boiling.

Some tests on deerbrush seeds (*C. integerrimus*) indicate that very short periods of boiling will condition only part of the seeds of a sample for germination. For example, seeds of collection Q–087 (age 26 months) were boiled for various short periods. Final germination was as follows: boiled 4 seconds, 20% germination; 8 seconds, 78%; 16 seconds, 63%; 32 seconds, 68%; and 64 seconds, 73% germination. The four-second treatment obviously was too short to be effective on the majority of seeds of this two-year-old collection. Likewise seeds of sample Q–026 at age of 28 months were boiled for short periods, stratified at 2.2°C. for 102 days, and germinated in the greenhouse. Germination follows: boiled 30 seconds, 60% germination; 1 minute, 76%; and 2 minutes, 64% germination. Most lots of snowbrush seed seem to be adequately treated by shorter periods of boiling than deerbrush seeds. No very short and obvi-

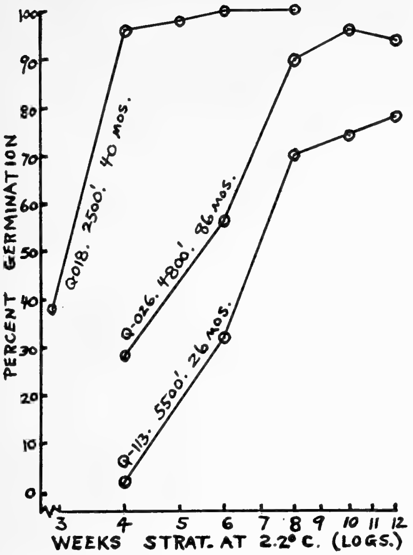

Fig. 4. Length of stratification and germination of deerbrush (*Ceanothus integerrimus*) seeds. (Seed collection number, altitude of collection, and seed age in months.)

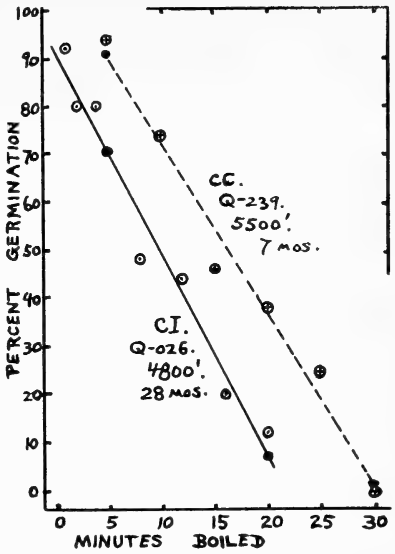

Fig. 5. Germination of ceanothus seeds after long boiling in water. (Species of ceanothus, seed collection number, altitude of collection, and age of seed in months.)

ously inadequate treatments of snowbrush seeds with boiling water, such as described above for deerbrush seeds, have been observed.

Statistical Generalization

When small lots of ceanothus seeds of a single sample are boiled for various short periods, then stratified and germinated, a graph of results commonly appears to fit a curve rather than a straight line (fig. 1). From theoretical considerations of the effects of boiling water on horny seed coats, an exponential scale on the time axis of a graph would be expected to fit the data better than an arithmetic scale. This generalization can be conveniently handled in linear regression analysis by using logarithms of time units rather than time units as such (Snedecor, 1938, pp. 308–312). Another common method of "fitting" a curve is to add, as a second variable, the square of the independent variable—in this case the square of the time units (Snedecor, 1938, pp. 313–316).

Figure 3 graphs data resulting from eight cultures of boiled snowbrush seed. Plotted first in this figure is the straight-line regression in which time of boiling is handled arithmetically as number of seconds. Also on the graph is a logarithmic regression, computed by linear regression methods, in which time (the independent variable) was the common logarithm of seconds boiled. The third line on the graph is the multiple regression curve in which two time variables, (1) seconds boiled, and (2) square of seconds boiled, were used.

The straight-line equation appears to be an oversimplification of the data involved. The multiple regression equation in which the square of seconds boiled was added as a separate variable is not a valid generalization because it predicts a minimum germination percentage at about 70 seconds of boiling and a steadily rising germination percentage after 70 seconds. The logarithmic transformation appears to be the best generalization of the three presented and will be used hereafter whenever a straight-line relationship is not considered adequate.

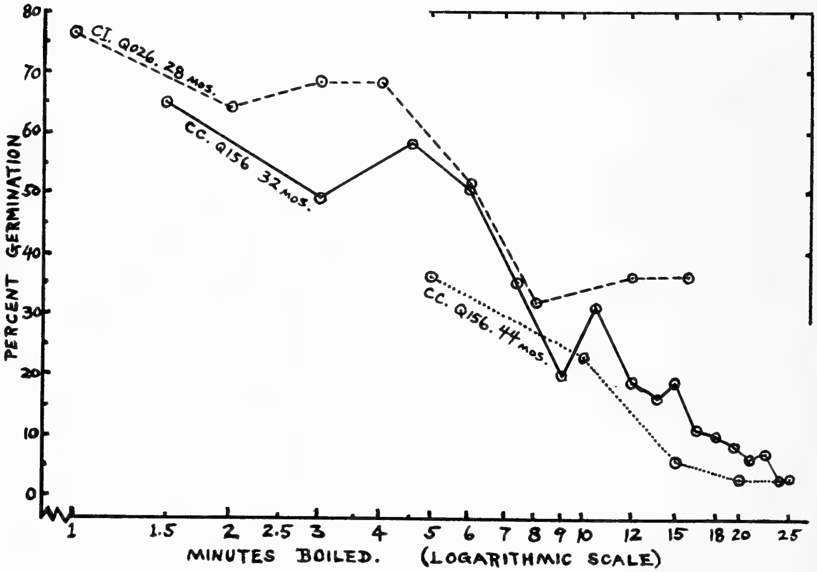

Fig. 6. Additional tests on long-boiled ceanothus seeds. (Species of ceanothus, seed collection number, and age of seed in months.)

Stratification Time and Temperature

A reasonably effective temperature and period of stratification must be known before conclusions about effects of other variables in germination of ceanothus seed can be considered precise. Work reported by Quick (1935) indicates one treatment (2.2°C. for 3 months) that seems generally effective, but offers no comparison with other time-and-temperature combinations. Figure 2 reports results of a series of stratification tests on deerbrush seed of sample Q–018. Obviously any one of three stratification temperatures will satisfactorily condition water-permeable deerbrush seed of this lot for germination. Other experiments have shown that snowbrush seeds react similarly, but commonly are best stratified at 2.2°C. or 0°C. rather than at 5°C.

Differing severities of hot-water treatment might conceivably change the time-and-temperature reactions of ceanothus seeds to subsequent

TABLE 2. GERMINATION OF OLD CEANOTHUS SEEDS

Seed Collection No. (Quick)	Species of *Ceanothus*	Approximate Collection Altitude, Feet	Seed Age, Years and months	Seeds per culture	Seeds Boiled, Seconds	Stratification, Days	Germination, Percent
014	*C. arboreus* Greene[1,2]	225	20-5	50	6	none	38
370	*C. arcuatus* McMinn	6000	9-5	50	20	90	66
155	*C. cordulatus* Kell.	4800	15-4	100	10	108	71
156	" " "	5800	15-4	100	10	108	87
239	" " "	5500	12-3	100	10	108	90
317	" " "	5800	13-4	100	20	90	81
318	" " "	6600	13-3	100	20	90	86
056	*C. cuneatus* (Hook.) Nutt.	2700	17-5	100	10	98	98
024	*C. divaricatus* Nutt.	----	19-6	100	5	108	46
183	*C. impressus* Trel.[1]	400	17-7	25	5	none	88
026	*C. integerrimus* H. & A.	4800	24-4	100	20	90	90
015	" " "	4800	21-3	100	20	90	100
087	" " "	4800	21-3	100	20	90	93
018	" " "	2500	20-5	100	20	90	93
158	" " "	6300	15-3	100	10	108	98
238	" " "	5500	12-3	100	10	108	97
057	*C. lemmoni* Parry	2700	17-5	100	10	108	96
247	*C. prostratus* Benth.	5800	12-5	80	10	108	100
028	*C. sorediatus* H. & A.[3]	750	22-1	100	10	73	85
017	" " "	800	17-5	100	10	86	96
025	*C. spinosus* Nutt.[2]	250	19-4	66	5	108	93
246	*C. velutinus* Dougl.	4300	12-4	100	10	108	92

[1] *C. arboreus* and *C. impressus* not stratified prior to germination.

[2] Seeds from landscape planting.

[3] *C. sorediatus* stratified at 5°C. (41°F.), all other species at 2.2°C. (36°F.).

stratification. However, two series of cultures of deerbrush seed, sample Q–018, one of seeds boiled for 20 seconds and the other for 70 seconds, reacted the same to stratification, insofar as could be told from inspection of the data.

Quick (1935) found that requirements for optimal stratification of ceanothus seed apparently varied among the species in relation to the altitude at which the species commonly grew. Results from series cultures of three collections of deerbrush seeds from different altitudes are summarized in figure 4. Deerbrush seeds from lower altitudes appear to respond progressively to shorter periods of stratification.

TOLERANCE TO BOILING WATER

Immersion in boiling water for 10 to 20, or perhaps 30 seconds will satisfactorily condition most ceanothus seeds for germination, if subsequently the seeds are adequately stratified. The limit of tolerance of both deerbrush and snowbrush seeds to boiling water was tested in Berkeley by individually boiling subsamples from 1 to 20 or 30 minutes. Figure 5 graphs the results from long-boiling treatments on one lot of deerbrush seed, Q–026, and one of snowbrush seed, Q–239.

The regression equation for the deerbrush series of treatments is $E = 91.64 - 4.214X$ ($r = 0.982$), where X is simply minutes boiled. This equation predicts that on the average 4.2 percent of germination is lost for each minute the seeds of lot Q–026 are boiled. The corresponding equation for the snowbrush series is $E = 108.67 - 3.571X$ ($r = 0.989$). The regression line for deerbrush seeds crosses the time axis—zero germination—at 21.75 minutes, and for snowbrush seeds at 30.43 minutes! These two tests indicate that snowbrush seeds may be more resistant to boiling water than deerbrush seeds. Additional tests of resistance to boiling water were made. Results are presented in figure 6.

It is amazing that ceanothus seeds can stand such prolonged periods of boiling. The seed coats presumably exclude water from the seed proper; the embryo and endosperm are in effect subjected to dry heat for the period of the boiling. It is unknown whether death of over-boiled seeds is due to the effects of dry heat on embryo or endosperm or to the final penetration of boiling water or steam through the seed coats. Effects of dry heat on seeds from which coats have been removed have not been determined.

SEED LONGEVITY

In an ecological sense many ceanothus species are pioneer plants and therefore might be suspected of having durable, long-lived seeds. Seeds of some species are known to be generally distributed in the duff and soil of Sierra Nevada forests (Quick, 1956). Actual germination tests of old ceanothus seeds would be of some ecologic interest. Table 2 presents a few records of longevity for seeds of known age.

Many factors may condition results of germination tests on old seeds, and high levels of consistency between species and collections, ages and individual tests are not necessarily expected. Additional tests will be required to define maximum seed life under the pertinent conditions of seed collection, handling and storage. The reported data, however, confirm the fact that seeds of many ceanothus species are long-lived.

Berkeley, California

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NOTES AND NEWS

THE DISCOVERY OF THE LICHEN PARMELIOPSIS PLACORODIA IN WESTERN NORTH AMERICA.—The foliose lichen *Parmeliopsis placorodia* (Ach.) Nyl. is a locally common epiphyte of pine in the eastern United States. Six years ago I presented a map of its distribution from a study of materials from many herbaria. The species was found in twelve states from Maine to North Carolina and northwestward to Michigan and Wisconsin (Culberson, Revue Bryol. Lichénol. 24:334–337. 1955). Many new localities in the eastern states have since been found, most of them by Dr. Mason E. Hale. These new localities, including those in West Virginia and Kentucky (specimens at US) where the species had not before been recorded, fall within the previously delimited range.

In a current study of some *Parmelia* specimens from various herbaria, I found a misidentified specimen of *Parmeliopsis placorodia* from Arizona. It was collected in 1946 by Dr. R. A. Darrow, but it was not determined by him. Dr. Hale then sent me a 1957 collection from Arizona by Dr. W. A. Weber and Dr. S. Shushan. In the spring of 1959, in correspondence about these western specimens, Dr. Weber wrote that he and Dr. Shushan had just found the species in Colorado and sent a sample; later his student, Mr. R. A. Anderson, also sent me material from South Dakota. The known western localities for *P. placorodia* are then:

ARIZONA. Santa Cruz County: Santa Rita Mountains, 8,600 feet elevation, *Darrow 4351* (Darrow Herbarium, College Station, Texas; WIS). Cochise County: Chiricahua Mountains west of Portal, 8,500–10,000 feet elevation, *Weber* & *Shushan S8980* (US). COLORADO. Boulder County: Boulder Canyon, north slope, 8,000 feet elevation, *Weber* & *Shushan S17,954* (COLO). SOUTH DAKOTA. Lawrence County: Black Hills, vicinity of Roubaix Lake, 5,450 feet elevation, *Anderson S20,941* (DUKE). Pennington County: Black Hills, Rockerville Camp Ground, 4,000 feet elevation, *Anderson S20,893* (DUKE).

The habit of the western specimens, all with apothecia, is identical to that of specimens from the eastern states. The western specimens also contain the depside thamnolic acid identified in microchemical analysis by the presence of typical crystals of the aniline condensation product.

In the five new localities, the species was collected on the bark of *Pinus ponderosa* Laws. *sensu lat.* (including var. *arizonica*). All known epiphytic specimens from the eastern United States are likewise from pines, but the species also occurs on old fence rails in some places in New England. In the East, *Parmeliopsis placorodia* habitually grows with *Cetraria fendleri* (Nyl.) Tuck., another North American lichen of ecologic amplitude very similar to that of *Parmeliopsis placorodia. Cetraria fendleri*, however, has been known for some seventy years from pine and "dead wood" in New Mexico and Colorado. Although in the eastern states *C. fendleri* may be somewhat more broadly distributed than *Parmeliopsis placorodia*, the high ecologic similarity and doubtless the similar distributional history of the two species seem to be borne out by the western finds reported here. WILLIAM L. CULBERSON, Department of Botany, Duke University, Durham, North Carolina.

OBSERVATIONS ON ARCEUTHOBIUM VAGINATUM IN MEXICO.—The dwarfmistletoe *Arceuthobium vaginatum* (Willd.) Presl is a common parasite of pines in Guatemala, Mexico, and the southwestern and central Rocky Mountain areas of the United States. The taxonomic status of the parasite, particularly in the southern parts of its range, is unsettled. Gill (Conn. Acad. Arts & Sci. Trans. 32:111–245. 1935) designated a northern form on *Pinus ponderosa* var. *scopulorum* Engelm. as *Arceuthobium vaginatum* forma *cryptopodum* (Engelm.) Gill. Gill did not subdivide *A. vaginatum* as it occurs in Mexico, but listed it on *Abies religiosa* Schl. and Cham., *Pinus leiophylla* Schl. and Cham., and *P. hartwegii* Lindl. Sosa (Bol. Dept. Forest. y Caza y Pesca [Mexico] 4:123–156. 1939) recorded this parasite on *Pinus montezumae* Lamb. as did Kuijt (Bot. Rev. 21:569–626. 1955) for *P. tenuifolia* Benth. Gill (loc. cit.) also noted the predominantly Mexican form of *A. vaginatum* on *Pinus engelmannii* Carr., *P. leiophylla* var. *chihuahuana* (Engelm.) Shaw, and *P. ponderosa* var. *arizonica* (Engelm.) Shaw in southern Arizona and southern New Mexico. To this list of hosts may be added *P. pseudostrobus* Lindl., which was parasitized by *A. vaginatum* (*Hawksworth 51*; March 10, 1956) in Atzimba National Park between Zitacuaro and Morelia in the State of Michoacan, Mexico. This parasite probably occurs on other Mexican pines as there are several reports of it in the literature that do not classify the host species of *Pinus*.

Arceuthobium vaginatum is common on *Pinus montezumae* (*Hawksworth 49*; March 10, 1956) along Highway 15 between Toluca and Zitacuaro in the State of Mexico. No infection was seen on *P. leiophylla* in the stands examined, although this tree was closely intermixed with infected *P. montezumae*. *Pinus leiophylla* is attacked by *A. vaginatum* elsewhere in Mexico so this suggests the possibility of rather specific host preferences among races of this parasite, as was reported by Gill (loc. cit.) for *A. campylopodum* in Western North America.

In central Mexico *Arceuthobium vaginatum* is a robust plant with shoots frequently more than thirty centimeters high. In Arizona and New Mexico, shoots of *A. vaginaum* f. *cryptopodum* rarely exceed twenty certimeters in length. An additional differences is that witches' brooms caused by the dwarfmistletoe are not nearly as conspicuous in Mexican pines as in *Pinus ponderosa* var. *scopulorum* in the southwestern United States.

The biology and taxonomy of the dwarfmistletoes of Mexican conifers are poorly known and present a challenging opportunity for critical study.—FRANK G. HAWKSWORTH, Rocky Mountain Forest and Range Experiment Station, U. S. Forest Service, Fort Collins, Colorado.

ADDITIONS TO THE AQUATIC FLORA OF ARIZONA.—The aquatic flowering plants of Arizona have not been adequately studied, consequently it is not surprising to find species previously unreported for the state in such habitats. The following three new records were obtained during the summer of 1958 while the junior author assisted with collecting for the herbarium of the Museum of Northern Arizona (MNA); the fourth was sent by the collector to the University of Arizona for identification.

ELATINE CALIFORNICA Gray (*Hevly* s.n., 17 August 1958, MNA) and *Limosella aquatica* Sesse & Mocino (*Hevly* s.n., 17 August 1958, ARIZ, MNA) occur in White Horse Lake south of Williams, Coconino County, altitude 6500 feet. This lake was created by the relatively recent damming of a tributary to Sycamore Creek; it is suggested that migratory birds making use of this new environmental area may have introduced these species.

POTAMOGETON RICHARDSONII (Benn.) Rydb. was collected at Wheatfields Lake, Apache County, on the Arizona-New Mexico boundary (*Hevly, Haskell* and *Deaver* s.n., 23 July 1958, ARIZ, MNA). The introduction of this species might also be attributed to migratory birds.

TYPHA ANGUSTIFOLIA L. was collected south of Yuma in the marshes along the Colorado River, Yuma County (*D. Tuttle* s.n., 14 September 1959, ARIZ). Both *T. latifolia* L. and *T. domingensis* Pers. also occur in the Arizona flora.—CHARLES T. MASON, JR. and RICHARD H. HEVLY, University of Arizona, Tucson, Arizona.

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CLATHRACEAE IN CALIFORNIA

WM. BRIDGE COOKE AND GEORGE NYLAND

Although the Phallales are found mainly in tropical regions there are a few representatives known from temperate areas. Of the two families comprising this order of fungi, the Phallaceae are better represented in the north temperate zone than are the Clathraceae. Nevertheless, many collections have been reported in the United States of some members of the latter family.

The literature on those clathraceous fungi which have been collected in North America is very scattered. In eastern North America, Burt (1894) described *Anthurus borealis* from material collected in New England, and Murrill (1912) added a report, illustrated with a colored plate, of a collection of this species from Blackwell's Island, New York. It is possible that Burt's species and Murrill's record were based on imported material since it has been shown that *Anthurus borealis* Burt is a synonym of *Lysurus sulcatus* (Cooke & Massee) G. H. Cunningham, a species usually found in Australia. *Lysurus texensis* Ellis appeared as a *nomen nudum* in a casual collector's report (Gerard, 1880), and Long (1917) later published a description of another collection from Texas which he provisionally assigned to *L. texensis* Ellis. Lloyd's Synopsis (1909) has not been very useful for North American workers. It is a compilation in which several species are described briefly and illustrated, sometimes poorly; some of these descriptions may prove to represent the same taxon. In "The Genera of Fungi" by Clements and Shear (1931), both *Anthurus* and *Lysurus* are illustrated, the classic illustration of *Lysurus mokusin* credited to Cibot being copied there. Likewise, this illustration is used by Gäumann and Dodge (1928) but credited to "Cibot and Fischer" rather than to "Cibot in Fischer." Coker and Couch (1928) present a description of *Anthurus* and cite the above-mentioned illustrations.

The structure and development of the fruiting body of *Anthurus borealis* were described in considerable detail both by Burt in 1894 and by White in 1944. White referred the material that he studied to *Lysurus sulcatus*. A summary of these two studies was made by Rea and Heidenhain (1955) and a comparison of the characteristics of this species with those of *Lysurus mokusin* was made. This publication, based on the extensive observations made by Rea on specimens from Santa Barbara, California, of *Lysurus mokusin* (Cibot ex Pers.) Fries, represents the first detailed study of material collected in the western part of the United States.

Following his retirement from the directorship of the Santa Barbara Natural History Museum, Paul Marshall Rea devoted much time to

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mycological studies in the Santa Barbara area. His collections and notes are deposited in the Herbarium of the University of Michigan, Ann Arbor, where, through the courtesy of Dr. A. H. Smith, the senior author had the opportunity of studying Dr. Rea's collections of phalloid fungi. Dr. Rea noted the first specimens of *Lysurus mokusin* in Santa Barbara in March, 1941. From that time until the end of his collecting activities he acquired, through his own efforts and those of his neighbors, no less than 130 collections of this species from the Santa Barbara region.

The present paper has grown out of a study of recent collections of clathraceous fungi which appeared in Bermuda grass [*Cynodon dactylon* (L.) Pers.] lawns in Fresno, Yolo, and Sacramento counties, California, particularly after the areas had received an excess of irrigation water. For making available to us the specimens collected in their area, we wish to thank John Bartels, Agricultural Commissioner's Office, Woodland, California, and K. A. Kimble and H. A. McCain, Department of Plant Pathology, University of California at Davis.

The family Clathraceae includes those phalloid fungi (stinkhorns) whose receptacles are stipitate or sessile, clathrate, columnar, or divided into several arms, and whose mucilaginous spore mass is borne on the interior or exterior of the arms or between the arms. In 1931 Cunningham divided the family into three tribes containing eleven genera. The tribe Stellateae, the only one with which we are concerned in California, included the following four genera as keyed out by him:

Arms apically organically united or united by a membrane.
  Glebiferous layer composed of irregular pseudoparenchymatous processes . . . *Mycopharus*
  Glebiferous layer consisting of walls of the chambers of the arms . . *Anthurus*
Arms apically free, connivent or expanded.
  Arms connivent (usually), attached to the apex of a simple cylindrical (or fluted) stem . . . . *Lysurus*
  Arms attached laterally to a horizontal discoid expansion of the apex of the cylindrical stem . . . . *Aseroë*

The other seven genera of Clathraceae were placed in the tribes Columnateae and Clathrateae. In a later treatment, Cunningham (1942) placed *Mycopharus* in synonymy with *Lysurus*; the same organization into tribes was retained. Fischer (1933) recognized fifteen genera in the Clathraceae, but he did not arrange them into tribes. He recognized the four genera listed in the key above, as well as *Pseudocolus*, which Cunningham considered to be a synonym of *Anthurus*.

Mycopharus was established by Petch as a segregate from *Lysurus* in which the glebiferous surface of the receptacular arms is formed of a series of minute shingle-like plates in contrast with that of *Lysurus* in which this surface is merely strongly wrinkled longitudinally, possibly as a result of the compact arrangement of the walls of the stipe chambers in this portion of the receptacle. In 1931 Cunningham accepted this basis for differentiation, but in 1942 he reverted to the earlier position that the two genera were synonymous. In this report Cunningham's 1931 interpretation is being followed and the two genera are considered distinct.

With the exception of some of the Santa Barbara material, which exhibits characters similar in many respects to those of *Mycopharus*, the California specimens studied to date appear to belong in *Lysurus*.

LYSURUS Fr. Syst. Myc. 2: 286. 1822.

Phallus Pers., Syn. Meth. Fung. 245. 1801. *pro min. parte.*

Aseroephallus Lepr. & Mont., Ann. Sci. Nat., Bot. III, 4: 360. 1845.

Anthurus sensu Burt, Mem. Bost. Soc. Nat. Hist. 3: 504. 1894.

Clathraceae; with an egg-like membranous volva; receptacle composed of a glebiferous surface raised on a hollow cylindrical or fluted stipe; stipe white or tinted near the receptacular arms; receptacular arms seated at the top of the stipe, of a more compact tissue, divided into 4–7 arms, arms separate or organically united, grooved on the outside, rounded toward the inside, longitudinally wrinkled, not continuous in the center with the hollow portion of the stipe, covered on the rounded inner glebiferous surface with the ill-smelling gleba.

Type. *Lysurus mokusin* (Cibot ex Pers.) Fr.—only species described in original publication of genus.

KEY TO CALIFORNIA SPECIES OF LYSURUS

Stipe weakly to strongly angular-fluted, upper area red . . . . . *L. mokusin*
Stipe cylindrical, upper area brown . . . . *L. sulcatus*

LYSURUS MOKUSIN (Cibot ex Pers.) Fries, Syst. Myc. 2:286. 1822. Figs. 1, 2. *Phallus mokusin* Cibot, Nov. Comm. Petrop. 19:373–378, t. 5. 1775. *P. mokusin* Cibot ex Pers., Syn. Meth. Fung. 245. 1801. *Mutinus pentagonus* Bailey, Queensland Bot. Bull. 10:35. 1895. *Lysurus beauvaisii* Möll., Rev. Gen. Bot. 12:61. 1900. *Mutinus pentagonus* var. *hardyi* Bailey, Queensland Agr. Jour. 16:494. 1906. *M. hardyi* Bailey, Comp. Cat. Queensland Pl. 747. 1910. *Lysurus sinensis* Lloyd, Myc. Notes 5: 718. 1917.

Peridium white, 3–6 (–11) cm. long, with white rhizomorphs at base; receptacle 6.5–7.5 cm. long to apex of usually connivent arms; stipe 5 cm. long, 4–7 mm. in diameter, narrow at base and expanding upward, white to orange-pink below, dark orange-pink to reddish above, internally divided into hollow chambers, fluted, the flutings 2–3 mm. deep, continuing above into midribs of receptacular arms; receptacular arms 4–6, 1.5–2 cm. long, red, the texture similar to that of stipe, but wrinkled and more compact, the tips of arms pointed; gleba brownish in color, becoming purplish-black when dry; spores hyaline to pale yellowish, rod-shaped, somewhat rounded at ends, (3.8–) 4.5–5 × (1.2–) 1.5–2.0μ.

California collections examined.

In Bermuda grass [*Cynodon dactylon* (L.) Pers.] lawn, Fresno, Fresno County, summer, 1952 (DAV). The stipe in this specimen is hollow, 5 cm. long, 4 mm. in diameter at the base and expanding upward, and pentagonal in cross-section, with the surface flutings 1 cm. from tip to tip of the adjoining pairs. The arms are five in number.

In loam in flowerbed at edge of lawn, Bakersfield, Kern County, April 11 and 22, 1936, *Mrs. A. Ashley* and *Mrs. F. Hamlin* (UC 553876), The collectors thought the fungus might have been introduced from Maine with some cultivated plants. When first picked, the stipe in the later collection was orange above, cream below, and the volva was white; a few days later, the stipe had become entirely orange, the arms red, and the glebal mass madder. The odor was described as that of "acetum squill." Too rapid development because of artificial watering caused cracking and abnormalities. Receptacles with both five and six arms are represented in the collection. In more robust specimens, the receptacular arms may be capped by a portion of the volva. The stipes are made up of at least two, possibly three, layers of chambers.

In lawn, Cajon Street, Redlands, San Bernardino County, May, 1944, *G. J. Hollenberg* (UC 695849). When fresh its color was described as pale pinkish. The specimen is evidently immature; the spores measure 3.8 × 1.2µ, and the stipe (the specimen was collected without the peridium) measures 4 cm. in length and 6 mm. in diameter at the top in the dry condition.

The collection of a specimen in Sacramento late in 1956 is represented only by a colored illustration (fig. 1) made by Norma O'Neil of Sacramento. This illustration, which was sent by the Agricultural Extension Office in Sacramento to the University of California at Davis for determination, clearly represents a sporophore of this species. No herbarium specimen is available.

In garden, Santa Barbara, Santa Barbara County, November 18, 1936, *Miss Caroline Hazard* (UC 568835). Upon the arrival of the specimens at Berkeley, Mrs. Vera M. Miller observed that the stipe was not white anywhere, but pinkish throughout, shading down from a color somewhat lighter than that of the arms to an Ibis pink (Maerz and Paul, 1950, Pl. 1, B–10) where the stipe went into the volva, to a very delicate pink at the lower end of the stipe. The stipe is coarsely chambered above, acuminate below, bearing apically the receptacular arms which were united at their tips. One of the receptacles in the collection bears four arms, while the other has six arms. The glebiferous layer is wrinkled and continuous over the unfused area of the arms and the base of the arms above the stipe. The collector reported that when a hot day was followed by a cool night, the texture of the specimens was crisp, while a cool day followed by a cool night resulted in limp receptacles.

In gardens, Santa Barbara, Santa Barbara County, at least 130 collections made between 1941 and 1952 or later by Dr. P. M. Rea or Mrs. Rea or by residents who gave the specimens to Dr. and Mrs. Rea, the collections all deposited at the Herbarium, University of Michigan, Ann Arbor, and dated as follows: March, 1941; June, 1943; April through Novem-

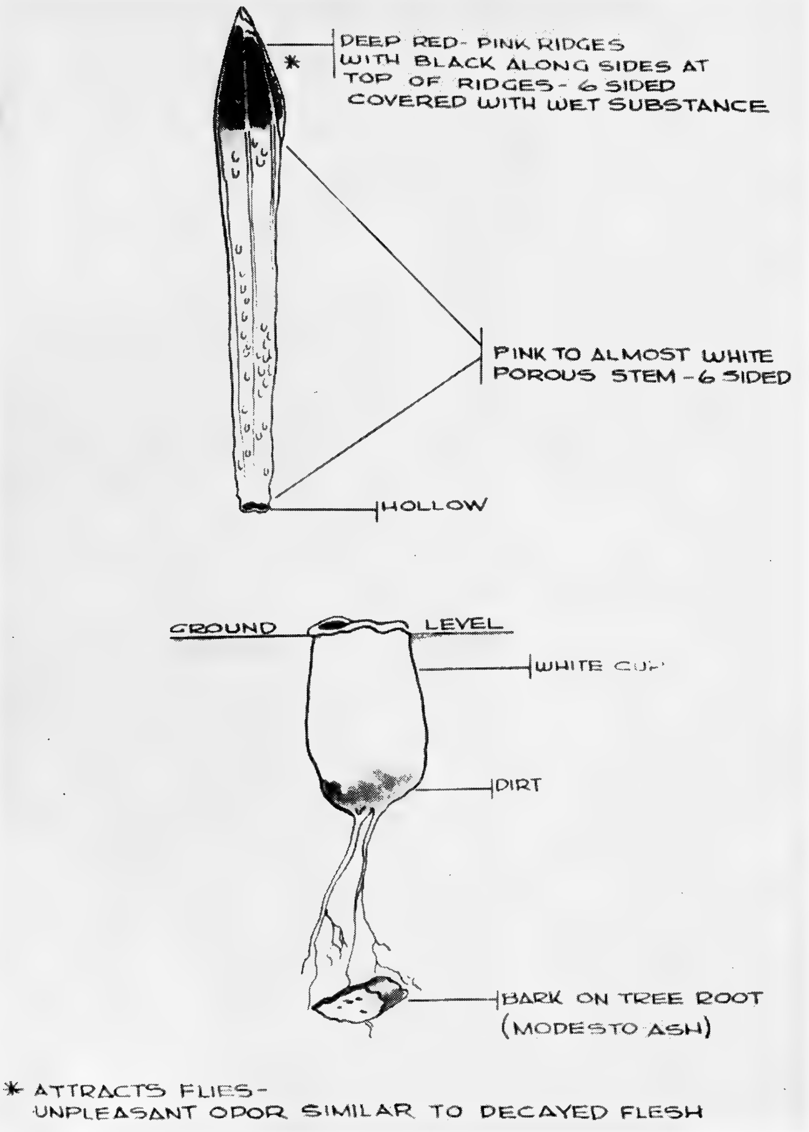

FIG. 1. *Lysurus mokusin* showing habit and mature receptacle. The gleba is shown as occurring between the receptacular arms, not covering their outer surface. Drawing by Norma O'Neil, Sacramento.

ber, 1944; May through September, 1945; May, June, October through December, 1946; January through March, 1947; October, 1952. A wide range of morphological variation is found among these collections as is evidenced in the notes Dr. Rea made from fresh material. On the large mass of earlier material, he took voluminous notes, among which are three different versions of a paper he was preparing on this species. This material was assembled and developed into a paper for publication by Berta Heidenhain (as co-author) at the University of Michigan (1955). The report gives a complete description of *Lysurus mokusin* throughout its development from the very young buttons or eggs to mature and senescent receptacles.

The senior author has made the following general observations from several representative collections of the above series. Dr. Rea sectioned nine peridia and mounted them on black paper. These sections show that in the unopened receptacle the gleba appears to lie on the outer surface of the receptacular arms and not on the inner surface. The gleba is separated, by plates arising from the center of the backs of the arms, into as many units as there are arms. As was pointed out by Rea and Heidenhain (1955), the glebal masses actually lie between the arms and are attached to their sides, but do not invade the central chamber. The backs, or outer surfaces, of the arms are thus free from glebal material. These surfaces are concave or flat in mature receptacles. However, it has been observed by the present authors that as the arms mature and are raised from the volva, the gleba appears to shift in position and surround the receptacular arms on all surfaces except the backs of the arms.

The receptacular arms in the specimens accumulated by Dr. Rea vary from those in specimens in which they are completely free through those which are connivent, those which are held together by fragments or caps of volva material, and those which are organically united by a very small bit of tissue to those which are united in such a way that the receptacular arms form an expanded structure similar to a Chinese lantern and join above the glebiferous surface into an apical spire at least 1.5 cm. long. The longest dry receptacle observed in the Rea collections was 11 cm. long.

Some of the specimens of *Lysurus mokusin* from Santa Barbara, both those of the Reas deposited at the University of Michigan and that of Hazard at the University of California (UC 568835), have characteristics

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EXPLANATION OF FIGURES 2–4.

FIGS. 2–4. Development of receptacles in *Lysurus*. FIG. 2. *L. mokusin*. Each of the four fresh specimens shows a different amount of sterile tissue projecting beyond the glebiferous area. Flutings on stipe are apparent and continuous with the outer edge of the receptacular arms between which lies the gleba. Previously unpublished photo by Paul Marshall Rea, Santa Barbara, California. Courtesy of the Herbarium, University of Michigan. FIG. 3. *L. sulcatus*. Cluster of four receptacles in various stages of development. Lower left: young receptacle just breaking through the peridium, the receptacular arms hold the gleba between them; lower right: receptacle with stipe nearly completely elongated, gleba still intact; center: gleba nearly completely removed; upper left: mature receptacle collapsed after removal of gleba. Note cylindrical stipe. Collected at Woodland, and photographed at University of California, Davis, October 1, 1958. FIG 4. *L. sulcatus*. Single receptacle collected at Woodland, September 23, 1958, showing receptacular arms with wrinkled glebiferous surface.

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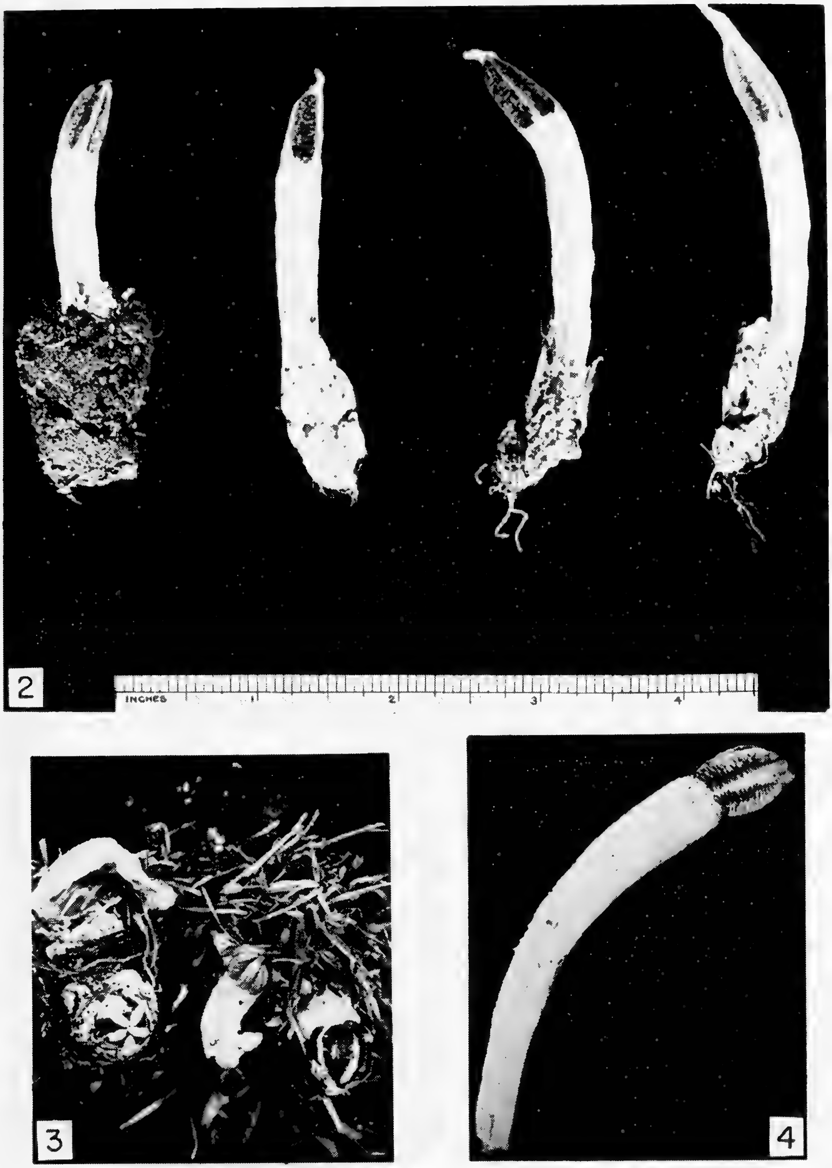

FIGS. 2–4. Development of receptacles in *Lysurus*.

which in many respects are similar to those of *Mycopharus gardneri* (Berk.) Petch of Ceylon. This latter species was first placed in *Lysurus* by Berkeley, then in *Colus* by Fischer. Petch (1919) established for it the new genus *Pharus*, and later, finding the name *Pharus* to be preoccupied, he (1926) renamed the genus *Mycopharus,* distinguishing it from *Lysurus* on the basis of the type of glebiferous surface on the receptacular arms. He illustrated the genus as having the arms slightly separated from one another below the glebiferous surface. Although, as stated above, some of the characteristics of *Mycopharus gardneri,* the type and at first the only species of this genus, are to be found in some of the Santa Barbara collections of *Lysurus mokusin*, the present authors consider that there are sufficient differences between the two species to justify the separation of the two genera. They differ primarily in the nature of the glebiferous surface, which is composed of tightly packed scales of "pseudoparenchymatous processes" in *Mycopharus* and of tightly packed wrinkles in *Lysurus*; in addition, the stipe is weakly fluted in *Mycopharus* and strongly fluted in *Lysurus*. Among the many specimens of *Lysurus mokusin* from the Rea collection of Santa Barbara, however, there is a wide variety of stipe surfaces, the stipes varying from deeply fluted or winged to shallowly or weakly angular.

LYSURUS SULCATUS (Cooke & Massee) G. H. Cunningham, Proc. Linn. Soc. N. S. W. 56 (3):189, pl. viii, figs. 3, 4. 1931. *L. texensis* Ellis in W. R. Gerard, Bull. Torrey Club 7:30. 1880, *nomen nudum*. *Mutinus sulcatus* Cke. & Mass., Grev. 17:69. 1889. *Lysurus australiensis* Cke. & Mass., Grev. 18:6. 1889. *Anthurus australiensis* (Cke & Mass.) Fisch., Denksch. Schweiz. nat. Gesell. 33:27. 1893. *A. borealis* Burt, Mem. Bost. Soc. Nat. Hist. 3:504. 1894. *Lysurus borealis* (Burt) P. Henn., Hedw. 41:167. 1902. *L. borealis* var. *klitzingii* P. Henn., Hedw. 41:173. 1902. *L. tenuis* Bailey, Comp. Cat. Queensland Pl. 745. 1910. *L. texensis* Ellis (?) in Long, Mycologia 9:271–274. 1917.

Peridium at dehiscence 2–2.3 cm. tall, 2 cm. in diameter at the widest point, rhizomorphic; receptacle 7.5–10.5 cm. long; stipe 6.5–9.0 cm. long, tapering downward, 5–6 mm. in diameter below, 10–13 mm. in diameter at apex just beneath receptacular arms, cream-colored below to yellowish above, composed of one layer of chambers, hollow, apex open, at top of stipe a collar on which are produced 5–7 hollow receptacular arms on the rounded inner surfaces of which is the glebiferous layer; glebiferous layer longitudinally strongly wrinkled, dark olive to blackish; receptacular arms orange-buff to buff to tan in color, composed of very compact tissue with a different appearance from that of stipe, even in length, 6–15 mm. long, 3.5–4 mm. in diameter, tapering to a rather sharp point, more or less flattened on outer grooved surface, the outer surface 1–2 mm. wide, smooth; spores rod-shaped, with rounded ends, slightly yellowish, 3.8–4.3 × 1.5–1.8µ.

In 1880, Gerard noted that Ellis had received a species of *Lysurus* from

Texas which he considered to be new and thus had provisionally named it *L. texensis*. No description was given. In 1917, Long described a *Lysurus* collection from Texas, designating it as *Lysurus texensis* Ellis (?), since this *nomen nudum* had been applied to an undescribed *Lysurus* from Texas. He stated that his material might be only a red form of *Anthurus borealis*. *Lysurus texensis* Ellis in Long is placed in synonymy with *L. sulcatus* because Long's description appears to be based on material of the *L. sulcatus* type rather than of the *L. mokusin* type. In spite of the interpretation by Rea and Heidenhain (1955), Long's description of the stipe is interpreted here as indicating that the walls of the chambers in the stipe wall are polygonal rather than that the stipe itself is polygonal, fluted or winged. Cunningham (1931, 1942) places *L. texensis* in synonymy with *L. sulcatum*, but he lists only Ellis' *nomen nudum* and makes no mention of Long's description.

California collections examined.

In Bermuda grass lawn, Woodland, Yolo County, September 23, 1958, *John Bartels*; October 1, 1958, *K. A. Kimble* (DAV). The specimens usually appeared after occasional heavy spray irrigation. They were either solitary in occurrence, grouped in small clusters, or disposed in large numbers in the lawn. In one specimen, the receptacle, instead of bearing six arms of equal length, bore three arms 1.7 cm. long which alternated with three shorter arms, 1.4–1.5 cm. long.

West Sacramento, Yolo County, October, 1958, *H. A. McCain* (DAV).

In lawn, Fresno, Fresno County, September 16, 1941, *George W. Graves* (UC 660274). Each of the three somewhat immature receptacles bears six arms. The length of the receptacles in the dried condition is 3 cm., while that of the arms is 5 mm.; the stipe is white, with no indication of the original color, had it been other than white when fresh.

Santa Barbara, Santa Barbara County (P. M. Rea collection, University of Michigan, Ann Arbor). Two small specimens are present in this collection.

In flower garden, "The Flower Shop," San Diego, San Diego County, September, 1913, *A. M. Rainford* (specimen in alcohol, deposited by Professor W. A. Setchell in the collection of class demonstration material, Botany Department, University of California, Berkeley). According to Dr. Lee Bonar, who reported the existence of this specimen to the senior author (letter, December 11, 1958, the stipe of this specimen is 6.5 cm. long, 2 cm. in diameter at the apex, and 1 cm. in diameter at the base. There are five receptacular arms, which are free at their tips. Of the five arms, one is shorter than the other four; the short arm is 1.7 cm. in length, while the others are 2.1 cm. in length.

SUMMARY

Even though members of the Clathraceae are not commonly found in California, a large number of specimens of *Lysurus* have been found in a few isolated localities. The two species of *Lysurus* that have been reported from California, *Lysurus mokusin* and *L. sulcatus*, are distinguished primarily on the basis of color and the nature of the surface of the stipe. Since basidia and spores tend to be similar in appearance and size, gross morphological features such as color, the shape of the stipe in cross-section, the type of glebiferous surface, and the extent of the connection of the apices of the receptacular arms serve as the basis for determining the species in the genus *Lysurus*. On the whole, these characters seem to the writers to be of importance only at the species level at our present stage of knowledge of the Phallales. However, the nature of the glebiferous surface of the receptacular arms is considered to be of sufficient importance to separate the two genera, *Lysurus* and *Mycopharus*.

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FOLIAR XEROMORPHY OF CERTAIN GEOPHYTIC MONOCOTYLEDONS[1]

Baki Kasapligil

Introduction

Xeromorphy in the vegetative organs of plants and especially in foliage leaves has long attracted the interest of morphologists and ecologists. There is now considerable information about foliar xeromorphy and its relation to factors of the environment (Clements 1905, Harshberger 1908, Starr 1912, Hanson 1917, Hayden 1919, Pool 1923, Mothes 1932, Evenari 1938, Shields 1951a). Most of these studies deal mainly with dicotyledons, while the monocotyledons, with the exception of xeric grasses, have received less attention. As a matter of fact, dicotyledons are more abundant than monocotyledons in arid and semi-arid regions; however, certain "drought resistant" monocotyledons do occur widely in xeric habitats.

Geophytic monocotyledons, i.e., those having subterranean bulbs, corms, rhizomes, or tuberous roots, are quite common in the steppic flora of central Anatolia. In the vicinity of Ankara, there are over fifty such species in the Gramineae, Araceae, Liliaceae, Iridaceae, and Orchidaceae; they form about thirty-seven per cent of the total number of known species of monocotyledons in the local flora (cf. Krause 1937). In the present study the foliar xeromorphy of eighteen of these species, representing five families, has been investigated anatomically.

The geophytic monocotyledons in central Anatolia produce aerial shoots as early as February and complete their flowering and fruiting stages during March and April. After forming seeds they usually return to subterranean dormant stages before the drought period starts. In their habit of resting during the dry season, they resemble ephemeral annuals. Some botanists may not consider the ephemerals and geophytes as true xerophytes, since both of these groups escape instead of endure the critical drought period. This argument may be answered by considering the dormant seeds or subterranean fleshy organs as adaptational drought-enduring stages in the continuous life cycles of these plants. The geophytes thus fit the "drought evading" class of Shanz (1927). Furthermore, the geophytes can also be considered as succulent xerophytes since they are well adapted to withstand prolonged drought by means of their fleshy subterranean organs in which water, carbohydrates, and mucilaginous substances are stored (cf. Warming 1909).

In this paper, the term "xerophyte" is used as a convenient qualitative term to designate the plants of xeric habitats where the available soil water is limited. The classical concept of this term refers to plants living in places with limited water supply and which are equipped with various arrangements to reduce transpiration (cf. Willis 1957, p. 692). Although

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[1] This paper was supported in part by a faculty research grant from Mills College.

Bakee (1914) concluded that xerophytes have higher indices of transpiring power than mesophytes, recent experimental studies have demonstrated that there is no direct correlation between structural modifications and transpiring powers of xerophytes. The degree of drought resistance cannot be judged simply according to the xeromorphic features (Maximov 1931, Evenari 1938, Weaver and Clements 1938, Shields 1950, Daubenmire 1959).

There is general agreement that xerophytes can by morphological and physiological means either escape or resist permanent injuries caused by excessive loss of water (Maximov and Maximov 1924), and leaf xeromorphy is, in addition to geophytic xeromorphy, another such means. Studies on leaf xeromorphy and its relation to physiological and structural influences are discussed comprehensively in a recent review article by Shields (1950); therefore the present paper will not attempt to give a detailed account of the environmental and genetic causes of the foliar xeromorphy. However, I should like to point out briefly the factors of the steppic environment in central Anatolia that contribute to the structural modifications of xeromorphic leaves in the eighteen geophytic monocotyledons chosen for investigation. In Ankara the atmosphere is very dry and induces strong transpiration. The wind velocity is high during the winter months when foliage leaves of many geophytic monocotyledons develop. The wind increases the rate of transpiration. The light intensity, one of the factors contributing to foliar xeromorphy (Shirley 1929, Turrell 1940, Shields 1951a) is very strong due to high altitude (from 830 m. at the railroad station to 1855 m. on the Elmadag mountain), cloudless skies, with the exception of a few rainy and snowy days distributed irregularly through fall and winter, and to the reflection of solar radiation from gray steppic soils and calcareous rocks of the mountains which are poorly covered by vegetation. The precipitation is low, and the drought period usually extends from May to October (Colasan 1946, Walter 1955 a and b). The limited water supply of the steppic soils is further decreased by direct evaporation from the soil surface, and the soil solution acquires the high osmotic pressure which is so typical of arid and semi-arid regions. Also, the steppic soils in this habitat are extremely deficient in nitrates, which is another important factor contributing to foliar xeromorphy (cf. Mothes 1932).

The monocotyledons in this study exhibit certain uniformities in addition to their geophytism, reduced leaf surface, and phenological periodicity. Their root systems are fibrous and very shallow and are limited to the uppermost soil layers (Birand 1938, Karamanoglu 1955). The latter author points out the anatomic similarities in regard to epidermis, exodermis, cortical parenchyma and endodermis in the roots of *Iris*, *Ornithogalum* and *Muscari* species, although these tissues show minor differences from one species to another in regard to thickness of tissues. Furthermore the geophytic monocotyledons studied by Birand (1938) exhibit low osmotic pressures since they complete their activities above ground during the moist season. The present study was initiated primarily to see if there is any parallelism in the structural modifications and in the adaptational degree of foliar tissues among unrelated species of geophytic monocotyledons.

In this study the following widely accepted xeromorphic characters have been considered:

A. General habit of the plant and gross morphology of leaves
  1. Reduction of the surface
  2. Revolute margins
  3. Folding and fusion of the blade
  4. Involution upon wilting
  5. Increased thickness of the blade
B. Epidermis
  6. Strong cutinization
  7. Increased thickness of the epidermal cell walls
  8. Water storage in depression of stomata
  9. Cutinization and ledge formation on the guard cells
  10. The occurrence of trichomes
  11. Water storage in the epidermal cells
C. Mesophyll
  12. Isolateral organization of the palisade
  13. Strongly developed palisade parenchyma at the expense of spongy parenchyma
  14. Compactness of the tissues
  15. Decreased size of cells
  16. Development of a water storing tissue
  17. Abundance of excretory idioblastic cells
D. Vascular system
  18. Strong development of vascular bundles
  19. Compactness of vascular bundles, i.e., lateral proximity of veins
E. Sclerenchyma
  20. Strongly developed fibers, tracheoid and sclerenchymatous idioblasts (cf. Foster 1956 for these idioblasts).

MATERIALS AND METHODS

The leaves were collected from plants growing in different localities of the steppe of Ankara. Portions of leaves were fixed in a solution of formaldehyde–propionic acid–acetic acid, then transferred into 70 per cent ethyl alcohol. Transverse leaf sections were made by free hand and stained with safranin for general histological study and mounted in gelatin-glycerin. Additional sections were stained with phloroglucinol and hydrochloric acid for lignin test. Sudan IV was used for the cuticle (Foster 1949). Leaf portions, cleared in 3 per cent sodium hydroxide, stained with safranin, dehydrated with xylene and mounted permanently in Canada balsam (cf. Kasapligil 1951 for method), were entirely satisfactory to observe the orientation of various tissues and their cellular morphology. Drawings of leaf sections were prepared by camera lucida. Herbarium specimens of the plants were also prepared and distributed among the herbaria of the University of Ankara, University of California, Berkeley, and the Royal Botanic Garden, Edinburgh.

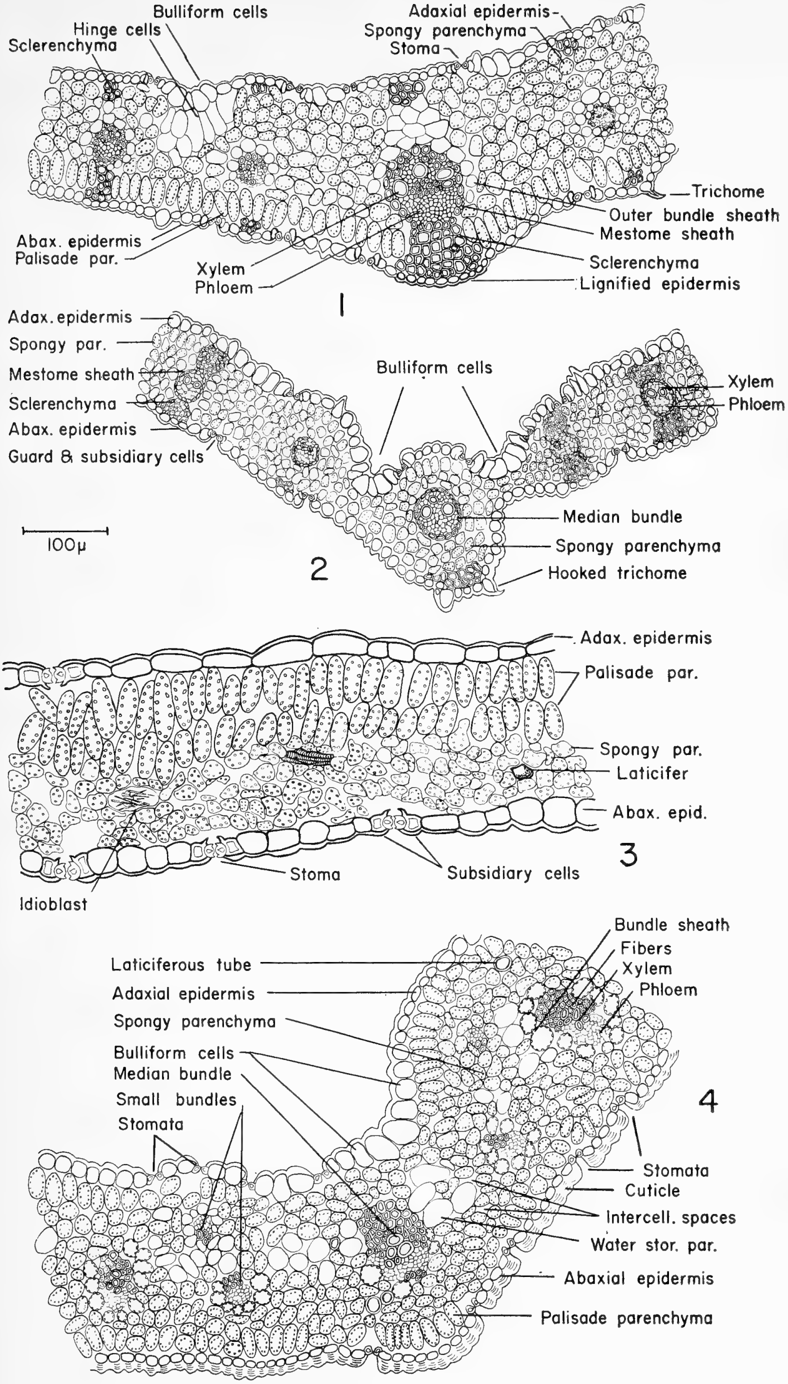
DESCRIPTIONS OF PLANTS AND THEIR COMPARATIVE FOLIAR ANATOMY

GRAMINEAE

HORDEUM BULBOSUM L. (fig. 1) is a tall perennial grass of cultivated lands as well as of the mountains of the steppe. The flat stiff blades are characteristically involute upon wilting. The blades are 6–10 mm. wide, 230–300 microns thick along the median bundle and 150–160 microns thick in the lateral portions. The cormous basal nodes are aggregated in large clumps.

Epidermal cells are elongated with undulate cell walls, and alternate with short silica cells. Outer cell walls of the epidermal cells are thicker than their inner tangential walls. Cutinization of the cell walls is not prominent, but the epidermal cells adjacent to sclerenchyma strands on both adaxial and abaxial surfaces of the blade have lignified cell walls. The stomata are not sunken, and they occur on both surfaces. The guard cells are dumb-bell shaped and have lignified cell walls. Each stoma is accompanied by a pair of subsidiary cells. Bulliform cells are situated along the grooves of the adaxial surface in 4–6 rows. They have straight cell walls. Hinge cells underlying the bulliform cells are filled with water, contain very few chloroplasts and form one or two layers. Two different types of unicellular trichomes were observed: short and hooked trichomes with thick silicified walls along ridges on the abaxial surface and along margins of the blade; long slender trichomes with lignified cell walls near the abaxial base of the blades.

Leaves are dorsiventral and a single layer of palisade parenchyma is situated on the abaxial side. Cells of the mesophyll are small and very compactly arranged. Prismatic crystals are abundant in the spongy parenchyma cells along the bundles. Collateral bundles are surrounded by mestome sheath (Schwendener 1890) as well as by bundle sheath. Bundle sheath extensions (Esau 1953) are well developed, especially along the median bundle of the blade, and connect the vascular bundles to the adaxial fibre strands as seen in transverse sections. Vascular bundles are close together and are interconnected by small bundles. Fibres are more strongly developed on the abaxial sides of the bundles than on the adaxial ones. Abaxial fibre strands are connected directly with the lignified epidermis and the mestome sheath of the bundles, while the adaxial fibre strands are "separated" from the bundles either by bundle sheath extensions along large bundles or by spongy parenchyma cells along small bundles. Strands of 8–15 fibres extend along both margins of the blade, beneath the epidermis.



FIGS. 1–4. Transverse sections of leaves: 1, *Hordeum bulbosum*; 2, *Poa bulbosa*; 3, *Arum orientale* var. *elongatum*; 4, *Allium rotundum*.

Poa bulbosa L. (fig. 2) is a small perennial grass which is very common in the steppe as well as in the fields and fallow lands. It has short and narrow leaves, involute upon wilting. The blades are 2–4 mm. wide and 4–7 cm. long. Thickness of the blades ranges from 180–220 microns along median bundles and from 60–125 microns in the lateral portions. The basal portions of the shoots are swollen and enveloped by thickened bases of leaves forming clumps of small bulbs.

Epidermal cells are long tabular cells with straight walls. Outer walls are thicker than the inner ones and are moderately cutinized. The bulliform cells are 5–6 cells wide, situated along two grooves of the adaxial surface on two sides of the median bundle. Bulliform cells are not accompanied by hinge cells. The stomata are slightly sunken and occur in both surfaces of the blade above assimilatory tissue. Guard cells are dumbbell shaped, and each stoma has two very small subsidiary cells which are also sunken. Unicellular hooked trichomes are situated along both margins and dorsal ridges of the blade.

Mesophyll is not differentiated into palisade and spongy parenchyma. It consists of very small isodiametric parenchyma cells closely packed together. Mesophyll is only two cell layers thick beneath the bulliform cells, while its thickness in other portions of the blade is 5–6 cell layers. Prismatic crystals are abundant throughout the mesophyll parenchyma.

The collateral vascular bundles are surrounded by mestome sheaths, but differentiated border parenchyma or bundle sheath extensions are not present. The median bundle is "imbedded" directly within assimilatory tissue and is not connected with the dorsal strand of fibres. On the other hand, most of the small bundles are connected to upper and lower epidermis by strongly developed fibre strands. Groups of 3–6 fibres extend along leaf margins beneath the epidermis. Comparatively speaking, the vascular bundles in the *Poa* leaf are more compactly arranged than the vascular bundles of the *Hordeum* leaf, and likewise anastomosing veins are more frequent than those in the previous species.

Araceae

As far as this author knows, this family is represented only by one species in the steppic flora.

Arum orientale M. Bieb. var. elongatum Engl. (fig. 3) is a herbaceous perennial plant which grows in little soil pockets on eroded and exposed limestone or within narrow rock crevices at the highest altitudes of the steppic region. Broadly-hastate leaves are 15–25 cm. long. The lamina is tender and 250–270 microns thick. The adaxial surface of the lamina is darker green than the abaxial one. The plants have rounded tubers, slightly adpressed.

The epidermal cells are polygonal and appear isodiametric in face view. They are about 50–70 microns long and 40–50 microns deep in transectional view. The epidermal cells along the vascular bundles are narrow tabular in form. A few chloroplasts were observed within the epidermal cells. Outer tangential walls of the epidermal cells are cutinized moderately and these walls are thicker than the inner tangential and radial ones. Stomata are not sunken and appear on both surfaces of the lamina, more frequently on the dorsal side. As an average, the guard cells are 45 microns long and 15 microns wide, although their sizes are variable. The inner and outer ledges of the guard cells are distinctly developed. Each stoma is subtended by a pair of lateral subsidiary cells which are thick walled. Each subsidiary cell is equipped with a curved ledge on its inner tangential wall adjacent to the guard cell. Possibly these ledges produce complete closure of stomatal openings and form an additional air chamber between the guard cells and the substomatal air cavity. Trichomes and idioblasts are absent in the epidermal tissue.

Mesophyll is dorsiventral and provided with a biseriate palisade parenchyma on the adaxial side. Palisade parenchyma cells are large and occupy the upper half of the mesophyll. The spongy parenchyma consists of 5–6 layers of large irregular and loosely arranged cells. As a whole the mesophyll has very conspicuous intercellular spaces presenting a mesomorphic rather than a xeromorphic structure. Idioblasts containing raphides are distributed within the spongy parenchyma. Individual raphides are 180–200 microns long and form crowded bundles within the idioblasts. Druses are also present, but are not as common as raphides. Another feature of the spongy mesophyll is the presence of articulated laticifers which were noted also by Solereder and Meyer (1928). Sclerenchyma is not present in any form.

Vascular bundles are reticulate and the leaf resembles a dicotyledonous leaf in this respect. The veins of first, second, third, and fourth orders are closed and form vein islets, while the veins of fifth and sixth orders frequently end freely in mesophyll. Marginal bundles run very close to the leaf edge. The major veins are surrounded by a vaguely differentiated bundle sheath.

LILIACEAE

This family is represented by eight genera in the steppic flora. The largest genus, *Allium*, is represented by ten species occurring in the steppic region under a wide variety of conditions, from moist places along streams to extreme xeric habitats of saline depressions and mountain steppe. Two species, which seem to endure drought longer than other species, were studied.

ALLIUM ROTUNDUM L. (fig. 4) is a tall slender plant reaching a height of 40–50 cm. The leaves are filiform, tapering gradually to the tips. Although the leaves are typically unifacial in their ontogeny, the adaxial surface is flat, the abaxial one ridged (cf. Esau 1953 and Hayward 1938 for the ontogeny of the leaf of *Allium cepa*). There is no central cavity in the blade. Upon wilting, involution takes place through a folding action along the median bundle of the lamina halves. The leaves are 2–3 mm.

wide and 280–300 microns thick. The thickness decreases very slightly toward the margin of the blade. The small bulbs are oval in outline.

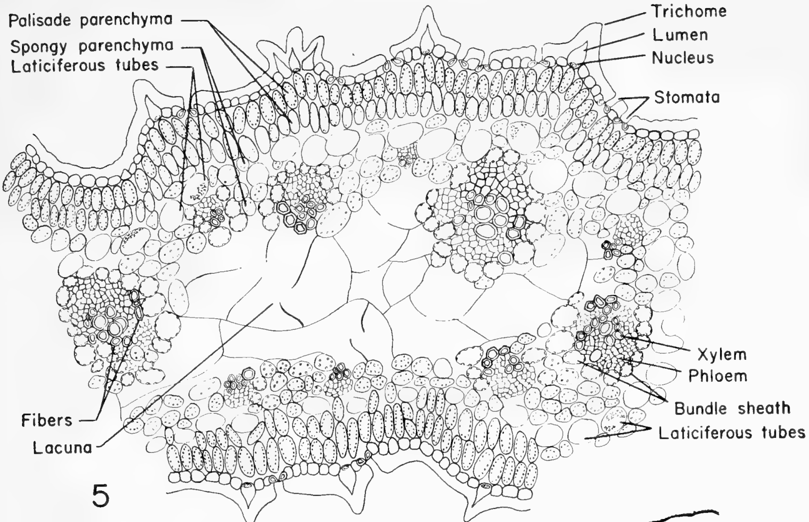
The epidermis, as seen from the surface, consists of long, tapering cells with straight lateral walls. The lower epidermis bears a much heavier cuticle than the upper and its outer walls are characterized by lamellation. The lumina of the lower epidermal cells are extremely small. Bulliform cells of the upper epidermis extend along the groove above the median bundle and form a row of 5–7 cells. They are not accompanied by any specialized hinge cells in the underlying tissue. Stomata occur on both upper and lower surfaces and are sunken below the epidermal level. Subsidiary cells are not present, and trichomes in the epidermis are missing.

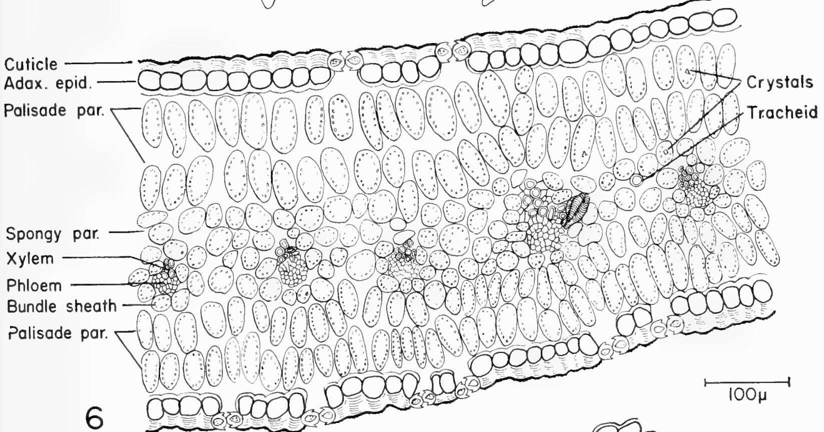
Mesophyll includes a uniseriate palisade on both sides. The abaxial palisade is strongly differentiated, while the adaxial one is weakly developed. The spongy mesophyll is composed of small isodiametric parenchyma cells which form 10–15 layers with conspicuous intercellular spaces. A well differentiated water-storing parenchyma in the central portion of the mesophyll consists of enlarged cells lacking chloroplasts. Articulated laticifers and patches of tracheoid idioblasts are abundant in the mesophyll and are distributed at random. Well developed vascular bundles are densely arranged in longitudinal directions. They are transconnected by means of small bundles. Reversal of the bundles in regard to the position of xylem and phloem is obvious. Apparently this situation is caused by the peculiarity of the leaf apex (cf. Esau 1953, fig. 16.19). Clearly differentiated bundle sheaths have cells characterized by prominent central vacuoles and peripherally arranged chloroplasts.

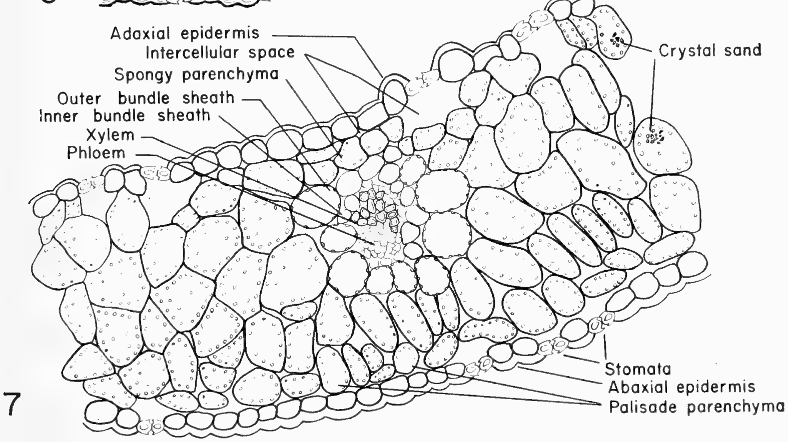
Fibers associated with the vascular bundles are strongly developed, the xylem fibers, especially, forming very thick and compact strands along major veins.

ALLIUM STAMINEUM Boiss. (fig. 5) is a small plant about 20–25 cm. high with tunicated oval bulbs. The leaves are smaller and more tender than those of the previous species. They are 1.5–2 mm. wide and appear reniform in transverse section. Involution upon wilting is not pronounced. The thickness of the leaves ranges from 450 to 550 microns. As in *Allium rotundum*, the leaves are unifacial, but both the upper and lower surfaces are ridged. The epidermal cells are tabular in form, and their outer walls are extremely thick and heavily cutinized throughout both surfaces of the leaves. Consequently the lumina of the epidermal cells are very small. Stomata occur in deep depressions of abaxial and adaxial surfaces. Unicellular, short, conical trichomes with very thick cell walls are arranged in regular rows along the ridges. Trichomes are living cells, and their nuclei are always situated at the bottom of the enlarged basal portions of the cells.

The mesophyll is quite different from that of *A. rotundum*. First of all it has a well developed biseriate palisade on both upper and lower sides,







FIGS. 5–7. Transverse sections of leaves: 5, *Allium stamineum*; 6, *Colchicum biebersteinii*; 7, *Gagea arvensis* var. *semiglabra*.

followed by a layer of articulated laticiferous tubes. These laticifers possess perforation plates similar to sieve plates. The spongy parenchyma is very weakly developed, forming a layer of 2–3 cells inside the "ring" of laticifers. As the leaves reach maturity, remarkably large water-storing parenchyma cells in the center of the leaf collapse and form lacunae. Collateral bundles are surrounded by bundle sheaths. "Parallel" running major bundles are more or less spaced from each other, but they are transconnected by minor bundles. There are a few xylem fibers associated with the bundles, but phloem fibers are very rare. Sclerenchymatous idioblasts are abundant and seem always to be associated with interconnecting transverse bundles or to occur terminal to freely ending veinlets.

COLCHICUM BIEBERSTEINII Rouy (fig. 6) is a stout plant which grows in foothills and on mountain slopes protected from the wind. It blooms as early as in February, right after a few sunny winter days. The basal leaves arising from tunicated bulbs lie on the ground. They are flat, narrow, dark green and coriaceous in texture, 8–10 mm. wide and 380–450 microns thick. Involution does occur, although the leaves are not provided with any specialized motor cells. A similar situation was observed in *Oryzopsis hymenoides* (Roem. et Schult.) Ricker by Shields (1951b). The epidermal cells are long tabular cells with straight anticlinal walls. Abaxial and adaxial sides of the epidermis are coated with a thick cuticle layer which exhibits very fine dentation as seen in transectional view. Outer tangential walls of the upper and lower epidermis are exceedingly thick and are marked with distinct lamellation (25 microns or even thicker) while the inner tangential walls are moderately thickened. Radial walls of the epidermal cells however do not show a noticeable thickening. The stomata occur on both surfaces, but are more frequent on the abaxial surface. They are not sunken, but lie at the same level with cuticle and thick outer walls of the epidermal cells. The guard cells also possess very thick cell walls and are provided with well developed inner and outer ledges. Subsidiary cells are not present. Unicellular, short, conical trichomes with blunt tips occur along leaf margins only. These trichomes are dead cells with extremely thick walls and practically no lumens.

The leaves of *Colchicum biebersteinii* present an isolateral organization with a biseriate palisade on both upper and lower sides of the mesophyll. Palisade parenchyma is strongly developed at the expense of the spongy parenchyma. It occupies two thirds of the mesophyll. Palisade parenchyma has thin walls in general, but the outer cell walls of the outer parenchyma layer are remarkably thickened toward the leaf margins. The spongy parenchyma is scanty and represented by 2–5 layers of isodiametric cells in the central portion of the mesophyll. Prismatic crystals occur in both palisade and spongy parenchyma cells. Large and small vascular bundles imbedded within the spongy mesophyll are sheathed by border parenchyma. The median bundle is not different from other bundles. The general pattern of venation is striate, but the veins running along the longitudinal axis of the leaf are interconnected by small bundles at frequent intervals so that a strongly developed and compact network of veins with many vein islets of varying sizes results. Isolated tracheids with spiral thickenings are found occasionally outside the bundles. Vascular bundles are not accompanied by fibers. Strands of 7–8 collenchyma cells with highly reduced lumens occur along leaf margins under the epidermis.

Gagea arvensis Dum. var. semiglabra Beck (fig. 7) is a bulbous plant occurring commonly in fields, fallow lands and in thickets under the protection of small steppic shrubs. The smooth, flat, lanceolate, light green, tender leaves are 7–8 cm. long, 5–6 mm. wide and 350–380 microns thick. Involution occurs upon wilting, although there are no specialized motor cells.

The epidermis consists of long tabular cells with straight radial walls. The outer tangential walls of epidermal cells are 12–14 microns thick on both surfaces. However, the outer tangential walls of the upper epidermis project and become almost papillate especially in the cells adjacent to the stomata. Apparently the adaxial epidermis is involved in water storage. A finely striate cuticle covers the entire leaf. The stomata are not sunken, and they occur on both the upper and lower epidermis at nearly equal frequencies. The guard cells are 20 microns wide, 45 microns long and 20 microns thick. They are equipped with well developed inner and outer ledges. Subsidiary cells are not present. The long unicellular trichomes occurring along leaf margins are dead, thick walled cells with papillate projections all around them. The leaf structure is dorsiventral, and the mesophyll is provided with a single layer of palisade on the abaxial side. The palisade parenchyma is poorly differentiated, although sometimes it appears to be biseriate. The greater part of the mesophyll consists of large spongy parenchyma cells, 4–5 cell layers thick. These cells are more or less isodiametric and variable in size, but cells with a diameter of 100–120 microns are not uncommon. The spongy parenchyma cells, with large central vacuoles filled with sap, are mainly responsible for the succulent texture of the leaves. Crystal sand is found in the spongy parenchyma cells, but no specialized idioblasts occur.

Vascular bundles are not accompanied by fibers, but interestingly enough are sheathed by two layers of border parenchyma, thin walled cells which appear round in transectional view. The inner bundle sheath consists of smaller cells than those of the outer bundle sheath. There are no sheath extensions on either side of the bundles. Vascular bundles present a typical striate pattern. They converge near the leaf apex, but interconnecting veinlets have not been observed. They are more widely spaced than in any other species studied. Isolated vascular strands lie parallel to adjacent vascular bundles. These strands consist of a few helical tracheids and terminate in undifferentiated procambial cells at both ends. There is no evidence of bundle sheaths around the isolated vascular strands.

Leaves of *Gagea* do not present striking xeromorphic features. They represent a leaf type at the border line between mesomorphic and xeromorphic structures.

Merendera trigyna (Adam) Woron. (fig. 8) is a bulbous plant with strap shaped, flat leaves which are 3–4 mm. wide and 300–350 microns thick. It occurs in the mountain steppe and blooms during February and March. The leaves are isolateral and involution occurs upon wilting.

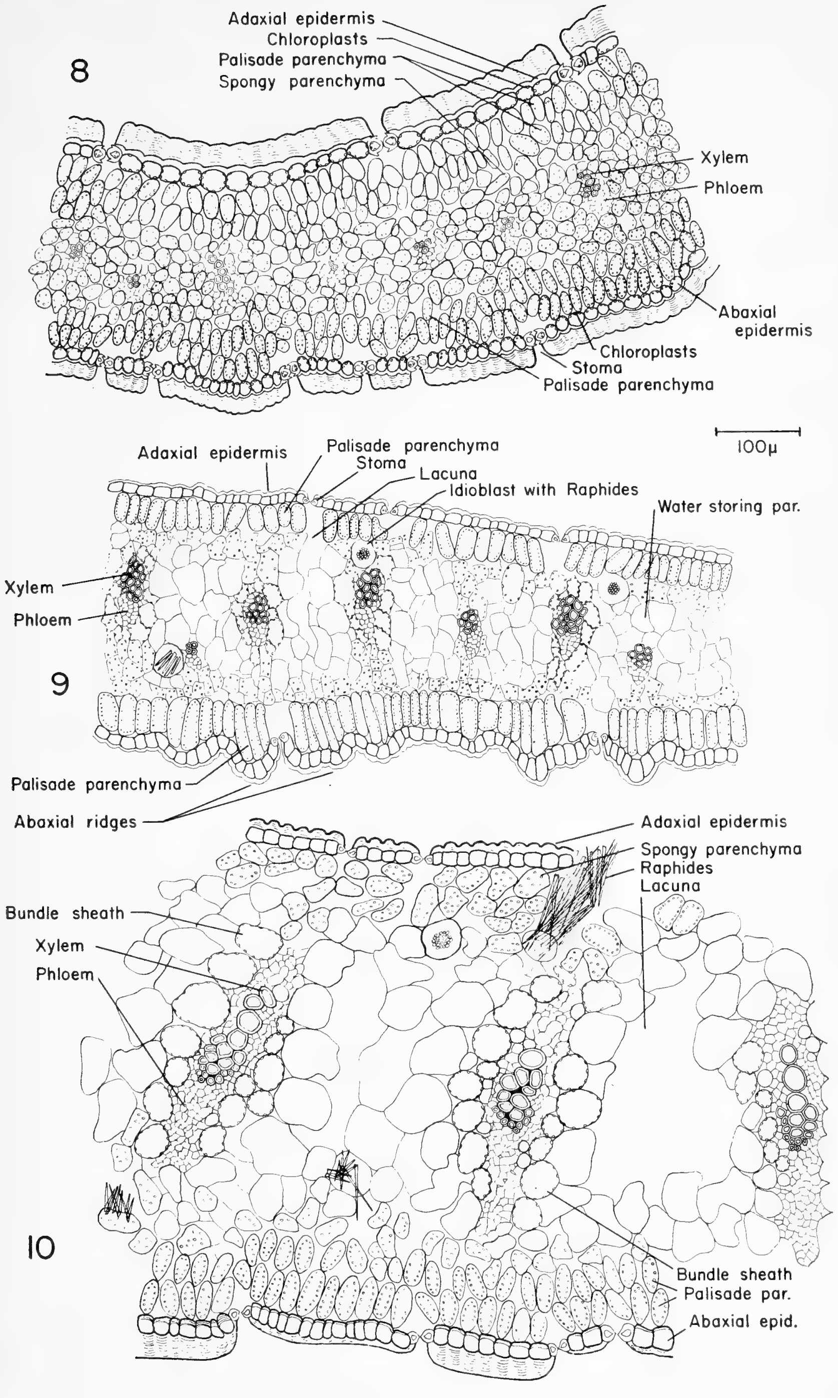
The epidermis consists of rectangular cells, 14 microns wide and 70 microns long. Upper and lower epidermis are coated by a striate cuticle 2–3 microns thick. The outer tangential walls of the epidermal cells are remarkably thick, and cell lumina are extremely reduced. Both upper and lower epidermal cells contain chloroplasts. The stomata are sunken and distributed on both adaxial and abaxial surfaces. Guard cells are 12 microns wide and 32 microns long as seen in face view. Inner and outer ledges are well developed, the outer ones being cutinized. Subsidiary cells are not present. Short unicellular trichomes occur along leaf margins. The cell walls of the trichomes are very thick and appear refringent under polarized light.

The mesophyll has a biseriate palisade on both adaxial and abaxial sides. Palisade parenchyma cells are small and densely arranged. They occupy two thirds of the mesophyll as seen in transverse section. Spongy parenchyma consists of 5–6 cell layers between upper and lower palisade. Crystal sand occurs in spongy parenchyma cells. There are no specialized idioblasts in the mesophyll.

Vascular bundles are closely spaced and transconnections occur very frequently. Border parenchyma cells containing very few chloroplasts are restricted to outer edges of xylem and phloem. Consequently they do not form a continuous sheath around bundles. There are no fibers associated with the vascular bundles, but strands of partially lignified, hypodermal fibers extend along leaf margins.

Muscari comosum Mill. (fig. 9) is a bulbous plant which grows in mountain steppe as well as in cultivated lands. Strap-shaped leaves, slightly deflexed at their tips, are 10–15 cm. long, 1–1.5 cm. broad and 250–350 microns thick. Incomplete involution takes place upon wilting.

The upper epidermis is smooth, while the lower epidermis exhibits a wavy surface although there are no ridges on the abaxial side. Epidermal cells are almost prosenchymatous, 10–15 microns wide and 150–200 microns long. The cuticle is thin and the outer tangential walls of the epidermal cells are moderately thick. Stomata occur on both surfaces of the leaves. They are nearly at the same level with the rest of the epidermal cells of the adaxial surface, but the stomata of the abaxial surface are hidden within the furrows caused by the plication of the epidermal



FIGS. 8–10. Transverse sections of leaves: 8, *Merendera trigyna*; 9, *Muscari comosum*; 10, *Muscari racemosum*.

tissue on this side. Guard cells are not accompanied by subsidiary cells and there are no trichomes.

Leaves are typically isolateral; mesophyll is provided with a uniseriate palisade on adaxial and abaxial sides. Palisade parenchyma cells are nearly cylindrical in shape and are compactly crowded. Cells of the abaxial palisade are almost twice as long as the cells of the adaxial palisade. Together the two palisade layers occupy about one third of the thickness of mesophyll. Spongy mesophyll consists of 7–8 layers of cells which are loosely arranged, leaving conspicuous intercellular spaces between them. Chlorenchymatous cells are located around vascular bundles and adjacent to the inner edges of the palisade layers. Spongy parenchyma cells, located centrally in the mesophyll, are larger than the cells of the peripheral spongy parenchyma and contain few chloroplasts and large vacuoles. This water storing parenchyma gives a fleshy texture to the leaves. It is interesting to note that this tissue becomes lacunate as the leaves reach maturity. Cylindrical idioblastic cells containing raphides are abundant in the spongy mesophyll.

Vascular bundles are surrounded by a single layer of bundle sheath. Large and small bundles which are distantly spaced and which alternate with each other run along the longitudinal axis of the leaves. Small veins interconnecting the "parallel" veins are common. Sclerenchyma cells are not present.

With the exception of isolateral structure of leaves and presence of water storing tissue, *Muscari comosum* does not present any appreciable xeromorphic feature and lies rather on the mesomorphic side, especially in respect to the presence of lacunae and prominent intercellular spaces and high proportion of spongy parenchyma as compared to the proportion of palisade parenchyma. It can well be regarded as a mesoxeromorphic leaf.

MUSCARI RACEMOSUM Mill. (fig. 10) is a larger bulbous plant than *Muscari comosum* Mill. It grows in the mountain steppe. The leaves are lanceolate to almost ovate, tapering gradually toward apex. They are coated with a waxy substance which gives a glaucous appearance to the leaves. The upper surfaces of the leaves are flat and the lower surfaces are ridged. Involution takes place upon wilting although there are no bulliform cells in the epidermis.

Epidermal cells are prosenchymatous, 18–20 microns wide and 220–280 microns long. The cuticle is thicker than the cuticle of the preceding species. Outer walls of the epidermal cells are very thick and are characterized by lamellate cutinization. The wall thickness is more prominent in the epidermal cells on the abaxial surface than in those on the adaxial surface. Inner tangential walls of the abaxial epidermal cells are also thickened considerably. Portions of the abaxial epidermis beneath vascular bundles have exceedingly thick outer cell walls reaching 25 microns in thickness. These thick-walled epidermal cells contribute to the formation of abaxial ridges on the leaves since there are no hypodermal fibers along ridges. Outer cell walls of the abaxial epidermis adjacent to the mesophyll between vascular bundles are relatively thin walled. Consequently thin and thick walled portions of the lower epidermis alternate with each other following the spacing of vascular bundles and dorsal ridges as seen in transverse section. Stomata are sunken and occur on both surfaces. There are no subsidiary cells or trichomes.

Unlike the previous species, the leaves of *Muscari racemosum* are dorsiventral with a biseriate palisade on the lower side. The central portion of mesophyll is occupied by an extensive water storing tissue which takes up two thirds of the thickness of the mesophyll between vascular bundles. Water storing parenchyma cells contain very few chloroplasts. Assimilatory cells of the spongy parenchyma are situated at the peripheries of the water storing tissue and are very loosely arranged, leaving conspicuous air spaces between them. Sizable lacunae are present in the centers of water storing tissues. Although these lacunae seem to be schizogenous cavities, there is ample evidence for collapsed cell walls, suggesting that they are partly lysigenous in origin (cf. Newcombe 1894). Bizarre idioblasts containing raphide bundles are abundant in the mesophyll.

Vascular bundles are surrounded by bundle sheaths and are devoid of fibers. However, converging bundles of the leaf apex are associated with many tracheoid idioblasts. Vascular bundles are widely spaced, as in the preceding species. Transverse veinlets occur frequently, either connecting the longitudinal bundles or terminating blindly in mesophyll.

The leaves of *Muscari racemosum* also can be considered as meso-xeromorphic, especially considering the presence of large lacunae. This lacunate condition, however, may also be considered as an ancestral feature, if we follow the classical belief that the xeromorphic leaves are derived from mesomorphic leaves during evolution.

Ornithogalum is represented by ten species in the steppic flora. Only two species are considered in this paper.

ORNITHOGALUM ARMENIACUM Bak. (fig. 11) is a bulbous plant which grows in the valleys of the mountain steppe. Linear leaves are 2–3 mm. wide and 250–400 microns thick. The upper leaf surface is flat, the lower one ridged by prominent thickenings of the outer walls of epidermal cells. Involution occurs upon wilting (fig. 11B).

Epidermis is covered by a heavy cuticle. Epidermal cells of both surfaces are more or less tabular in shape, 20–22 microns wide and 247–330 microns long. Stomata are not sunken and occur on both surfaces. Guard cells are thick-walled and equipped with cutinized external ledges only. Guard cells are 13 microns wide and 39 microns long, and are not accompanied by subsidiary cells. Trichomes are not present.

The leaf is isolateral and mesophyll is provided by a uniseriate palisade on adaxial and abaxial sides. It is interesting to note that the adaxial palisade is interrupted by water storing parenchyma cells above the median vascular bundle (fig. 11a and b). Assimilatory parenchyma cells of the spongy mesophyll form one or two layers bordering the palisade layers. The central portion of mesophyll is occupied by water storing parenchyma and schizogenous lacunae. Raphide containing excretory idioblasts are abundant particularly in the spongy mesophyll and along the leaf margins.

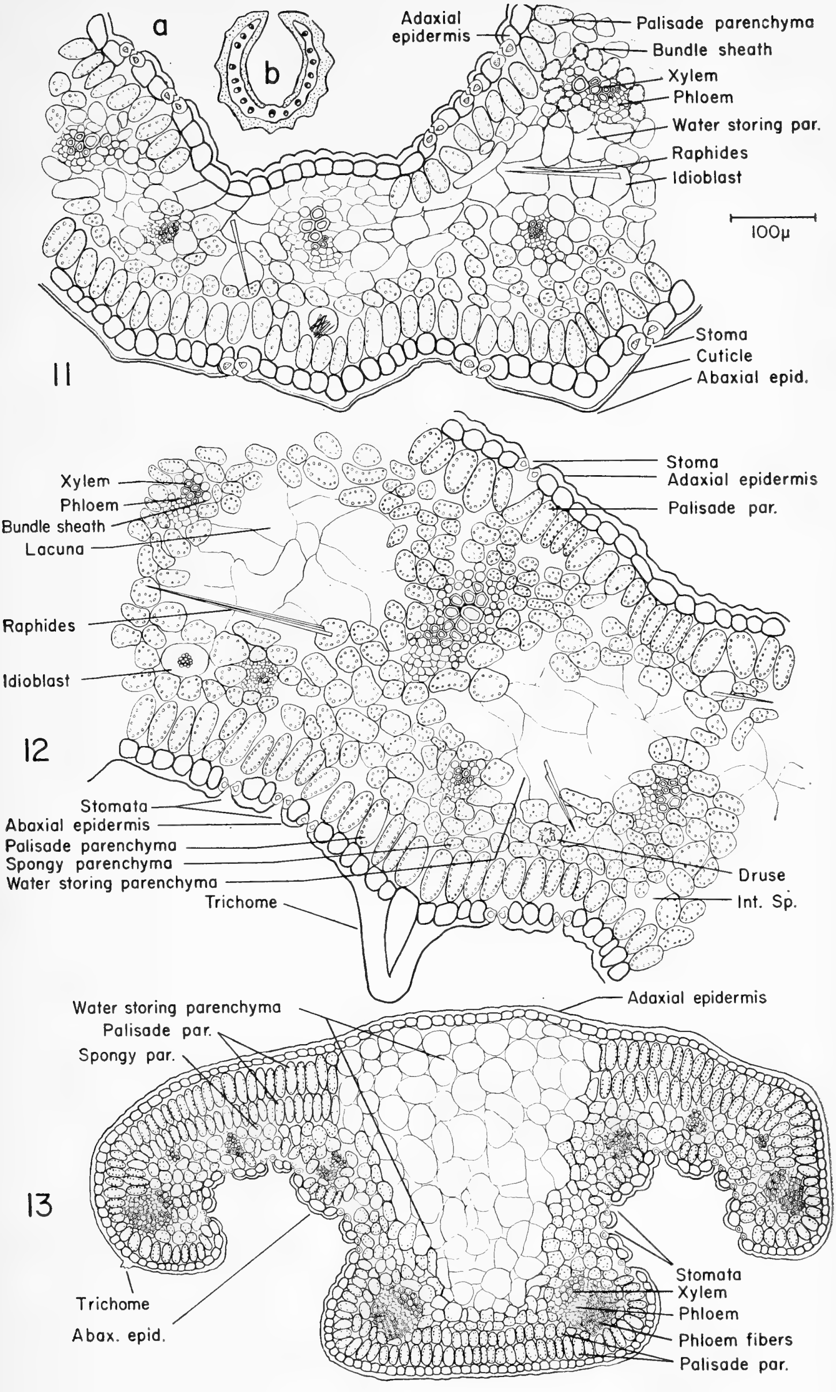
Vascular bundles lack sclerenchyma and are sheathed by bundle sheaths. Large bundles are closer to the adaxial leaf surface than are the alternating small bundles. Transverse veinlets interconnect large "parallel" veins obliquely or perpendicularly, very often without making any contact with the alternating smaller longitudinal bundles.

ORNITHOGALUM NARBONENSE L. var. PYRAMIDALE Boiss. (fig. 12) is a bulbous plant which grows in fields and fallow lands as well as in the mountain steppe. Strap-shaped, fleshy leaves are 20–30 cm. long, 1–1.5 cm. wide and 500–600 microns thick. Upper surfaces of the leaves are flat; lower surfaces are more prominently ridged than those of *O. armeniacum*. Slight involution occurs upon wilting.

The epidermis consists of very narrow cells, tapering toward the ends. Epidermal cells are 618–825 microns long, 25–30 microns wide, and 35–38 microns deep. Superficial walls of the epidermal cells project on both adaxial and abaxial sides. Outer walls of the epidermal cells are thick and heavily cutinized. Stomata are distributed throughout both surfaces of leaves and are sunken distinctly on the lower epidermis. Guard cells are 12 microns wide and 32 microns long; they are not accompanied by subsidiary cells. Two kinds of unicellular trichomes have been observed: very thick walled conical trichomes 100–110 microns long which occur along the abaxial ridges; and cylindrical trichomes 345–450 microns long which are confined to the leaf margins.

Leaves are isolateral and the mesophyll has a uniseriate, well-developed palisade on abaxial and adaxial sides. Again the adaxial palisade is interrupted by a few large cells without chloroplasts along the median groove. These cells may function as motor cells together with other cells between median bundle and epidermal cells lining the groove. Spongy parenchyma is more prominent than it is in the leaves of the preceding species. The central portion of mesophyll is occupied by a water storing tissue which consists of very large irregular parenchyma cells of 4–5 layers. Schizogenous lacunae develop within this water storing tissue in mature leaves. Excretory idioblastic cells containing druses or raphides of calcium oxalate are abundant in spongy mesophyll. Individual raphide crystals are 4–5 microns thick and 206–230 microns long. Very long isolated individual fibers occur in the mesophyll. These fibers are about 20 microns thick and 8–14 millimeters long, extending along the longitudinal axis of the leaf, not far from large vascular bundles.

The vascular bundles are more closely spaced than those of the pre-



FIGS. 11–13. Transverse sections of leaves: 11, *Ornithogalum armeniacum*; 12, *Ornithogalum narbonense* var. *pyramidale*; 13, *Crocus ancyrensis*.

ceding species. Large and small veins are interconnected by small veins which always run into major veins obliquely and never perpendicularly. Bundle sheaths are well developed around large and small bundles.

IRIDACEAE

This family is represented by *Crocus*, *Gladiolus* and *Iris* in the steppic flora. The genus *Crocus*, which has tunicated, fleshy, underground corms, is represented by six species, two of which will be considered in this paper. *Gladiolus* possesses a tunicated corm which is not so deeply buried as the corms of crocuses. *Gladiolus* is represented by a single species. The genus *Iris* is represented by four species in the steppic flora, all of them having fleshy rhizomes which become slightly woody in age.

CROCUS ANCYRENSIS Maw (fig. 13) is an endemic species abounding in the mountain steppe and blooming from February to April. It has very narrow, stiff, dark green and shiny leaves which are not differentiated into petiole and lamina. These leaves, which remind one of pine needles, represent an extremely reduced leaf type among geophytic monocotyledons of the steppic flora. Their length ranges from 5–8 cm., their width is 800–900 microns and their thickness in the middle portion of the leaf, across the dorsal ridge, is 400–450 microns. The transectional outline of the leaf is almost "T"-shaped. Lateral flaps of the leaf are revolute, 120–162 microns thick. Possibly, change of turgor pressure in the abaxial epidermal cells of the lateral flaps is responsible for the revolution mechanism.

The epidermis consists of very narrow and elongated cells which appear almost fusiform in surface view. Epidermal cells are 290–300 microns long, 14–16 microns wide and 18–24 microns deep. The cuticle is 1–2 microns thick and covers the entire leaf surface. Both outer and inner tangential walls of the epidermal cells are strongly thickened, the outer walls being much thicker than the inner ones. The lumina of the epidermal cells are highly reduced, particularly along the margins of the lateral flaps of the leaf. The stomata are sunken and appear on the abaxial surface of the foliar flaps and along the upper portions of the thickened abaxial ridge of the leaf. The adaxial surface of the leaf and the abaxial surface of the dorsal ridge are devoid of stomata. Guard cells are very small, 7–8 microns wide and 18–20 microns long. Very few unicellular trichomes occur along the margins of foliar flaps and along lateral corners of the dorsal ridge.

Leaves are isolateral in a peculiar way. A strongly developed, biseriate palisade consists of small and tightly arranged cells. Palisade is interrupted by water storing parenchyma cells on the adaxial side. Spongy mesophyll is differentiated into assimilatory and water storing tissues. Small chlorenchymatous cells of the spongy mesophyll form 2–5 rows in foliar flaps as well as in dorsal ridge, beneath palisade parenchyma. The central portion of the mesophyll is occupied by water storing tissue which extends from the dorsal ridge to the adaxial epidermis in a "V"-shape as seen in transectional view. Water storing parenchyma cells lack chloroplasts. They appear as a white band on the adaxial sides of the leaves. Crystals and idioblasts are not present.

Vascular bundles are strongly developed and run very close to each other and to the abaxial epidermis. A median bundle is not present. Each foliar flap and each "corner" of dorsal ridge is provided with a major bundle which is characterized by the presence of a well-developed bundle cap. Minor bundles have small amounts of phloem fibers or none. The minor bundles anastomose highly and interconnect the major bundles. Xylem fibers are not present and bundle sheaths are not clearly differentiated.

CROCUS SUTERIANUS Herb. (fig. 14) is another endemic species which occurs in the mountain steppe of Asia Minor. It has a spherical corm protected by a fimbriate tunic. The leaves are linear, 10–15 cm. long, 2–3 mm. wide and 200–300 microns thick in foliar flaps. With the exception of a white adaxial stripe, the leaves are dark green and stiff. The dorsal ridge is more pronounced than that of the preceding species and the transectional outline of the leaf is T-shaped (fig. 14b). The foliar flaps are revolute and roll backwardly upon wilting. Ridged middle portion of leaves is 1–1.5 mm. thick, which is twice or three times as thick as that of *Crocus ancyrensis*.

Epidermal cells, which are very slender and fusiform as seen in face view, are 130–243 microns long, 20–26 microns wide and 25–28 microns deep. The entire leaf surface is covered by a thick cuticle which reaches a thickness of 4 microns on the adaxial epidermis and on the abaxial epidermis of the dorsal ridge. Inner and outer tangential walls of the epidermal cells are very thick. Abaxial epidermal cells of foliar flaps are characterized by dome-shaped outer walls. These highly vacuolated cells are relatively thin-walled and may function as motor cells. Stomata are sunken and restricted to the abaxial epidermis of foliar flaps and to the lateral sides of the dorsal ridge. Guard cells are very small, 14 microns long and 7 microns wide. There are no subsidiary cells. Unicellular, dead trichomes occur only along the margins of the foliar flaps. Trichomes are 120 microns long and 15 microns thick.

The leaves are peculiarly isolateral as described in the preceding species. The adaxial palisade consists of narrow cylindrical cells which are tightly arranged and biseriate, but the cells tend to be in three layers near water storing tissue. The palisade tissue is strongly developed at the expense of spongy parenchyma in the foliar flaps and occupies more than half of the thickness of the mesophyll. Again the spongy mesophyll is differentiated into assimilatory and water storing tissues (fig. 14a and b) as described for *Crocus ancyrensis*. Assimilatory spongy parenchyma cells are small, tightly arranged and form four layers on the abaxial side of the foliar flaps and in dorsal ridge. Water storing parenchyma cells are large and have prominent air spaces between them. Idioblasts containing large prismatic crystals are abundant in the assimilatory spongy tissue. These crystals are 15–16 microns thick and 97–146 microns long. The idioblasts are situated around the bundle caps and occasionally occur also "scattered" within the assimilatory spongy mesophyll.

Vasculation of the leaves is similar to that of *Crocus ancyrensis* with minor differences. The major bundles along the margins of foliar flaps and those at the "corners" of the dorsal ridge are accompanied by xylem and phloem fibers. Furthermore, the bundle sheaths are more distinctly differentiated and the vascular bundles more compactly arranged than those of *C. ancyrensis.*

GLADIOLUS ATROVIOLACEUS Boiss. (fig. 15) is a cormous plant 30–55 cm. high. It has a wide distribution in the Middle East. It grows in fields, fallow lands as well as in mountain steppe. The leaves are strap-shaped, firm, strongly ribbed, 15–20 cm. long, 4–5 mm. wide and about 0.5 mm. thick. From the morphological point of view, these leaves present a very peculiar structure. Typically, the leaves are unifacial, with inverted bundles, but the presence of two marginal bundles and a prominent marginal groove (fig. 15a and b) along one edge of the blade and the presence of a single bundle with a well developed ridge along the other edge of the blade suggests the folding and fusion of two halves of the blade during ontogeny. However, there is no evident line of fusion in the mesophyll. The problem may be solved by an ontogenetic study. Corms are ovoid, tunicated and buried superficially in ground.

If the interpretation of the foliar structure given above be true, the epidermis of upper and lower leaf surfaces may represent the abaxial epidermis only. The epidermal cells are tabular in form, 48 microns long, 30 microns wide and 20 microns deep. The cuticle is 2 microns thick on the blade surface and 4–5 microns thick along leaf margins. Epidermal cells form 2–5 papillose projections. Stomata are sunken and occur on both leaf surfaces. Epidermis of the projecting ribs has no stomata or trichomes.

The leaves are isolateral in the sense that abaxial and adaxial sides of the leaves present identical structure, but the mesophyll is not differentiated into palisade and spongy parenchyma. The mesophyll consists of very small, tightly arranged, elliptical cells which resemble palisade, but they lie parallel to the leaf surface. Water storing parenchyma cells are situated between opposite major ribs of the blade (fig. 15b). Idioblasts containing prismatic crystals are distributed at random within mesophyll. Crystals are 16 microns thick and 65–160 microns long. Tracheoid idioblasts occur commonly in mesophyll.

Major vascular bundles are accompanied by bundle caps and project on leaf surfaces as well as along leaf margins. Major bundles extend "parallel" but the minor bundles which are imbedded in mesophyll anas-

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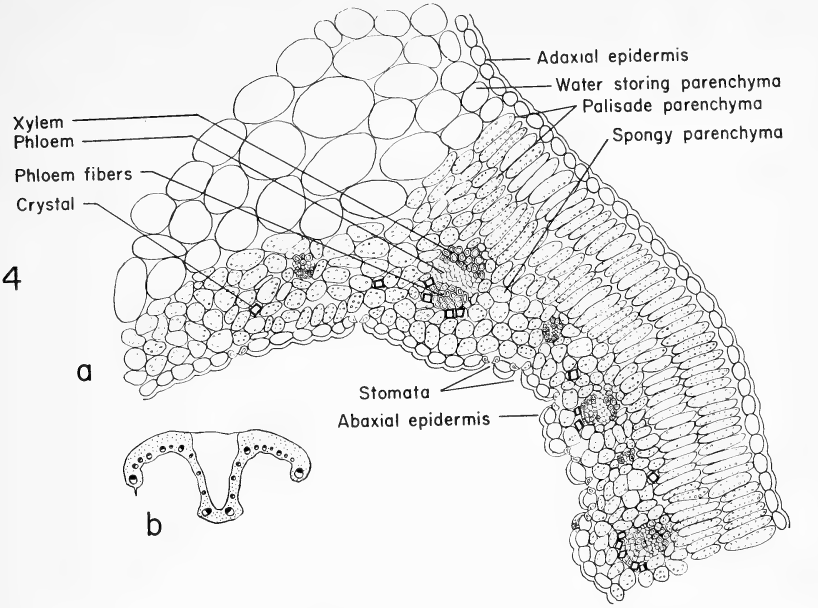

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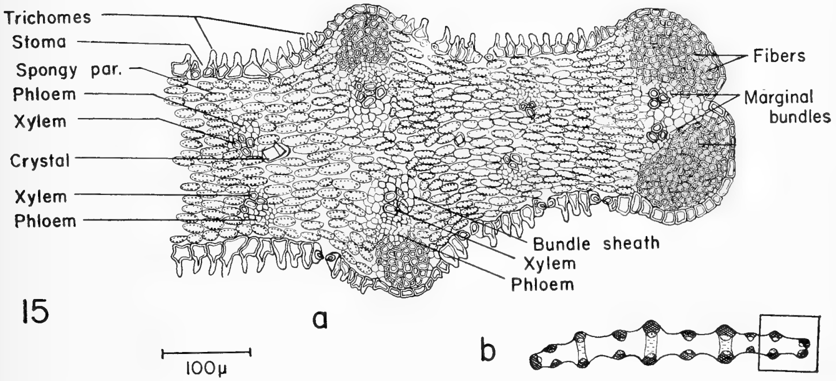


Figs. 14–15. Transverse sections of leaves: 14, *Crocus suterianus*; 15, *Gladiolus atroviolaceus.*

tomose frequently and interconnect the major bundles. Minor bundles lack fibers and are surrounded by bundle sheaths. As a whole, the leaves present a compact vascular system.

Iris aphyllus L. (fig. 16) is a rhizomatous plant occurring in the mountain steppe and in the openings of forest remnants of the steppic region. Bluish-green, sword-shaped, erect leaves are 10–15 cm. long, 1–1.5 cm. broad and 800 microns thick in the lower sheath portion, 400 microns thick in the upper blade portion. Unifacial structure of leaves with inverted vascular bundles is seen clearly (fig. 16a, b, and c).

Epidermal cells are 227 microns long, 48 microns wide and 39 microns deep and rectangular in form. Stomata are sunken and occur on both surfaces of the blade. However, there are no stomata on the adaxial epidermis of the flaps in sheathing lower portions of leaves. Considering the development of these unifacial leaves, it is understandable that a similar epidermis occurs all around the upper blade portions of leaves; therefore the actual distribution of stomata would be confined to abaxial epidermis only. The guard cells are typically reniform, 50 microns long and 25 microns wide. There are no subsidiary cells. Unicellular, thick walled trichomes occur on the abaxial epidermis only and there are no trichomes on the adaxial epidermis of sheathing flaps. The trichomes are 40 microns long and conical in shape.

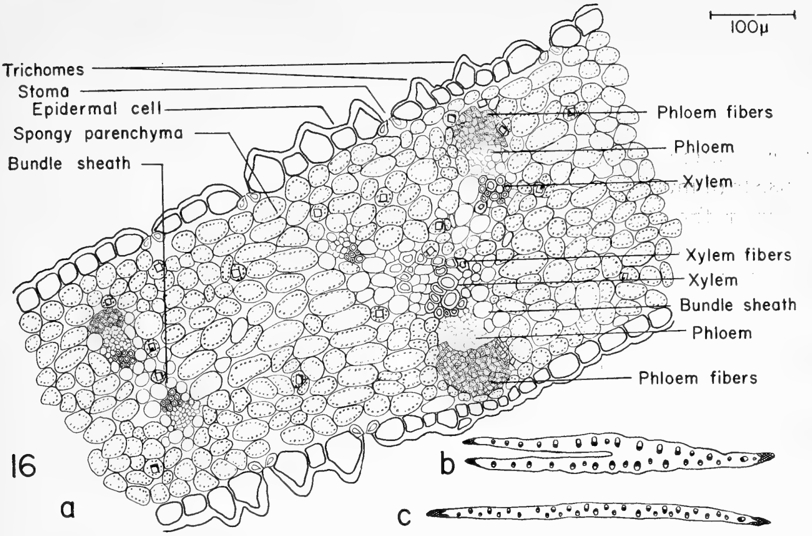
The blades are isolateral in the sense that both sides of the blades are similar in regard to uniform mesophyll and inverted bundles, although there is no palisade tissue. On the other hand sheathing flaps present a dorsiventral structure since mesophyll is differentiated into water storing parenchyma on the adaxial side and assimilatory parenchyma on the abaxial side. Furthermore xylem tissues of vascular bundles face the adaxial epidermis in sheathing flaps (fig. 16b). The mesophyll of the blade consists of elliptical spongy parenchyma cells lying with their longitudinal axes parallel to leaf surfaces. This is quite similar to the situation found in *Gladiolus* leaves except that the parenchyma cells in *Iris* leaves are at least twice as big as the assimilatory parenchyma cells of *Gladiolus* leaves. Extensive water storing tissue occupies the central part of the mesophyll in lower sheathing portions of leaves. Idioblasts containing prismatic crystals are abundant in mesophyll. These crystals are very similar to those found in the leaves of *Crocus suterianus* and *Gladiolus atroviolaceus*.

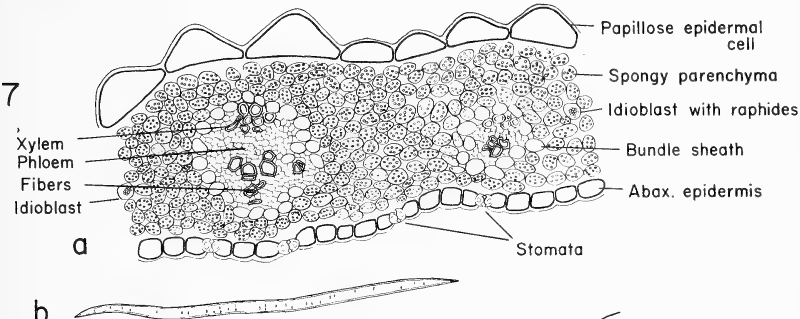
Vascular bundles of the leaves are strongly developed, but are not as compact as the bundles in *Crocus* and *Gladiolus* leaves. The bundle caps also are strongly developed along major veins, but do not project as ribs on the leaf surface. Xylem tissues of the major veins possess a few fibers. Phloem fibers are lignified while thick walls of xylem fibers do not show any sign of lignification. Veinlets interconnecting the major bundles occur frequently. Some of the veinlets terminate blindly in mesophyll and very often are associated with tracheoid idioblasts at their tips. Strands of fibers occur along the margins of sheathing blades as well as along both edges of blades (fig. 16b and c).

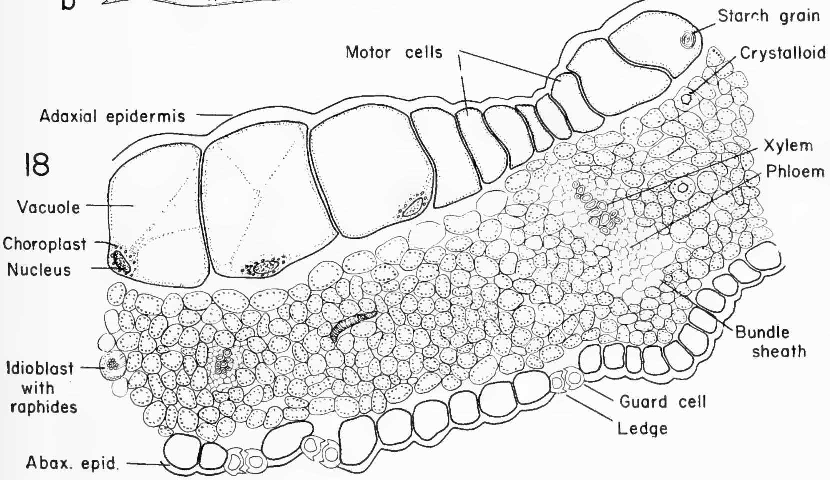
ORCHIDACEAE

This family is represented by a number of terrestrial orchids which grow in moist places of the steppic region. The specimens of *Limodorum abortivum* and *Orchis mascula* subsp. *pinetorum* were collected from an open pine forest in Beynam at an altitude of 1450 meters.

LIMODORUM ABORTIVUM (L.) Sw. (fig. 17) is a saprophyte with well developed fleshy rhizomes. Scale-like leaves are small, very tender and nearly surround the scape. Apical portions of these leaves slightly diverge







FIGS. 16–18. Transverse sections of leaves: 16, *Iris aphyllus*; 17, *Limodorum abortivum*; 18, *Orchis mascula* subsp. *pinetorum*.

from the scape and form a short blade about 2–3 cm. long, 1–1.5 cm. broad and 250–300 microns thick. Involution occurs slightly upon wilting.

The adaxial epidermis consists of large tabular cells with papillose outer walls. Water storage takes place in upper epidermis. The abaxial epidermis consists of much smaller cells than those of the adaxial epidermis. Stomata occur on the abaxial epidermis only and are not sunken. Guard cells are 65 microns long and 23 microns wide. Each stoma is surrounded by six subsidiary cells, each guard cell being subtended by three of them. The presence of four *Tradescantia*-type subsidiary cells was reported by Solereder and Meyer (1930) in some orchidaceous genera. The radial walls of subsidiary cells extend toward the stomatal opening, the stomatal apparatus as a whole resembling a rosette in face view.

Mesophyll is not differentiated into palisade and spongy parenchyma and consists of more or less uniform isodiametric parenchyma cells arranged tightly. Patches of tracheoid idioblasts, fibers and mucilage- or raphide-containing excretory idioblasts are present in mesophyll. The occurrence of such a great variety of idioblasts together in one species was not observed in other species of the present study.

Major vascular bundles present a striate pattern, but minor bundles anastomose frequently and form also peculiar zigzags extending back and forth and interconnecting major bundless eventually.

ORCHIS MASCULA L. subsp. PINETORUM Boiss. (fig. 18) has tuberous fleshy roots protected by a dark brown cork tissue. The leaves are basal, flat and very tender, 10–15 cm. long, 1.5–2 cm. wide, 350–450 microns thick. Upper leaf surface is grooved along the median bundle and the lamina halves fold over along the median bundle when a water deficit develops.

The adaxial epidermis consists of remarkably large tabular cells 340–550 microns long, 100–150 microns wide and 120–200 microns deep. These cells are characterized by thick outer walls, peripheral cytoplasm and large vacuoles. Their nuclei are pushed against inner tangential walls. They contain chloroplasts and concentric starch grains. Epidermal cells along the adaxial groove are specialized as motor cells and are much smaller than adjacent water storing epidermal cells. Adaxial epidermis is mainly responsible for the fleshy nature of the leaves. The occurrence of water storing epidermis was reported by Metzler (1924) for other orchidaceous genera such as *Dendrobium, Otochilus, Pholidota* and *Pleione*. The abaxial epidermis consists of much smaller cells. Stomata occur on the abaxial epidermis only and are not sunken. Guard cells are 70 microns long, 35 microns wide and are equipped with strongly developed inner and outer ledges. Subsidiary cells and trichomes are not present.

Mesophyll consists of small isodiametric parenchyma cells which are arranged rather tightly. Idioblasts containing protein crystalloids (Kuester 1935) and raphide bundles associated with mucilage occur at random in the mesophyll. There is no sclerenchyma, but a strand of a few hypodermal collenchyma cells occurs occasionally on the dorsal side of the ridge.

Vascular bundles are widely spaced. Major and minor veins anastomose frequently. Bundle sheaths are differentiated distinctly around major bundles.

The leaves of *Limodorum abortivum* and *Orchis mascula* subsp. *pinetorum* do not show striking xeromorphic features with the exception of folding of blades, epidermal water storage, compactness and decreased cell size in the mesophyll, and abundance of excretory idioblasts. On the other hand they exhibit a prevailingly mesomorphic structure, and may be considered as mesoxeromorphic.

The present study shows that not all xeromorphic characters occur universally in the leaves of the geophytic monocotyledons investigated. Each plant exhibits a different combination of xeromorphic features. Furthermore, there are quantitative differences in the degree of development of each particular xeromorphic feature. I believe many of these xeromorphic characters are genetically fixed as the result of a natural selection in this semi-arid environment. Consequently these plants are morphologically and physiologically adapted to tolerate the factors of the environment. Drought is one of the most severe factors and the plants in question are well adapted to survive drought. On the other hand some of the features described may represent xeroplastic characters which may be subject to qualitative and quantitative changes under varied conditions of the environment. It would be very desirable to conduct an experimental study using controlled conditions to determine the extent of plasticity of the foliar xeromorphic features.

SUMMARY

The foliar histology of eighteen species of geophytic monocotyledons representing Araceae, Liliaceae, Gramineae, Iridaceae and Orchidaceae has been described. The research materials were collected wholly from the central Anatolian steppic region. They exhibit certain uniformities such as geophytism, shallow root distribution, leaf shape, osmotic concentrations, and phenological periodicity.

Xeromorphic characters observed in gross morphology and in anatomical structure do not occur universally in the leaves of all plant species studied, but each species exhibits combinations of certain foliar xeromorphic features as follows. Reduction of the leaf surface: *Allium stamineum, Crocus ancyrensis, C. suterianus*; revolute margins: *Crocus ancyrensis, C. suterianus*; unifacial leaves: *Allium rotundum, A. stamineum, Gladiolus atroviolaceus, Iris aphyllus*; involution or folding of blade upon wilting: *Hordeum bulbosum, Poa bulbosa, Allium rotundum, Colchicum biebersteinii, Gagea arvensis, Merendera trigyna, Muscari comosum, M. racemosum, Orchis mascula*; increased thickness of the blade: *Allium stamineum, Crocus ancyrensis, C. suterianus*; strong cutinization of epidermis: *Allium rotundum, A. stamineum, Colchicum biebersteinii, Gagea arvensis, Merendera trigyna, Muscari racemosum, Ornithogalum armeni-*

acum, O. narbonense, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus; increased thickness of the epidermal cell walls: *Allium rotundum, A. stamineum, Colchicum biebersteinii, Merendera trigyna, Ornithogalum armeniacum, O. narbonense, Crocus ancyrensis, C. suterianus, Orchis mascula*; depression of stomata: *Poa bulbosa, Allium rotundum, A. stamineum, Merendera trigyna, Muscari racemosum, Ornithogalum narbonense, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus, Iris aphyllus*; the occurrence of trichomes: *Allium stamineum, Gagea arvensis, Merendera trigyna, Ornithogalum narbonense, Crocus suterianus, Gladiolus atroviolaceus, Iris aphyllus*; epidermal water storage: *Gagea arvensis, Limodorum abortivum, Orchis mascula*; isolateral leaf: *Allium rotundum, A. stamineum, Colchicum biebersteinii, Merendera trigyna, Muscari comosum, Ornithogalum armeniacum, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus, Iris aphyllus*; strongly developed palisade parenchyma at the expense of spongy parenchyma: *Allium stamineum, Merendera trigyna, Ornithogalum armeniacum, Crocus ancyrensis, C. suterianus*; compactness of the tissues: *Poa bulbosa, Allium rotundum, Merendera trigyna, Crocus ancyrensis, C. suterianus*; decreased size of cells: *Poa bulbosa, Allium rotundum, Merendera trigyna, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus, Orchis mascula*; water storing tissue in mesophyll: *Allium rotundum, A. stamineum, Gagea arvensis, Muscari comosum, M. racemosum, Ornithogalum armeniacum, O. narbonense, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus, Iris aphyllus, Limodorum abortivum*; relative compactness of vascular bundles: *Hordeum bulbosum, Poa bulbosa, Allium rotundum, Colchicum biebersteinii, Merendera trigyna, Ornithogalum narbonense, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus*; strongly developed fibers: *Hordeum bulbosum, Poa bulbosa, Allium rotundum, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus, Iris aphyllus.*

The leaves of *Arum orientale, Gagea arvensis, Muscari comosum, Limodorum abortivum* and *Orchis mascula* have been designated as mesoxeromorphic, since they exhibit structural features intermediate between mesomorphic and xeromorphic leaves.

In spite of the adaptive responses of any particular tissue to the xeric environment, the anatomical structures of the monocotyledonous leaves studied are highly specialized and the pattern of tissue organization is quite distinct even between species of the same genus.

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REVIEWS

Die Evolution der Angiospermen. Von Professor Dr. Armen Takhtajan, Leningrad. Aus dem Russischen übersetzt von W. Höppner, Berlin. viii + 344 pages, 43 figures. VEB Gustav Fischer Verlag, Jena. 1959.

The review of this book by our fellow-member of the California Botanical Society, Dr. Lincoln Constance (Science 132:801. 1960), led me to order it from Messrs. Stechert-Hafner. It is not available in this country. Sent from East Germany, it arrived in about three months, with a bill for $11.65, including postage.

About two thirds of the work may be described as prolegomena. The workings of evolution in general are described; as details, the frequency of neoteny (this term is distinguished from *paedomorphosis*, and preferred to it), and of parallel development, are noted; the hypothesis of a profound difference in mechanism between macroevolution and microevolution is denied. The generally accepted hypotheses as to the usual directions of evolution in the plant body, the xylem, phloem, vascular anatomy of the node, the leaf, the flower and its parts, the fruit and seed, are duly set forth. The telome theory, which denies the foliar nature of stamens and carpels, is rejected.

The flowering plants are held to be genuinely a natural group, being of a single evolutionary origin. The original flowering plants are believed to have been large-leaved trees of tropical mountains.

Surely, the original flowering plants were homoxylous, i.e., without vessels in the wood. The plants now living which are homoxylous as a primitive character (Lemnaceae, at least, are homoxylous by reduction) are primitive in all of their characters. Nevertheless, these few appear to be related to widely divergent heteroxylous groups. Takhtajan suggests the independent origin of vessels in at least five distinct lines of descent. Winteraceae, allied to Magnoliaceae, appear to represent the origin of the bulk of the dicots. Trochodendraceae and Tetracentraceae appear to lead into Amentiferae, and *Amborella* and *Sarcandra* into minor lines. The Nymphaeaceae appear to represent the ancestry of the monocots. Thus certain hypotheses maintained by Bailey and Cheadle are at the same time applied and convincingly supported: the presentation is *elegant* in the sense in which our mathematical and physical colleagues use the term.

Referring primarily to the body of opinion which has just been sketched, Constance remarks, "If in all this there is very little that is startlingly new to Western students of plant evolution, it is interesting to discover that the climate of opinion is not radically different between East and West." I think that there is something more to say. The Russian botanists know everything that we know; Takhtajan cites Bailey and Cheadle, Gundersen and Cronquist. We, on the other hand, can not be certain that political and linguistic barriers have not withheld from us much pertinent information. How many American botanists have cited Koso-Poljansky?

These same opinions of Takhtajan are available also in two essays which have been translated into English by Mrs. Olga Hess Gankin, edited by G. Ledyard Stebbins, published by the American Institute of Biological Sciences, and reviewed by Constance, along with the book, as cited above. In one of these translations, the mere skeleton of Takhtajan's system of the flowering plants is included as an appendix.

In the book, Takhtajan's conception of the phylogeny and the system of the flowering plants constitutes the remaining one-third of the text. The extent of this presentation makes possible a statement of the reasons which have guided him in the placement of each family. I did not note among the prolegomena a statement that no division of the flowering plants into major natural groups, beyond the distinction of dicots and monocots, can be made by any small number of definite characters; that among apetalae, choripetalae and sympetalae, between woody plants and herbaceous, or in any similar system, at least some of the groups are artificial. Neither did I find the correlative statement, that the true system is perceived by recognizing the connections between groups, no matter what may be the characters which indicate these connections. Without stating these principles, Takhtajan has evidently been guided by them. Some years ago, I dared predict that the main outlines of the natural system of the flowering plants would become essentially completely known within our lifetime. I consider that Takhtajan has essentially fulfilled this prediction. Delaying discussion of the taxonomic pattern which he has produced, I shall sketch the phylogeny as Takhtajan sees it, interpolating remarks, among which only the few references to plants which I have personally studied have any claim to authority.

As noted, Takhtajan derives the Amentiferae from something of which the Trochodendraceae and Tetracentraceae are the surviving representatives; these being immediate derivatives of the unknown original flowering plants. The Hamamelidaceae-Platanaceae group is an important secondary center among the Amentiferae, which include also the Juglandaceae and associated families, and the odd monotypic American family Leitneriaceae.

Lauraceae and their allies, including *Amborella*, and the Englerian Piperales, including *Sarcandra*, are treated as minor lines of descent as ancient as any among flowering plants; and Aristolochiaceae (among which the most ancient have apocarpous flowers), with associated families, are treated as another such line.

The remainder of the Englerian Ranales (Winteraceae, Magnoliaceae, Ranunculaceae, Berberidaceae, etc.) lead to the remainder of the dicots. A first offshoot includes the Centrospermae (including Cactaceae) and Papaveraceae.

Starting again from Ranales, the Dilleniaceae-Theaceae group is recognized as a second node in the main line of descent of the dicots. Offshoots at this node include Ericales, Ebenales, a wide range of Parietales (including Salicaceae), and Malvales, with Euphorbiaceae in the same neighborhood.

I was surprised to find Cyrillaceae in Ericales. Cyrillaceae have many of the characters of Bicornes, but seemed excluded by formal characters, notably by the presence of a typical endothecium in the anthers. Takhtajan's Ericales is an extended group, including, with the authority of Schnarf, Saurauiaceae and Actinidiaceae. It now seems to me that if he had placed Cyrillaceae near these families, rather than near Empetraceae, he would have given satisfactory expression to the apparent relationships.

Capparidaceae and Cruciferae are placed near the Parietales. I would have thought that Eames' study of carpels had fixed the position of these families near Papaveraceae.

From the Dilleniaceae–Theaceae group, the main line of descent of the dicots goes on to a third note in Rosales *sensu lato*. From this group spring (1) Myrtales; (2) Rutales-Sapindales-Geraniales-Polygonales (I question this last); (3) Umbelliflorae; and (4) Celastrales-Rhamnales-Santalales. The great family Proteaceae, rather strange to us, is placed near Santalaceae. Since the Proteaceae have simple pistils, this association appears mistaken.

It is generally agreed that the bulk of the Sympetalae—the old orders Contortae, Tubiflorae, Rubiales, and Campanulatae—belong together. Cronquist treated them so. Without strongly committing himself, he appeared disposed to derive them from the Dilleniaceae–Theaceae group. Takhtajan derives them from the neighborhood of Celastraceae. To us, to whom Celastraceae are known merely by cultivated plants of *Euonymus japonica*, the connection is not evident.

A system of the monocots—derived from Nymphaeaceae, these in turn having as old an origin as Amentiferae, Laurales, Piperales, and the main line of the dicots—is duly set forth.

So much for Takhtajan's conception of the phylogeny of the flowering plants, in which only some three or four points have appeared to call for serious question. We shall not abandon detailed studies of species and groups; I expect, however, that the results of these studies will tend to strengthen the hypotheses of relationship which Takhtajan has set forth very much more frequently than they will tend to weaken them.

In the taxonomic expression of his phylogenetic hypotheses, Takhtajan has divided several families; recognized numerous orders of few families (of dicots and monocots together, he has provided eighty-two orders, grouped in eighteen superorders); and designated every order by the stem of a generic name with the termination *-ales*. These practices are the current style or mode-trend. I deprecate them. Is a well-founded opinion, that some two or three families belong together, of sufficient significance to require expression in the category of orders? On most occasions, I think not; what we wish to know of each family is to what group of a dozen or more families it belongs. And as to names, to write Theales (or Guttiferales), Ericales, Malvales, or Gentianales, is to contribute to erasing from memory some of the facts of history, namely that these groups were known, during a period of a century or more, as the orders Guttiferae, Bicornes, Columniferae, and Contortae.—HERBERT F. COPELAND, Sacramento City College, Sacramento 22, California.

Blakeslee: The Genus Datura. By AMOS G. AVERY, SOPHIE SATINA, and JACOB RIETSEMA. xli+289 pp., frontispiece, 67 figs, 34 tables. The Ronald Press Co., New York, 1959. $8.75.

This volume is a monumental review of investigations on the genus *Datura*. The authors, all collaborators of Dr. Alfred Francis Blakeslee, internationally recognized expert in genetics and leader of a devoted group of associates, have given a complete account of more than 40 years of scientific research on this justly famous genus. Focused on genetical studies, the research program was one of the broadest and most complete ever made of plants comprising a single genus. Included is a complete *Datura* bibliography of the 228 published papers of Dr. Blakeslee and associates. An interesting feature is a historical review of the taxonomy of the genus including descriptions, figures, and notes on the ten known species included in the sections *Stramonium, Dutra,* and *Ceratocaulis*. Section *Brugmansia,* regarded by many taxonomists as a separate genus, is not considered. The sole published summary of the *Datura* nomenclature from 1753 is also included. Nearly 1,400 collections of *D. stramonium,* the most widely investigated species, from many localities scattered all over the temperate zones were grown and studied.

The advanced student of genetics and the tyro alike should find much of interest in the preface, the foreword, and the historical review. The former will be reminded of the tremendous contributions to our understanding of fundamental genetical phenomena made through the investigation of one genus, of the ramifications which result from following up promising leads, and of the influence these researches have had on subsequent biological thinking and experimentation. If the tyro reads no more than the historical review by A. G. Avery, with its account of the medical, ceremonial, and cultural influences of this widely known solanaceous genus, his imagination should be stimulated. He should come away with an appreciation of the depth of genetical roots as he visualizes Kolreuter, Gaetner, Naudin, Godron, de Vries, and Bateson at work on these puzzling plants. In this account, as well as in Dean Sinnott's biographical sketch of Dr. Blakeslee, the career of a distinguished teacher, organizer, and investigator stands revealed in a stimulating manner, while attention is drawn to a magnificent cooperative venture.

A short chapter on the alkaloids of *Datura* by Edward Leete refers to the chemistry, distribution, pharmacology, and biogenesis of these useful substances and clearly indicates the need for further information at both practical and theoretical levels.

For many readers the chapters on "Chromosome Number and Morphology," "Polyploidy," and "Extra-Chromosomal Types" will strike responsive chords. They will be reminded of the use of Belling's iron-acetocarmine technique, of plant breeding methods, of the production of induced polyploids, and of the use of cold, injury, radiation, growth substances, and various other chemicals, including the pioneering work on the use of colchicine, as aids in experimentation. Interesting and valuable ideas were developed through combined cytological and genetical examination of the polyploids and extra-chromosomal types. Segmental interchange and ring formation, comparisons of the effects of single additional chromosomes with the duplication of complete sets of chromosomes, and the evolution of genetic systems come readily to mind as one flips the pages concerned with the details of these and other important phenomena.

Only two allelomorphic pairs of characters had been described prior to 1919 when Blakeslee and Avery reported the first of numerous mutations observed by the Cold Spring Harbor group. The total number of known gene pairs approaches 550 and, among plants, is probably exceeded only by those in *Zea*. These mutations affect all parts of the plant, have appeared either spontaneously or, more often, as a result of a variety of treatments, and are discussed at some length in the chapter on "Gene Mutations." Because of the enormous amount of work required, relatively little attempt was made to locate most of the genes. Nevertheless, genes responsible for 81 distinct mutations representing twelve linkage groups have been located. Methods for constructing maps of the several chromosomes are described. Certain markers have been very useful in various investigations of particular interest, including those investigations affecting male and female sterility.

Miss Satina's short, compact, and beautifully illustrated and organized chapter on "Chimeras" deserves careful reading. Here emphasis on the advantage of utilizing chimeras for obtaining information on the histogenesis of plant structures merits reiteration. The controversy on the origin, nature, and organization of apical meristems and other initials has engaged the attention of many botanists over a long period of years. Perhaps further study of chimeras along the lines suggested by the *Datura* work will help elucidate this perennial problem and will also offer evidence for the diverse functions of the epidermis which have been suggested. The use of periclinal chimeras as a tool in investigating a variety of morphogenetic problems should receive wider recognition.

A chapter on "Radiation Experiments" by A. G. Avery and Jean Cummings gives considerable detail on both methods and results. In this review, already becoming too lengthy, the chapter summary seems to be an efficient device for giving its essence:

> In *Datura,* as in so many other organisms, radiations have been very useful as inducers of genic and chromosomal mutants, and these in turn have been helpful in clarifying the answers to many questions of morphogenesis and physiology. On the other hand, it has been possible to use the knowledge gained from irradiated plants in the comparison of the effectiveness of different types of radiations—thermal and fast neutrons from various sources. To a great extent the conclusions seem clear-cut. All the radiations so far tested seem to cause the same types of both genic and chromosomal aberrations, but the effectiveness of the different radiations is quite different. Neutrons cause much greater effects, both genic and chromosomal, than do either x-rays or gamma rays for equivalent energies.

Geneticists have long since learned the need for a thorough knowledge of the life history of any experimental organism and the *Datura* team is no exception. Clear descriptions of the growth and activity of the tissues associated with reproduction, fertilization, and of the development of the embryo, endosperm, and seed coats are given by Satina and Rietesema in chapters 10 and 11.

"Barriers to Crossability: Prefertilization" and "Barriers to Crossability: Postfertilization" are two important chapters full of suggestions for future research. An inventive and imaginative approach to many experimental problems is presented.

Extensive studies of pollen viability, germination, and pollen-tube growth are summarized. The fate of embryos and endosperm in incompatible crosses, the growth of ovular tumors, and the physiological aspects of seed abortion are among the topics discussed.

In later years special attention has been paid to the vital link between generations, the seed. Problems of incompatability, sterility, and abortion required attention and led to the development of a method for the culture of embryos. Many observations have led to a partial understanding of the numerous complex processes going on simultaneously in the growing seed. Here are dozens of unsolved problems for which the *Datura* investigators suggest promising lines of attack.

In the chapter on "Segmental Interchanges and the Species Problem," Miss Satina assembles considerable material on prime types, racial differences, interspecific hybrids, and the characteristics of hybrids from incompatible crosses. The problems of chromosome analysis, ring formation, and of chromosome-end arrangements are examined. The abundant occurrence of segmental interchange present in the various races of *Datura* is unusual, but the condition is known in some other plants. In spite of intensive study, the exact relationship of the phenomenon to speciation remains obscure. We may agree with Blakeslee when he says that, "The frequency of interchange of chromosomal fragments in *D. stramonium* and the relation of this phenomenon to the formation of new pure-breeding types has led to the hypothesis that segmental interchange has accompanied the changes responsible for the formation of species in the genus *Datura*. Nevertheless, in spite of very intensive study the relationship of the phenomenon to speciation remains obscure." We may hope that some day *Datura* will be a valuable instrument in helping us work out the relationship between genes and chromosomes which will further our understanding of the evolutionary picture.

The scientific world owes its gratitude to Smith College and the National Science Foundation for contributing assistance, facilities, and finances towards the completion of this work. Congratulations are due the Ronald Press for its part in this fine enterprise, for the volume is pleasing in all aspects. High praise is due the committee of the Genetics Society of America which catalyzed the reaction which resulted in the publication of this labor of love.

Attention should be called to page three of the volume, which carries an invitation to investigators interested in securing material of the Jimson weed in order to add further chapters to our knowledge of the members of this fascinating genus.—ALTON H. GUSTAFSON, Department of Biology, Bowdoin College, Brunswick, Maine.

Vascular Plants of the Pacific Northwest. By C. LEO HITCHCOCK, ARTHUR CRONQUIST, MARION OWNBEY, and J. W. THOMPSON. Illustrated. University of Washington Press. Part 5, pp. 1–343. 1955. $7.50. Part 4, pp. 1–510. 1959. $12.00.

Present or future students of the Pacific Northwest flora will find their time well spent in carefully looking through the two volumes now available of the projected five-volume "Vascular Plants of the Pacific Northwest." It is a credit to the authors that they have drawn on their wide experience in the western flora to point out and discuss specific problems such as unusual variation patterns, possible hybridization, disjunct or vicarious distributions, and a host of other phenomena which suggest a number of areas requiring the attention of biosytematists, plant geographers, genecologists, and cytologists. This is merely a bonus added to a sound taxonomic treatment of the 4000 vascular plants (upon completion) either native or introduced in "all of Washington, the northern half of Oregon, Idaho north of the Snake River Plains, the mountainous portion of Montana, and an indefinite southern fringe of British Columbia." The area circumscribed is a natural floristic unit and excludes most of the interesting but large Great Basin flora occurring in the southern portions of Idaho and Oregon as well as the sizable cluster of endemic or California-centered species characteristic of southwestern Oregon.

The two volumes published to date are Parts 4 and 5 of the series: Part 5 is a monograph of the Compositae by Arthur Cronquist and Part 4 includes treatments by Cronquist (Polemoniaceae through Campanulaceae, except *Castilleja*), C. Leo Hitchcock (Ericaceae through Cuscutaceae), and Marion Ownbey (*Castilleja*). Although J. W. Thompson has not yet contributed texts, his valuable and extensive collections in the Northwest serve as a substantial basis for the present knowledge of the northwestern flora, hence his inclusion as a co-author is fully justified even in the absence of such textual material. The families are arranged in the Englerian sequence; the genera and species within a genus are arranged alphabetically. This practice eliminates the need for an index, although one to the synonyms of the larger genera and to common names is included. The chief difficulty with this alphabetical arrangement is that closely related species and genera are placed together only rarely, thus rendering a character-by-character comparison of two taxa (as is often done during the course of identification) rather more difficult. Taxonomic concepts are admittedly conservative, which results in the volumes being attractive for purposes of identifying species of such name-ridden genera as *Aster, Castilleja, Erigeron,* and *Senecio*.

In Part 5, Cronquist outlines his philosophy of taxonomy, which we assume to be the philosophy of the other authors as well in the absence of any statements to the contrary. His discussion is worth reading since he presents particularly well his views as an "orthodox" taxonomist on some of the attitudes held in the past by experimentally oriented workers. The term *variety* is preferred to *subspecies* when only one infraspecific level is recognized. In a few instances where it has been necessary to utilize two infraspecific levels, *variety* is subordinate to *subspecies*; *forma* is not used. It is a reflection of the authors' conservatism that infraspecific categories are widely used for entities which other workers prefer to recognize as species. In attempting to conform to their system, numerous changes in rank of many taxa have been made, involving transfers from subspecies to variety. Fortunately, these changes have been rendered somewhat inconspicuous by their placement among the synonymy of the species. The synonymy of each species is laudably complete and gives the full bibliographical citation, the collector, locality, and date of collection for the type of each synonym.

The volumes issued to date have served as vehicles for the publication of three highly localized species: *Chaenactis thompsonii, Hackelia davisii,* and *Luina serpentina*—appropriately endemic to Washington, Idaho, and Oregon respectively. In addition to these new species, numerous varieties are described for species of many genera. This emphasizes the fact that the Pacific Northwest is far from completely known botanically. In addition to these novelties, numerous changes of rank and transfers from one taxon to another are made. Hence this work can hardly be called an automatic compilation; rather it is an original, critical treatment of all the species it covers. The geographical ranges of the taxa are specifically outlined and, where known, ecological data regarding the habitat are included as well.

Although the authors have made extensive use of existing taxonomic monographs (many of which are cited in the text), they have obviously felt no obligation to follow these works in their own treatments. Undoubtedly they will receive criticism for their handling of many groups, but the citation of monographs and the lists of synonyms will make it easy for those who do disagree on some count to find other interpretations of the group in question. The Menyanthaceae and Gentianaceae are considered separate families; on the other hand, the Lobeliaceae are included in the Campanulaceae. Genera of the Vacciniaceae, Pyrolaceae, and Monotropaceae are found within the Ericaceae. *Ipomopsis* is relegated to *Gilia* and *Cacaliopsis nardosmia* will be found as a *Luina*.

The work serves as an interesting chronicle of the fate of many weedy introductions into the area. For instance, we learn that *Anthemis mixta* L. and *A. altissima* L. have both been collected only on the famous ballast heaps at Portland and presumably have failed to become members of the naturalized flora of the Pacific Northwest. This is quite different behavior from that of their cogeners *Anthemis* *cotula* L. and *A. arvensis* L., which have been extremely successful in becoming established in the region as weeds. *Conyza floribunda* H.B.K. and *Tournefortia sibirica* L. have apparently only persisted at their point of introduction and are not expanding in range. But by far the largest number of weeds have become widely distributed in the region and most, if not all of these are discussed in the text. These different patterns of behavior subsequent to introduction suggest a fertile field for genecological studies.

Notes on the cultivation and ornamental value of many of the native species included in Part 4 have been supplied by two accomplished Seattle horticulturalists: Carl English and Brian O. Mulligan. These men and a number of other northwestern gardeners have demonstrated the high desirability of native plants in the garden when they are grown properly. The ornamental value of the northwestern flora is not as widely appreciated in this country as it deserves to be; it is probably easier to purchase seeds of Northwest Pacific Coast indigens from British and European nurserymen than from American ones. It is true that attractive species such as *Gaultheria shallon, Arctostaphylos uva-ursi,* and *Arbutus menziesii* are rather widely grown, yet too few gardeners are aware of the potentialities of equally attractive species such as *Menziesia ferruginea, Vaccinium ovatum* and *V. parvifolium,* and *Polemonium carneum.* The majority of these species can be propagated or obtained in a manner which does not involve denudation of the countryside. Understandably, horticultural notes have not been included for the Compositae, whose contribution from the temperate zone of a large and diverse assemblage of weeds largely outweighs its contribution of a depauperate ornamental flora.

Chromosome numbers are included for most of the taxa in which they are known, although the literature sources for these numbers are not given. In the instances of circumboreal or polytypic species, or of polyploid complexes, it would be valuable to know the geographical source of the plants on which the counts are based.

Despite the necessity of using the same type throughout the entire work, the format of the book is enlivened by consistent use of indentations, capital letters, and underlinings for various kinds of information repeatedly appearing in each species description. Part 5 appears to be free of typographical errors; there are, however, several errors in Part 4 but none has been found which seriously impairs the meaning or usefulness of any section of the book. Each species discussed is illustrated; the Compositae were drawn by Dr. John Rumely and the taxa in Part 4 were done by Jeanne R. Janish, who is well known in the west for her work on Abrams' "Illustrated Flora of the Pacific States." Both artists have provided a felicitous combination of accurate scientific illustration with esthetically pleasing artistry. Dr. Rumely's drawings lack some of the three-dimensional qualities of Mrs. Janish's and are more obviously based on herbarium specimens; this may, however, prove to be something of a virtue in view of the high likelihood that most botanists would prefer to bring their specimens back from the field in press, rather than carry these bulky volumes with them in the field.

The keys are quite usable and generally include a number of characters which can be utilized in identifying an unknown species. Since the series is not yet complete, no glossary of terms or key to the families is provided. However, the publishers promise a family key in Part 1, and the authors promise that "a more nearly natural arrangement of the families and orders of dicotyledons will be presented at the beginning of Part 2." The high caliber of the work that has so far appeared makes us eagerly await the completion of this valuable contribution to the knowledge of the flora of the Pacific Northwest.—Robert Ornduff, Department of Botany, University of California, Berkeley.

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THE GENUS LEPIDIUM IN CANADA[1]

GERALD A. MULLIGAN

A world monograph of the genus *Lepidium* was published by Thellung (1906) and a further study of the genus by Hitchcock (1936). According to Hitchcock, Thellung did not have enough North American material at his disposal for an accurate interpretation of our plants. This prompted Hitchcock's comprehensive treatment of the genus *Lepidium* in the United States. However, Hitchcock did not see any material from Canadian herbaria and relatively few Canadian specimens were represented in his material from United States herbaria. Consequently it was not surprising to find on studying Canadian specimens that some of the taxa present in Canada are not included in even the most recent floras or lists. Apparently as the result of not having many Canadian specimens for study, Hitchcock included *L. bourgeauanum*, a common plant in the Canadian prairies, under *L. ramosissimum*. He erroneously applied Thellung's name, *L. bourgeauanum*, to another plant, *L. densiflorum* var. *bourgeauanum*. Specimens of *L. heterophyllum*, a species introduced from Europe, and previously unreported for North America, were found in the material studied.

This paper includes keys to all the *Lepidium* present in Canada and a description and discussion of each taxon. The life durations given are mostly based on information obtained by growing plants in nursery plots at Ottawa. The chromosome numbers given for Canadian material were determined from somatic root tip cells. The root tips studied were processed as in Mulligan (1959). Distribution maps (figs. 12 and 13) were prepared by mapping all the herbarium specimens seen, except where localities were closely duplicated.

A total of 935 herbarium specimens, exclusive of duplicates, was examined from the following Canadian herbaria: Department of Agriculture, Ottawa (DAO); National Museum of Canada, Ottawa (CAN); British Columbia Provincial Museum, Victoria (V); University of British Columbia, Vancouver (UBC). Type specimens were obtained from the Gray Herbarium, Harvard University, Cambridge (GH), the New York Botanic Garden, New York (NY); also seen were McCabe's British Columbia collections from the University of California, Berkeley (UC). I wish to express my appreciation to the curators of these herbaria for the loan of material. I am also indebted to workers at the Plant Research Institute, Canada Department of Agriculture, Ottawa, for their encouragement and assistance in this study.

LEPIDIUM L., Sp. Pl., 643. 1753; Gen. Pl. 291. 1754.

Annual to perennial herbs, glabrous to hirsute with simple hairs.

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[1] Contribution 79 from the Plant Research Institute, Research Branch, Canada Department of Agriculture, Ottawa, Ontario.

MADROÑO, Vol. 16, No. 3, pp. 77–108. July 12, 1961.

Flowers small, white to sulfur yellow in dense terminal racemes. Sepals usually somewhat pubescent along back. Petals lacking, or to twice length of sepals. Stamens 2, 4 or 6. Ovary with 2 ovules, style short, stigma capitate, sometimes 2 lobed. Fruit a dehiscent silicle, strongly keeled or winged (silicle indehiscent, not keeled or winged in closely related *Cardaria*). Usually one seed attached to the apex of each cell.

KEY TO THE SPECIES OF LEPIDIUM IN CANADA

a. Middle and upper leaves suborbicular, deeply cordate clasping with a closed sinus and slightly overlapping lobes, thus appearing as if perfoliate . 1. *L. perfoliatum*

aa. Middle and upper leaves narrower, linear to broadly lanceolate, if clasping, not appearing as if perfoliate.

  b. Silicles 5 to 6 mm. long.

    c. Middle and upper leaves clasping the stem, silicles on spreading pedicels.

      d. Annual or biennial with usually a single erect stem; anthers yellow; silicles covered with small white vesicles, style included to slightly exserted from shallow apical notch. . . . . 2. *L. campestre*

      dd. Perennial with numerous ascending stems; anthers violet; silicles with few or no vesicles, style mostly exserted from shallow apical notch. 3. *L. heterophyllum*

    cc. Middle and upper leaves not clasping, silicles on strongly ascending to appressed pedicels . . . . 4. *L. sativum*

  bb. Silicles 2 to 3.5 mm. long.

    e. Glaucous perennial 50 to 130 cm. high, with rhizomes; leaves thickish and rugose, lanceolate to broadly lanceolate . . . . . . 5. *L. latifolium*

    ee. Annual or biennial, 5 to 40 cm. high, leaves not thickish and rugose, linear to lanceolate.

      f. Silicle bidentate at apex, the sinus well developed and broad, its projecting shoulders abruptly contracted into widely divergent teeth, pedicels sigmoid. . . . . 7. *L. oxycarpum*

      ff. Silicles merely retuse or acuminate at apex with a shallow sinus, narrowed to abruptly curved into apical teeth; pedicels straight to arching.

        g. Silicles puberulent, at least on margin.

          h. Silicles 2.5 to 3 by 1.5 to 2 mm., nearly elliptic, narrowed into acute apical teeth; inflorescence congested into numerous axillary racemes as well as terminal ones. . . . . 11. *L. ramosissimum*

          hh. Silicles 3 to 3.5 by 2.5 to 3 mm., round-obcordate to short oblong-obovate, rounded to abruptly curved into obtuse apical teeth; inflorescence a single raceme or of sparsely branched racemes 9. *L. densiflorum*

        gg. Silicles glabrous.

          i. Silicles oval, orbicular to rotund; petals conspicuous, as long or slightly longer than sepals . . . . 8. *L. virginicum*

          ii. Silicles ovate, obovate to round obcordate, petals shorter than sepals or lacking.

            j. Silicles ovate to obovate, narrowed into acutish apical teeth.

              k. Middle and upper cauline leaves blunt tipped, lower cauline and rosette leaves bipinnatifid, petals absent . . 6. *L. ruderale*

              kk. Middle and upper cauline leaves acute tipped, lower cauline and rosette leaves incised, petals present, usually about half length of sepals . . . . 10. *L. bourgeauanum*

            jj. Silicles round obcordate to short-obovate, rounded to abruptly curved into obtuse apical teeth . . . . 9. *L. densiflorum*

1. Lepidium perfoliatum L., Sp. Pl., 643. 1753.

Annual or winter annual with single erect stem 1–5 dm. high, sparsely hairy, usually branched above; lower leaves bipinnate, the middle and upper leaves suborbicular, deeply cordate clasping; petals pale yellow, a little longer than the sepals; stamens usually 6; silicles usually glabrous, rhombic-ovate, on spreading-ascending pedicels, nearly as broad as long, 3–4 mm. long and 3–4 mm. broad; pedicels terete; style usually projecting beyond the shallow apical notch. $2n = 16$ (voucher: grown at Ottawa from seed collected at Lethbridge, Alberta, *Mulligan 1527*, DAO, fig. 1).

Rare along roadsides and in waste places in Ontario, Saskatchewan and Alberta. Occasional along roadsides in the Okanagan Valley of British Columbia and rare elsewhere in the Province (fig. 12). This plant, introduced from Eurasia, was first collected in Canada at Cranbrook, British Columbia, in 1931.

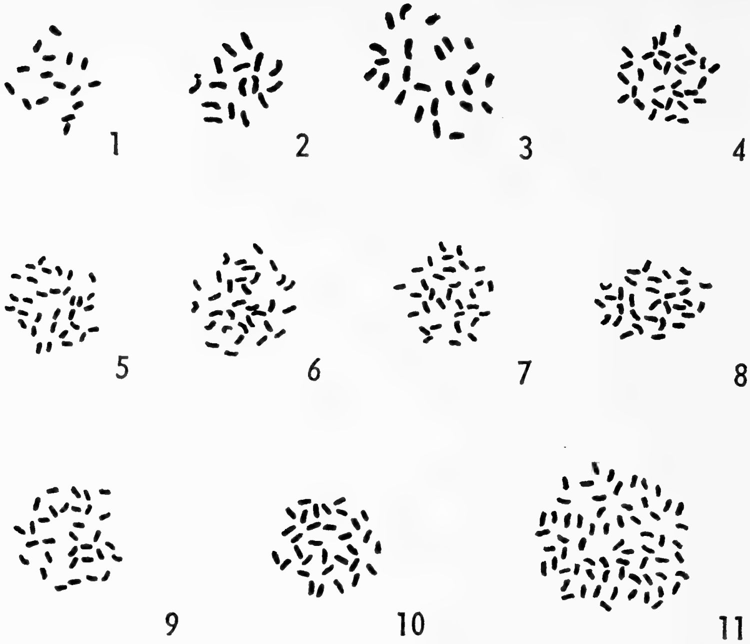
Representative material seen. ONTARIO: York County, at county line of Ontario County, *Shumovich 976* (DAO). SASKATCHEWAN: Swift Current, *Budd* in 1937 (DAO). ALBERTA: Lethbridge, *Bibbey 12* (DAO). BRITISH COLUMBIA: Cranbrook, *Groh* in 1931 (CAN); Kelowna, *McCalla 11598* (UBC, V); Osoyoos, *Lindsay & Woodbury 1128* (DAO).

2. Lepidium campestre (L.) R. Br., Ait. Hort. Kew, ed. 2,4:88. 1812.

Annual to biennial with dense short spreading hairs throughout, stem usually solitary, erect, 2–6 dm. high, branched above the middle, the branches ascending; lower leaves entire or lyrate, narrowed into a short petiole, the middle and upper leaves narrowly triangular, sessile, clasping the stem with long narrow pointed basal lobes; petals white, a little longer than sepals; stamens 6 with yellow anthers; pedicels spreading, slightly flattened; silicles densely covered with small white vesicles that become scale-like when dry, silicles oblong-ovate, 5–6 mm. long and 4 mm. broad; style included to slightly exserted from the shallow apical notch. $2n = 16$ (voucher: grown at Ottawa from seed collected in southwestern Ontario, *Mulligan 1499*, DAO, fig. 2).

Common in fields, roadsides and waste places in southern Ontario, Quebec and British Columbia. Sporadic along roadsides and in waste places in Newfoundland, Prince Edward Island, Nova Scotia, New Brunswick and Alberta (fig. 12). Introduced from Eurasia.

Representative material seen. NEWFOUNDLAND: Gander, *Bassett 383* (DAO). PRINCE EDWARD ISLAND: Souris, Kings County, *Erskine* and *Smith 2046* (DAO); Charlottetown, *Dore & Gorham* 45.314 (DAO). NOVA SCOTIA: South Sydney, Cape Breton, *Macoun* in 1886 (CAN); Kentville, *Lewis* in 1944 (DAO); Mabou, *Smith et al 8669* (DAO). QUEBEC: Grosse-Ile, Comté de Montmagny, *Marie-Victorin et al 40129* (CAN); Mont-Rolland, *Marie-Anselm 14* (DAO); Bristol, *Bassett* and *Mulligan* 1140 (DAO); Montreal, *Bernard* in 1952 (CAN, UBC). ONTARIO: Milton West, *Mulligan* and *Lindsay 818* (DAO); Snelgrove, *White* in 1897 (CAN); St. Thomas, *James 2478* (DAO); Kemptville, *Lindsay* and *Bassett 213* (DAO); Port Arthur, *Garton 2339* (DAO). ALBERTA: between Macleod and Pincher, *McCalla 11070* (DAO). BRITISH COLUMBIA: Chilliwack, *Faris 32* (DAO); Koksilah, V.I., *Tice* in 1937 (UBC, V); Sandspit, Moresby Island, Queen Charlotte Islands, *Calder 21111* (DAO).



FIGS. 1–11. Somatic chromosomes of *Lepidium*, camera lucida drawings, × 2150. 1, *L. perfoliatum*, 2n=16; 2, *L. campestre*, 2n=16; 3, *L. latifolium*, 2n=24; 4, *L. virginicum* (eastern material), 2n=32; 5, *L. virginicum* (western material), 2n=32; 6, *L. densiflorum* var. *densiflorum*, 2n = 32; 7, *L. densiflorum* var. *macrocarpum*, 2n=32; 8, *L. densiflorum* var. *elongatum*, 2n=32; 9, *L. densiflorum* var. *pubicarpum*, 2n=32; 10, *L. bourgeauanum*, 2n=32; 11, *L. ramosissimum*, 2n=64.

3. LEPIDIUM HETEROPHYLLUM (DC.) Benth., Cat. Pl. Pyr. 95. 1826. *L. smithii* Hook., Brit. Fl., ed. 3, 300. 1835.

Perennial herb with short spreading hairs on leaves and stem; stems many, ascending, 1.5–4.5 dm. high, often branched below as well as above the middle, the branches ascending; lower leaves oblanceolate or elliptical, narrowed into a short petiole, the middle and upper leaves narrowly triangular, sessile, clasping the stem with long narrow basal lobes; petals white, a little longer than sepals; stamens 6, anthers violet; pedicels spreading, slightly flattened; silicles with vesicles lacking or few, oblong-ovate, 5–6 mm. long and 4 mm. broad; style mostly exserted from the shallow apical notch. 2n=16, European material (Fl. Brit. Isles, 175. 1952).

Occasional along roadsides, in fields and waste places on Vancouver Island, British Columbia (fig. 12). This plant was first collected near Victoria in 1908. *Lepidium heterophyllum,* introduced from Europe, was first recognized as occurring in North America by Dr. C. Frankton in

1956 when he identified a specimen, collected near Courtenay, British Columbia, as *L. smithii.*

Material seen. BRITISH COLUMBIA. VANCOUVER ISLAND: vicinity of Victoria, *Macoun*, May 20, 1908 (CAN), June 19, 1908 (CAN); Telegraph Bay, *Copley 6657* (V); Mt. Finlayson, *Copley 6658* (V); Alberni, *Carter 2196* (V); Millstream Road, *Hardy 7558* (V); S. Saanich, *Newcombe 8917* (V); Sooke, *Hardy 22768* (V); Courtenay, *Molyneux 73* (DAO, UBC, V); 2 miles east southeast Langford, *Calder et al 20795* (DAO).

4. LEPIDIUM SATIVUM L., Sp. Pl., 644. 1753.

Annual with a solitary erect stem 2–8 dm. high, glabrous; lower leaves long-stalked, lyrate with toothed obovate lobes, the middle and upper leaves pinnatipartite or bipinnatipartite, occasionally entire and linear; petals white or reddish, up to twice as long as the sepals; stamens 6; silicles glabrous, broadly elliptical or nearly orbicular, 5–6 mm. long and 3–4 mm. broad; pedicels appressed, flattened; style not projecting beyond the deep apical notch. $2n=16$, European material (Jaretzky 1932).

Rare along roadsides and in waste places in Prince Edward Island, Nova Scotia, New Brunswick, Quebec, Ontario, Saskatchewan, Alberta, British Columbia and Yukon Territory (fig. 12). Introduced from Eurasia as early as 1882 but still only a casual escape from cultivation.

Representative material seen. PRINCE EDWARD ISLAND: 4 miles northwest Charlottetown, *Campbell 150* (DAO). NOVA SCOTIA: Harbourville, Kings County, *Lewis* in 1944 (DAO). NEW BRUNSWICK: St. Quentin, *Groh* in 1937 (DAO). QUEBEC: Ste. Annes des Monts, Gaspé, *Macoun* in 1882 (CAN). ONTARIO: Ottawa, *Scott* in 1890 (DAO, CAN). SASKATCHEWAN: Yorktown, *Macoun* and *Herriot* in 1906 (CAN). ALBERTA: Beaverlodge, *Brooks* in 1930 (DAO). BRITISH COLUMBIA: Victoria, *Newcombe 9259* (V); Nelson, *Eastham 3065* (UBC). YUKON TERRITORY: Dawson, *Macoun* in 1902 (CAN).

5. LEPIDIUM LATIFOLIUM L. Sp. Pl., 644. 1753.

Perennial herb with subterranean rhizomes, each branch of the rhizome giving rise to a single erect stem 5–13 dm. high, glabrous, much branched above; lower leaves long-petioled, simple and ovate with a toothed margin or pinnately lobed with a large terminal and 2 or more smaller lateral lobes, the lobes all rounded, the middle and upper leaves sessile, ovate or ovate-lanceolate, acute, entire or with distant teeth, the uppermost leaves often bract like and white margined near the apex; petals white, up to twice as long as sepals; stamens 6; silicles glabrous to pubescent, elliptical to orbicular, 2 mm. long and 2 mm. broad; pedicels ascending, terete; style very short with large rounded stigma, apical notch very slight or lacking. $2n = 24$ (voucher: grown at Ottawa from seed collected at Lethbridge, Alberta, *Mulligan 2147*, DAO, fig. 3).

This plant, introduced from Eurasia, was first collected in 1934 but has remained localized around Quebec City and Lethbridge, Alberta (fig. 12).

Representative material. QUEBEC: Quebec, *Marie-Anselm* in 1934 (DAO). ALBERTA: Lethbridge, *Moss* in 1940 (CAN).

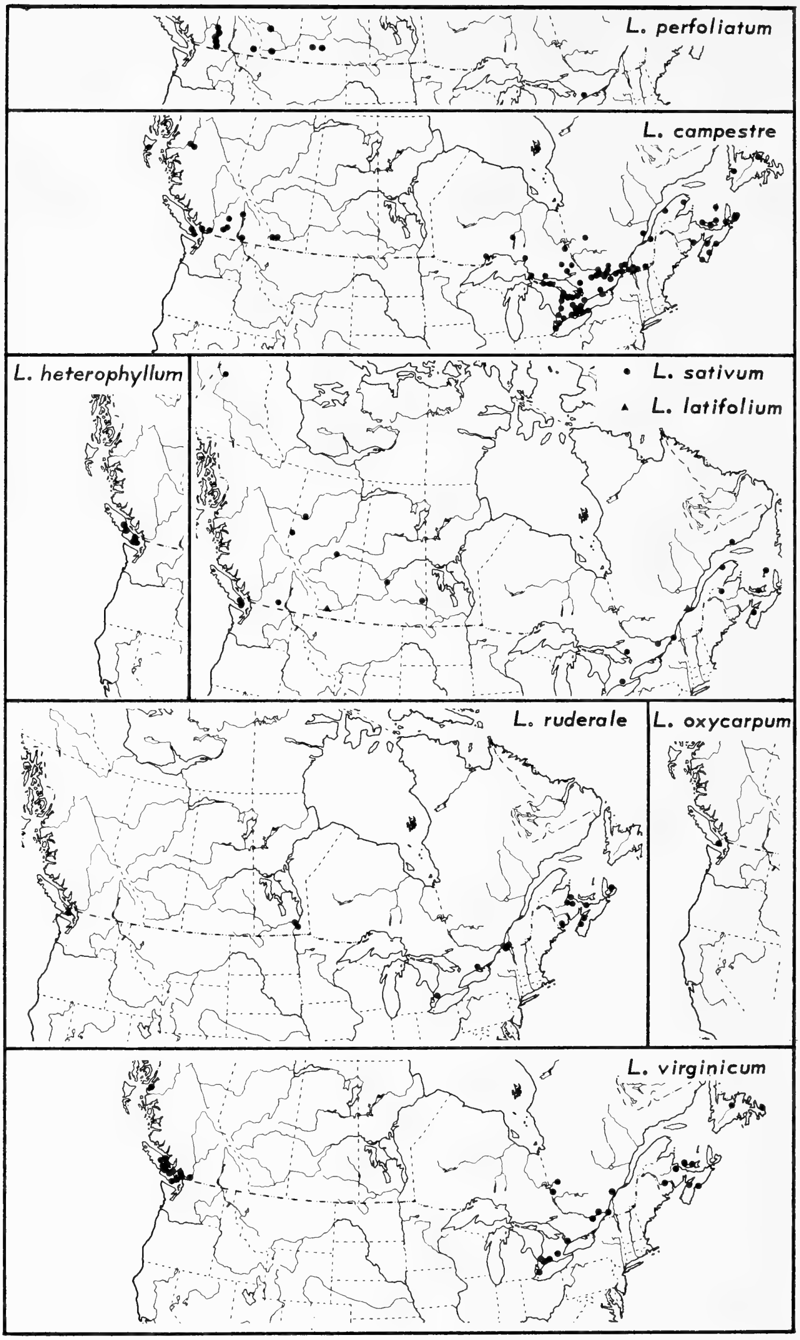


FIG. 12. Distribution maps of *Lepidium*.

6. Lepidium ruderale L., Sp. Pl., 643. 1753.

Annual to biennial with single erect or ascending stem 1–3 dm. high, plant almost glabrous, with occasionally a few short spreading hairs; stem branched above, the branches ascending; lower leaves long-petioled, deeply bipinnately divided into narrow entire segments, the middle and upper leaves sessile, narrowly oblong, entire, rounded at apex; petals usually absent; stamens usually 2; silicles glabrous, ovate or broadly elliptical, 2–2.5 mm. long and 1.5–2 mm. broad; pedicels spreading to ascending, slightly flattened; style at base of the shallow apical notch. $2n = 32$, European material (Jaretzky 1932).

Rare along roadsides and in waste places in Nova Scotia, New Brunswick, Quebec, Ontario and Manitoba (fig. 12). Introduced from Eurasia as early as 1868.

Representative material seen. NOVA SCOTIA: North Sydney, *Macoun* in 1883 (CAN). NEW BRUNSWICK: Bass River, Kent County, *Fowler* in 1868 (CAN). QUEBEC: Montreal, *Rolland-Germain 46008* (DAO, CAN). ONTARIO: Wellington, *Montgomery* and *Shumovich 997* (DAO). MANITOBA: Winnipeg, *Frankton* and *Bibbey 60* (DAO).

7. Lepidium oxycarpum T. & G., Fl. N. Am. 1:116, 688. 1838.

Slender, nearly glabrous annual, 0.5–2 dm. high, with many semi-erect stems branched above the middle; lower leaves linear, often with 2–4 pairs of linear lobes, middle and upper leaves usually linear and entire; petals white, rudimentary; stamens 4; silicles on slender somewhat sigmoid and flattened pedicels; silicles ovate, glabrous, and finely reticulate, 2.5–3.5 mm. long and 2–2.5 mm. broad, abruptly contracted at apex into a pair of widely divergent teeth; style at base of large apical notch.

The only Canadian specimen of *L. oxycarpum* seen (fig. 12) was collected at Cadboro on Vancouver Island (*Macoun* in 1893, CAN).

8. Lepidium virginicum L. sensu lat., Sp. Pl., 645. 1753.

Annual, freely branched, erect to spreading, 1.5–6 dm. high, glabrous to strongly pubescent; lower and middle leaves irregularly toothed or incised to pinnatifid, the divisions often again dissected, the upper leaves much reduced, usually entire or remotely toothed; petals white, equalling to much longer than the sepals; stamens usually 2; silicles glabrous, oval, orbicular to rotund, 2.5–4 mm. long and 2.5–4 mm. broad; pedicels spreading to ascending, slightly flattened to terete; stigma included in the shallow apical notch. $2n = 32$ (vouchers: grown at Ottawa from seed collected at St. Thomas, Ontario and Saanichton Spit, British Columbia, *Mulligan 2420* and *2421*, DAO, figs. 4 and 5).

In Canada, *L. virginicum* sensu lat. is represented by eastern and western elements (fig. 12). The positions of the cotyledons in the seeds of Canadian material, as in the United States material (Hitchcock 1936), are accumbent in eastern plants and oblique to incumbent in western plants. Eastern plants occur sporadically in Newfoundland, Prince Edward Island, Nova Scotia, New Brunswick, Quebec and Ontario. These plants are *L. virginicum* var. *virginicum* and are introduced from further south in the eastern United States. Western plants of *L. virginicum* sensu lat. are found only on Vancouver Island, and the adjacent islands and mainland. They are undoubtedly native to this area. Most of these western plants have morphological characters tending towards the varieties *pubescens* and *medium* as treated by Hitchcock (1936). However, it appears that two and possibly three varieties of *L. virginicum* sensu lat. come together in the southwestern corner of British Columbia and at this northern limit of their range, there is extreme morphological variability in the population. An understanding of the British Columbia plants would require an extensive study of all the western North American material of *L. virginicum* sensu lat. Such a study is outside the limits of this treatment.

Representative material seen. NEWFOUNDLAND: St. John's, *Green 1517* (DAO). PRINCE EDWARD ISLAND: Charlottetown, *Erskine 2332* (DAO). NOVA SCOTIA: Wolfville, *Groh* in 1932 (DAO). NEW BRUNSWICK: Fredericton, *Dore* and *Gorham 45165* (DAO). QUEBEC: Shawinigan Falls, *Groh* in 1927 (DAO, CAN). ONTARIO: near St. Thomas, *Macoun* in 1907 (CAN). BRITISH COLUMBIA: Saanich Spit, *Eastham* in 1939 (DAO, UBC); Parksville, Vancouver Island, *Carter 2195* (V); Jessie Island, Departure Bay, *Macoun* in 1908 (CAN); Mitlenatch Island, *Sweeney 15567* (V).

9. LEPIDIUM DENSIFLORUM Schrad. sensu lat., Ind. Sem. h. Götting. 4. 1832.

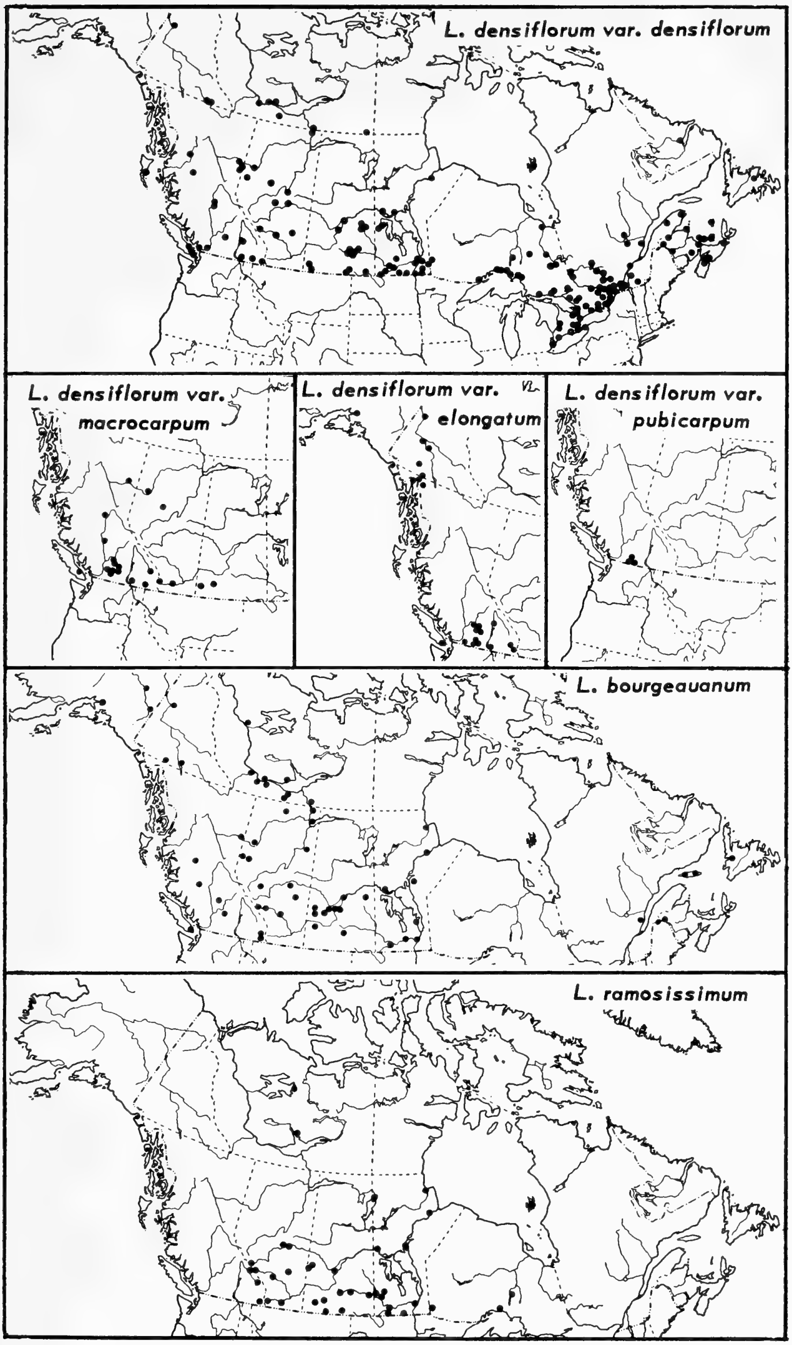
Annual to biennial, puberulent to pubescent; stem erect, 1–5 dm. high, usually branched above the middle, sometimes simple; lower leaves mostly oblanceolate, coarsely toothed to pinnatipartite, the divisions also toothed, the middle and upper cauline leaves reduced, slightly toothed or entire; petals white, rudimentary to sometimes equalling the sepals in western varieties; stamens 2; silicles glabrous to puberulent in some of western varieties, round-obcordate to short oblong-obovate, rounded to abruptly curved into obtuse apical teeth, 2–3.5 mm. long and 1.5 to 3 mm. broad; pedicels slightly ascending to nearly appressed, slightly to conspicuously flattened; stigma included in the narrow apical notch.

KEY TO VARIETIES OF L. DENSIFLORUM

a. Silicles averaging 2.5 mm. long, glabrous; pedicels slightly flattened, crowded, more than 9 pedicels per cm. . . . . 9a. var. *densiflorum*
aa. Silicles averaging 3–3.5 mm. long, puberulent except in var. *macrocarpum*; pedicels conspicuously flattened, less crowded, usually less than 9 pedicels per cm.
  b. Silicles glabrous . . . . 9b. var. *macrocarpum*
  bb. Silicles puberulent.
    c. Silicles puberulent only on margins . . . . . . 9c. var. *elongatum*
    cc. Silicles uniformly puberulent . . . . 9d. var. *pubicarpum*

9a. L. DENSIFLORUM Schrad. var. DENSIFLORUM. *L. densiflorum* var. *typicum* Thell., Bull Herb. Boiss., ser. 2, 4:706. 1904.

Plant erect, 1–5 dm. high, annual or winter annual with glabrous silicles, averaging 2.5 mm. long and 2 mm. broad, smaller than all western



L. densiflorum var. densiflorum

L. densiflorum var. macrocarpum

L. densiflorum var. elongatum

L. densiflorum var. pubicarpum

L. bourgeauanum

L. ramosissimum

FIG. 13. Distribution maps of *Lepidium*.

varieties. 2n = 32 (voucher: grown at Ottawa from seed collected at Ottawa, *Mulligan 1528*, DAO, fig. 6).

Widely distributed in all types of disturbed habitats: Newfoundland, Prince Edward Island, Nova Scotia, New Brunswick, Labrador, Quebec, Ontario, Manitoba, Saskatchewan, Alberta, British Columbia, Yukon Territory and Mackenzie District, Northwest Territories (fig. 13). Native to the Prairie Provinces, interior of British Columbia and probably some localities in eastern Canada. Weedy throughout its range.

Representative material seen. NEWFOUNDLAND: Gander, *Bassett 462* (DAO). PRINCE EDWARD ISLAND: Bideford, Prince County, *Smith 319* (DAO); French River, *Fernald et al 7508* (CAN). NOVA SCOTIA: Boylston, *Hamilton* in 1890 (CAN); Wolfville, *Groh* in 1928 (DAO). NEW BRUNSWICK: Point du Chene, *Bassett* and *Mulligan 2964* (DAO); Woodstock, *Macoun* in 1899 (CAN); Edmunston, *Malte 332* (CAN). LABRADOR: Goose Bay, *Gillett* and *Findley 5883* (DAO, UBC). QUEBEC: Nominique, *Lucien* in 1924 (CAN); Magog, *Bassett* and *Hamel 2322* (DAO); Shawville, *Mulligan* and *Lindsay 382* (DAO); Ville Marie, *Baldwin 5940* (CAN). ONTARIO: Leamington, *Macoun* in 1901 (CAN); Moosonee, *Baldwin 1453* (CAN); Goderich, *Senn et al 4759* (DAO); Point Pelee, *Bassett 1112* (DAO). MANITOBA: Douglas, *Lindsay 490* (DAO); Duck Mountain, *Scoggan* and *Baldwin 7793* (CAN); Fort Ellice, *Macoun* in 1879 (CAN); The Pas, *Krivda 1223* (DAO). SASKATCHEWAN: Dundurn, *Campbell 54* (DAO); Prince Albert, *Macoun* in 1876 (CAN); Cypress Hills, *Breitung 5001* (DAO); Bjorkdale, *Van Blaricom* in 1941 (DAO). ALBERTA, 7 miles north Fort Fitzgerald, *Cody* and *Loan 3863* (DAO); 20 miles west Selba, *McCalla 12313* (UBC); Fort Saskatchewan, *Turner 4873* (CAN). BRITISH COLUMBIA: 141 Mile House, *Cottle* in 1949 (UBC); Grand Forks, *Tice* in 1933 (V); Yahk, *Bassett* and *Cumming 3970* (DAO). NORTHWEST TERRITORIES: Fort Simpson, *Cody* and *Matte 8109* (DAO); Alexander Falls, Hay River, *Lewis 558* (DAO). YUKON TERRITORY: Watson Lake, *Gillett 2585* (DAO).

9b. L. DENSIFLORUM Schrad. var. **macrocarpum** var. nov. *L. densiflorum* var. *bourgeauanum* sensu Hitchcock, Madroño, 3:279, 1936, nec L. *bourgeauanum* Thellung.

Herba biennis erecta, saepius 1–3 dm., siliculis glabris, 3.0–3.5 mm. long., 2.5–3.0 mm. lat., 2n = 32 ex canadensibus.

Plant erect, 1–3 dm. high, biennial with glabrous silicles 3.0–3.5 mm. long and 2.5–3.0 mm. broad. 2n = 32 (voucher: grown from seed collected at Cache Creek, *Mulligan 2416*, DAO, fig. 7).

Native on dry open soil in western Saskatchewan, Alberta and British Columbia, as far north as Prince George, British Columbia (fig. 13).

Type. Lethbridge, Alberta, Platières de la rivière Sainte-Marie près de son embouchure, 23 juin 1958, *Boivin, Perron* and *Harper 12197* (DAO), fig. 14.

Material seen. SASKATCHEWAN: Webb, 7 miles au nord, *Boivin et al 12005* (DAO); Saskatchewan Landing, *Russell S58099* (DAO); 7 miles au sud de la Station Expérimentale de Manyberries, *Boivin* and *Alex 9651* (DAO). ALBERTA: 1 mile east of Canmore, south of Peace River, *Macoun* in 1903 (CAN); Canyon Creek, *Boivin* and *Perron 12744* (DAO); Lethbridge, *Boivin* and *Perron 12166* (DAO). BRITISH COLUMBIA: Tranquille, *Groh 246* (DAO); Lillooet, *Luyat* in 1928 (V), *Anderson 2197* (V), *Macoun* in 1916 (CAN); Kamloops, *Davidson* in 1912 (UBC), *Tisdale 40-410* (DAO), *Wattie* in 1915 (UBC); Kamloops, Thompson

River Flats, *Brink* in 1935 (UBC), a mixture of 1 plant var. *macrocarpum* and 2 plants var. *elongatum;* Spences Bridge, *Macoun* in 1899 (CAN); Hamilton Commonage, Nicola Valley, *Tisdale* in 1935 (DAO), *40-409* (DAO); Cache Creek, *Mulligan* and *Woodbury 1617* (DAO); Hat Creek Valley, *Thompson* and *Thompson 221* (DAO); Yahk, *Bassett* and *Cumming 3988* (DAO); Cecil Lake, *Merten* in 1958 (DAO); Riley's Ranch, Big Bear Creek, *Copley 6430* (V); Fairmont, *Anderson 225* (V); Merritt, *Copley 7312* (V); Nelson, *Eastham 3057* (UBC); Macalister, *Taylor* and *Lewis 286* (UBC); Prince George, *Eastham 14735* (UBC); Nanaimo, *Eastham 3058* (UBC); Lytton, *Dawson* in 1876 (CAN); Crow Nest Pass, *Macoun* in 1897 (CAN); 2½ miles south Merritt, *McCabe 4523* (UC); 21½ miles south Williams Lake, *McCabe 1312* (UC).

9c. L. DENSIFLORUM Schrad. var. ELONGATUM (Rybd.) Thell., Bull. Herb. Boiss., Ser. 2, 4:706. 1904; Monog. Lepid. 235. 1906. *L. elongatum* Rydb., Bull. Torr. Bot. Club, 29:234. 1902. *L. simile* Heller, Bull. Torr. Bot. Club, 26:312. 1899.

Plant erect, 1–3 dm. high (rarely taller), biennial with silicles puberulent only on margins, 3–3.5 mm. long and 2.5–3 mm. broad. $2n = 32$ (voucher: grown at Ottawa from seed collected at Ashnola River, Flatiron Mountain, British Columbia, *Mulligan 2422*, DAO, fig. 8).

Native on dry open soil in interior of British Columbia and as far north as Kamloops. Apparently also native along the Mackenzie River in Yukon Territory and in the northwestern corner of British Columbia (fig. 13).

Representative material seen. BRITISH COLUMBIA: 1 mile east Fort Steele, *Calder* and *Savile 9149A* (DAO); Fernie, *Bassett* and *Cumming 3986* (DAO); Goodfellow Creek, *Hardy 18.875* (V); Revelstoke, *Macoun* in 1890 (CAN); Windy-Arm, Yukon Boundary, *Gervaise* in 1914 (UBC); 2 miles north Skookumchuck, *McCabe 5031* (UC). YUKON TERRITORY: Carcross, *Gillett 3384* (DAO); Whitehorse, *Gillett 3508* (DAO); island in Klondike River, *Macoun* in 1902 (CAN).

9d. L. DENSIFLORUM Schrad. var. PUBICARPUM (Nelson) Thell., Bull. Herb., Boiss., Ser. 2, 4:706. 1904; Monog. Lepid., 235. 1906. *L. pubicarpum* Nelson, Bot. Gaz. 30:189. 1900.

Plant erect, 1–3 dm. high (rarely taller), annual or winter annual with puberulence scattered over all of silicle, 3–3.5 mm. long and 2.5–3 mm. broad. $2n = 32$ (voucher: grown at Ottawa from seed collected at Osoyoos, British Columbia, *Mulligan 2412*, DAO, fig. 9).

Known to occur in Canada only around Osoyoos and Penticton, British Columbia (fig. 13).

Material seen. BRITISH COLUMBIA: 19 miles east Osoyoos, *Mulligan* and *Woodbury 2010* (DAO); Osoyoos, *Lindsay* and *Woodbury 630* (DAO); Penticton, *Eastham 3056* (UBC), *7067* (UBC); Okanagan Valley at U.S. Boundary, *McCabe 5848* (UC).

10. LEPIDIUM BOURGEAUANUM Thell., Monog. Lepid., 237, 1906. *L. fletcheri* Rydb., Bull. Torr. Bot. Club, 34:428. 1907.

Biennial, 1.5–6 dm. high, sparsely to densely puberulent throughout; stem erect, with many ascending to nearly appressed branches bearing usually less than 5, rarely up to 10 racemes; lower leaves incised, middle

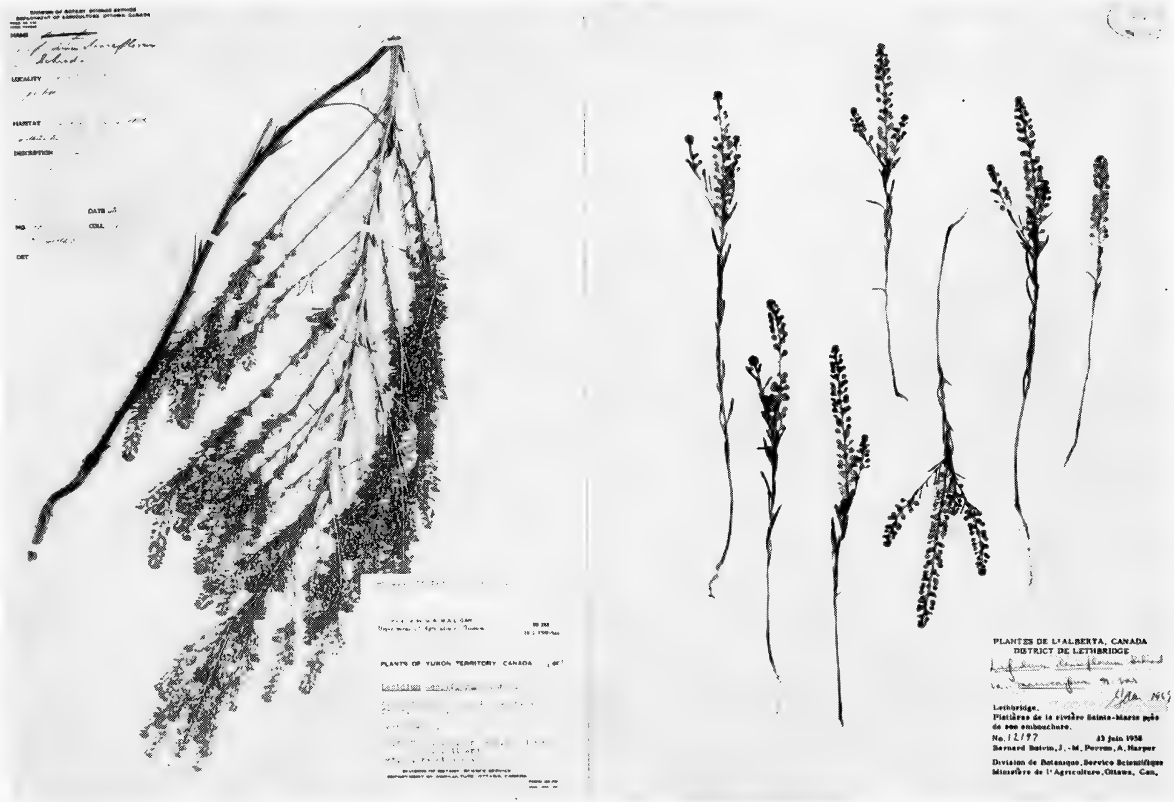


FIG. 14. *Lepidium densiflorum* var. *macrocarpum*, holotype, *Boivin, Perron* and *Harper 12197* (DAO), left; *Lepidium bourgeauanum*, a representative specimen, *Calder* and *Billard 4627* (DAO), right.

leaves incised or sometimes slightly toothed; upper leaves linear, entire, rarely slightly toothed; petals white, up to ¾ length of the sepals; stamens 2; silicles glabrous, ovate to obovate, 2.5–3 mm. long, and 1.5–2 mm. broad; pedicels spreading to ascending, slightly flattened; style included in the apical notch. $2n = 32$ (vouchers: grown at Ottawa from seed collected at St. Simeon, Province Quebec, Alexander Falls and Norman Wells, Mackenzie District, *Mulligan 2423, 2418* and *2419,* DAO, fig. 10).

Fairly common on open soil in Manitoba, Saskatchewan, Alberta, British Columbia, Yukon Territory and Northwest Territories, and probably native in all these areas. It also occurs at a few locations in Newfoundland, New Brunswick, Ontario and Quebec, where it has probably been introduced (fig. 13).

Lepidium bourgeauanum, described by Thellung (1906), was based on a collection of Bourgeau [Saskatchewan, 1857–8, Bourgeau (Pallisers Brit. N. Am. Exped.)—Herb. Petersburg]. Hitchcock (1936) applied this name to his *L. densiflorum* var. *bourgeauanum*, a plant that is relatively rare on the Canadian prairie. However, Thellung's description obviously refers to the plant here being treated (see fig. 14), not Hitchcock's *L. densiflorum* var. *bourgeauanum.* A Bourgeau specimen [labelled Lake Winnipeg Valley, 1857 (Pallisers Brit. N. Am. Exped.)] in the Gray Herbarium, Harvard University, is *L. bourgeauanum.* This specimen is possibly an isotype of *L. bourgeauanum* with more complete label data than the holotype in the Petersburg Herbarium. *L. bourgeauanum* has been included under *L. ramosissimum* by most botanists, but in addition to the differences in morphology and geographic distribution, the former plant has 32 somatic chromosomes while the latter plant has 64.

Representative material seen. NEWFOUNDLAND: Deer Lake, *Rouleau 1160* (DAO). NEW BRUNSWICK: 2 miles north northeast Edmunston, Madawaska County, along railroad tracks, *Mulligan* and *Spicer 2538* (DAO), not mapped on fig. 13. ONTARIO: Prescott, Grenville County, single plant near grain elevator, *Dore 18299* (DAO), not mapped on fig. 13. QUEBEC: 2 miles west St. Simeon, *Bassett* and *Hamel 2190* (DAO); Ellis Bay, Anticosti Island, *Johansen* in 1923 (CAN). MANITOBA: Lake Winnipeg Valley, *Bourgeau* in 1857 (GH, possibly isotype of *L. bourgeauanum*); Brandon, *Macoun* in 1896 (CAN); Churchill, *Beckett 3852* (DAO); Winnipeg, *Fletcher* in 1905 (DAO, isotype of *L. fletcheri*). SASKATCHEWAN: Cherryfield, *Macoun* and *Herriot 69881* (CAN, paratype of *L. fletcheri*); Dana, *Senn et al 2745* (DAO); 16 miles west Saskatoon, *Macoun* and *Herriot* in 1906 (CAN); Lee's Lake Reservoir, *Bird 1560* (DAO). ALBERTA: Fort McMurray, *Cody* and *Gutteridge* in 1953 (DAO); Beaverlodge, *Jenkins 123* (DAO); Calgary, *Macoun* in 1897 (CAN). BRITISH COLUMBIA: Sinkut Lake, *Eastham 16959* (UBC, V); 54 miles south Williams Lake, *Mulligan* and *Woodbury 1776* (DAO). NORTHWEST TERRITORIES. MACKENZIE DISTRICT: Wrigley Harbour, Brabant Island, *Lewis 998* (DAO); 2 miles east Trout River, *Cody* and *Matte 8637* (DAO); Indian Village on north shore of Mackenzie River, *Cody* and *Matte 8622* (DAO). YUKON TERRITORY: West Dawson, *Calder* and *Billard 4627* (DAO).

11. LEPIDIUM RAMOSISSIMUM Nelson, Bull. Torr. Bot. Club, 26:124, 1899. *L. ramosissimum* var. *robustum* Thell., Monog. Lepid., 236. 1906.

Biennial, 1–4 dm. high, sparsely to densely puberulent; stem erect, usually profusely branched throughout, with many spreading to ascending branches bearing usually more than 10, occasionally as few as 5 racemes; lower and middle leaves sessile, pinnately or bipinnately parted; upper cauline leaves usually with at least one pair of linear lobes towards the apex, rarely entire; petals white, up to ¾ length of the sepals; stamens 2; silicles puberulent, at least along margins, ovate to obovate, 2.5–3 mm. long and 1.5–2 mm. broad; pedicels spreading to ascending, slightly flattened; style included in the apical notch. $2n = 64$ (vouchers: grown at Ottawa from seed collected at Stirling and Edmonton, Alberta and Yellowknife, Mackenzie District, *Mulligan 2129, 2424* and *2417*, DAO, fig. 11).

Fairly common on open soil in Manitoba, Saskatchewan and Alberta; rare in western Ontario, British Columbia and Mackenzie District, Northwest Territory. Native in the Prairie Provinces, but possibly introduced elsewhere (fig. 13). The first Canadian collection seen was collected by Bourgeau, at Fort Ellice, Manitoba, in 1857.

Representative material seen. ONTARIO: Schreiber, *Hosie et al 689* (CAN). MANITOBA: Snowflake, *Bassett* and *Kemp 3504* (DAO); Norway House, off north end of Lake Winnipeg, *Scoggan 4233* (CAN); Churchill, *Beckett 3* (DAO); Buttes de Sables au Fort Ellice, *Bourgeau* in 1857 (GH). SASKATCHEWAN: Scott, *Groh* in 1933 (DAO); Twelve-Mile Lake, Wood Mountain, *Macoun* in 1895 (CAN); Saskatchewan, *Bourgeau* in 1858 (GH, isotype of *L. ramosissimum* var. *robustum*); Scott, *Groh* in 1933 (DAO). ALBERTA: Edmonton, *Frankton 895* (DAO); Fort Saskatchewan, *Turner 4948* (DAO, UBC); Craigmyle District, *Brinkman* in 1921 (CAN); Frank, *Bassett* and *Cumming 3975* (DAO). BRITISH COLUMBIA: Windermere Slough, Columbia Valley, *Eastham 16288* (V, UBC); Windermere, *McCabe 6365* (UC); Fernie, *Bassett* and *Cumming 3971* (DAO). NORTHWEST TERRITORIES. MACKENZIE DISTRICT: Yellowknife, *Cody* and *McCanse 3045* (DAO).

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ESCHSCHOLZIA COVILLEI GREENE, A TETRAPLOID SPECIES FROM THE MOJAVE DESERT[1]

THEODORE MOSQUIN

The purpose of this paper is to establish the validity of *Eschscholzia covillei* Greene (Papaveraceae) as a taxon of specific rank on the basis of a comparative study of morphological variation in relation to chromosome number and geographical distribution. *Eschscholzia covillei* is one of a group of closely related taxa in the deserts of southwestern United States and adjacent Mexico that has frequently been treated as conspecific with *E. minutiflora* Watson (e.g., Jepson, 1922, 1925; Munz, 1935; Abrams, 1944; Munz, 1959).

Lewis and Snow (1951) pointed out that *E. minutiflora* is hexaploid ($n=18$) and that a diploid species, *E. parishii* Greene ($n=6$), formerly considered a variety of *E. minutiflora*, is readily distinguishable from the latter on morphological grounds. They also pointed out that plants intermediate between these two taxa in Inyo County, California, might be tetraploid and genetically distinct from both *E. minutiflora* and *E. parishii*. This suggestion was confirmed in 1957 when a collection of the intermediate material from the White Mountains (*Lewis 1084*) was determined to be tetraploid ($n=12$). More recently Ernst (1959) has reported the tetraploid number of chromosomes for two collections from the same area (*Ernst 561, 564*). From study of my own collections, I have found that these intermediate specimens are consistently tetraploid and morphologically distinguishable from both the diploid, *E. parishii*, and the hexaploid, *E. minutiflora*. Consequently the tetraploid should be recognized as a distinct species. An examination of the literature and of the type specimens concerned indicates that the earliest specific name for the tetraploid is *E. covillei* Greene. This was clearly designated on the United States National Herbarium sheet (number 3340) by Greene.

ESCHSCHOLZIA COVILLEI Greene, Pittonia 5:275. 1905. Type: from Pete's Garden to 1000 feet below, Johnson Cañon, Panamint Mountains, Inyo County, California, elevation 1700 meters, *Coville* & *Funston 519* (US). *E. minutiflora* var. *darwinensis* M. E. Jones, Contr. West. Bot. 8:2–3, 1898. Type: on mesas, Darwin, Inyo County, California, *Jones* in 1897 (POM).

Glabrous annual herb, to 40 cm. tall, freely branched throughout; basal rosettes well-developed with leaves coarsely divided, numerous,

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[1] I am grateful to Dr. Harlan Lewis for suggesting this problem to me and for critical review of the manuscript. Special thanks are due to Dr. Peter H. Raven for his assistance in checking types and for other helpful suggestions. I also wish to thank Dr. Richard Snow for permission to publish his previously unreported chromosome number determinations, and for permission to examine the specimens in their care the curators of the following herbaria: the University of California, Berkeley; Pomona College; Rancho Santa Ana Botanic Garden; and the San Diego Museum of Natural History.

glaucous, 6–13 cm. long, the blade 0.5–4.5 cm. long, 0.5–4 cm. wide; upper leaves strongly reduced; mature buds elliptical, 6–9 mm. long, acuminate; pedicels 1–8 cm. long; torus turbinate; petals obovoid-cuneate, golden-yellow, 7–17 mm. long; stamens 8–15 per flower, 3.5–5 mm. long; pollen with 7–10 grooves (usually 8 or 9), 24–37 microns in diameter; seeds with finely reticulate grey-brown coat; chromosome number, $n = 12$.

Distribution. Slopes and washes of desert mountains, Inyo and San Bernardino counties, California (fig. 1).

Representative specimens. CALIFORNIA. Inyo County: Panamint Valley, 11 miles southwest of Ballarat on road to Ridgecrest, *Mosquin* & *Lewis 3241* (LA, UC); 0.7 mile from junction to Darwin on road to Darwin Falls, *Mosquin* & *Lewis 3251* (LA, UC); Panamint Valley, 7.2 miles east of junction to Trona on road to Stovepipe Wells, *Mosquin* & *Lewis 3255* (LA, UC); Emigrant Canyon, *Mosquin* & *Lewis 3256*, *3257* (LA, UC); 0.6 mile west of Bradbury Well entrance to Death Valley National Monument, *Mosquin* & *Lewis 3258–1* (UC); Westgard Pass road, *Lewis 1084* (LA); Nelson Range, *Austin* in 1906 (UC); Pleasant Canyon, Panamint Mountains, *Hall* & *Chandler 6965* (UC); Hole-in-the-Rock Spring, *Epling* et al. in 1930 (LA, UC); Hanaupah Canyon, Panamint Mountains, in 1922 (collector unknown, SD); Shepherds Canyon, Argus Mountains, *Keller 126* (SD); Black Canyon, White Mountains, *Duran 2668* (LA, UC); Bishop Creek, 5,200 feet, *Hall* & *Chandler 7249* (UC); Darwin, 4,600 feet, *Jones*, April 28, 1897 (POM); from Pete's Garden to 1000 feet below, 1,700 meters, *Coville* & *Funston 519* (US). San Bernardino County: 7 miles east of Daggett, *Munz* & *Keck 7843* (POM); 10 miles southwest of Garlic Springs, *Munz* & *Keck 7878* (POM).

Eschscholzia covillei is usually readily distinguishable from *E. minutiflora* (table 1), especially when the two are found in adjacent or mixed colonies. Where they occur in mixed colonies the two are distinguished by flower size and habit. It is perhaps more difficult to distinguish *E. covillei* from *E. parishii*, but the two are not known to grow together (fig. 1). In general, the latter two differ consistently in stamen number and in the number of grooves on the pollen. The specimens from San Bernardino County that are identified as *E. covillei* are geographically closest to *E. parishii* and it would be desirable to have additional chromosome number determinations from this area in order to confirm their identification. The hexaploid species, *E. minutiflora*, also grows sympatrically with *E. parishii*, and in such localities plants of the two species are readily distinguished, as is also true of most herbarium specimens, by the larger flowers and greater stamen number of *E. parishii*. All three species are found on comparatively moist alluvial slopes and fans, but unlike the other two species, the hexaploid *E. minutiflora* extends onto the desert floor.

Plants of *Eschscholzia parishii* from near Randsburg, Kern County (*Lewis* & *Mosquin 1117*; *Heller 7683*), the only locality for this species on the Mojave Desert, are intermediate in several morphological traits between *E. parishii* from the Colorado Desert and *E. covillei*. They may have as few as 14 stamens per flower, and they have an intermediate pollen morphology and stamen number. In the Heller collection, pollen

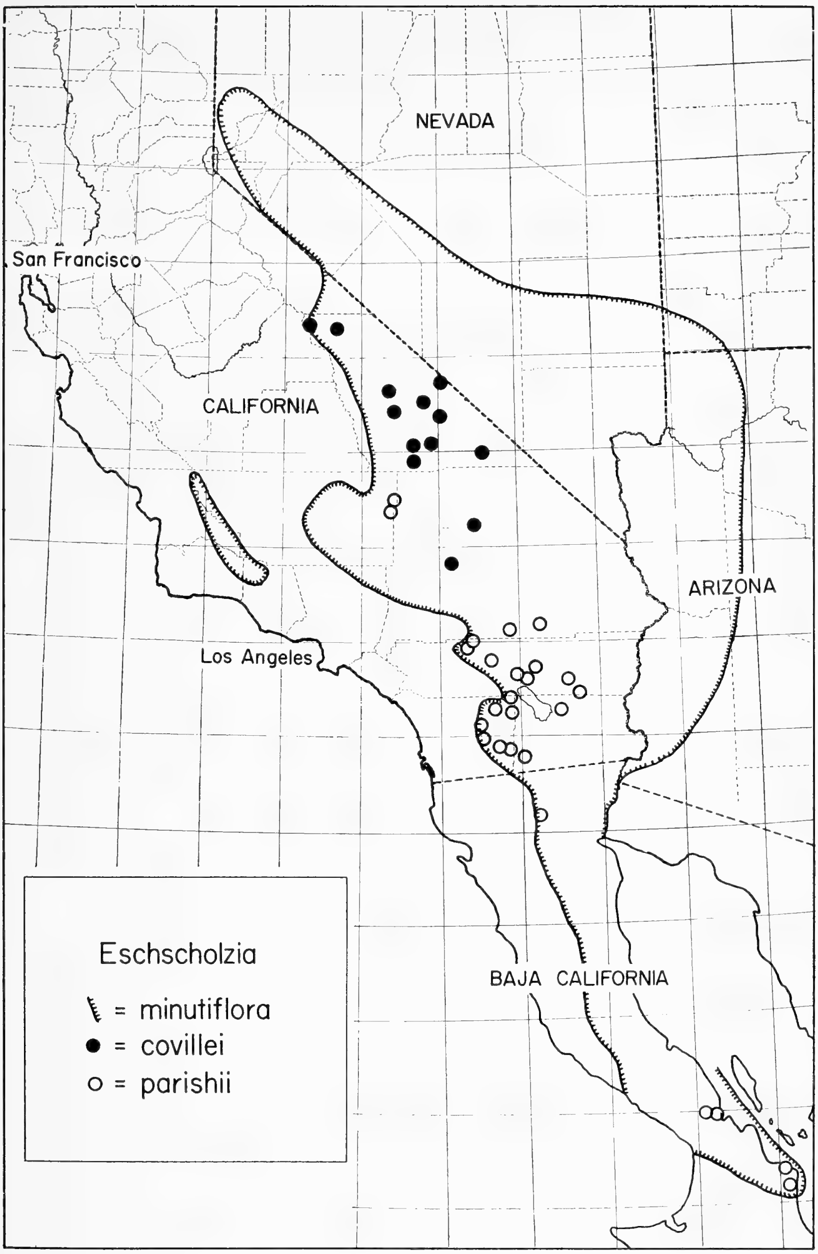

FIG. 1. General distribution of *Eschscholzia minutiflora* and selected localities of *E. covillei* and *E. parishii*.

size varied from 17–21 microns, and the two buds examined had, respectively, 14 and 15 stamens. The pollen had 7 and 8 grooves in approximately equal frequencies. In the Lewis and Mosquin collection, for which the chromosome number has been determined, pollen diameter varied from 20–32 microns, the pollen had 7, rarely 6, grooves per grain, and the stamen number varied from 16–18 per flower. In view of these morphological traits this might be considered a local subspecies of *E. parishii.*

The chromosomes of all three species are similar in size and morphology, with ring bivalents being more frequent than rods. The following list includes all known chromosome counts[2] made in this group:

ESCHSCHOLZIA PARISHII ($n = 6$). CALIFORNIA. Kern County: about 2 miles southeast of Searles Station, *Lewis & Mosquin 1117* (3 plants, 1 count from somatic cells). Riverside County: Morongo Wash, *Snow 11* (5 plants)[a]; about 5 miles west of road to Cottonwood Springs on United States Highway 60, *Lewis & Ernst* in 1949 (3 plants)[b]; Joshua Tree National Monument, *Lewis* in 1949[b]; Box Canyon, *Snow 7*[a]; *Raven 11478* (somatic count).

ESCHSCHOLZIA COVILLEI ($n = 12$). CALIFORNIA. Inyo County: *Mosquin & Lewis 3241* (2 plants), *3251* (3 plants), *3255–3, 3255–4* (2 plants), *3256* (2 plants), *3258–1*; *Lewis 1084*; Westgard Pass road, 2.8 miles west of Zurich, *Ernst 561*[d], 1.6 miles west of Zurich, *Ernst 564*[d].

ESCHSCHOLZIA MINUTIFLORA ($n = 18$). CALIFORNIA. Imperial County: road to 17 Palms, 0.3 miles east of United States Highway 99, *Lewis* in 1952. Inyo County: Panamint Valley, 15 miles north of road to Darwin on road to Stovepipe Wells, *Mosquin & Lewis 3240*; 4.6 miles from junction of State Highway 190 with road to Darwin Falls, *Mosquin & Lewis 3249, 3250* (total of 3 plants); 4.2 miles north of road to Darwin Falls on road to Darwin Springs, *Mosquin & Lewis 3254*; Panamint Valley, 7.2 miles east of junction to Trona on road to Stovepipe Wells, *Mosquin & Lewis 3255–1, 3255–2* (2 plants); 0.6 mile west of Bradbury Well entrance of Death Valley Natl. Mon., *Mosquin & Lewis 3258–2*; east of Darwin, *Snow 26* (approximate count)[a]; just below Darwin Falls, *Raven 12114.* Kern County: 2 miles southeast of Searles Station, *Lewis & Mosquin 1117–4.* Los Angeles County: 0.5 mile north of Pearblossom, *Mosquin 3265.* Riverside County: about 5 miles west of road to Cottonwood Springs on United States Highway 60, *Lewis & Ernst* in 1949 (3 plants)[b]; road to Cottonwood Springs, 7.2 miles north of United States Highway 60, *Snow 10*[a]; Box Canyon, *Snow 51*[a]. San Bernardino County: 0.8 mile north of Atolia, *Lewis* in 1950[b]; about 2 miles west of Lucerne Valley, *Snow 12*[a]; 10.2 miles east of Barstow, *Snow 23*[a]; United States Highway 395, 22 miles south of Inyo County line, *Snow 25–1*[a]; 15.9 miles south of Kramer Junction, *Lewis & Mosquin 1114*; 2 miles north of Needles, *Raven 13891* (approximate count). San Diego County: Mason Valley, near Vallecito Station, *Ernst 258*[c]. BAJA CALIFORNIA, MEXICO. 14.8 miles south of Mexican Highway 2 on road to San Felipe, *Raven 11630.*

Eschscholzia minutiflora also occurs in the South Coast Ranges of California (*Axelrod 260*, UC; *Axelrod 9170*, POM; *Schreiber 1045*, UC). The identification of this species is based on morphological considera-

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[2] Counts by Snow (unpublished) indicated by [a], those of Lewis & Snow, by [b], those of Ernst, 1958, by [c], and those of Ernst, 1959, by [d]. Vouchers for chromosome number determinations not previously reported are on file in the herbarium, University of California, Berkeley, or in the herbarium, University of California, Los Angeles. The first set of my own collections are deposited at the herbarium of the University of California at Berkeley.

TABLE 1. MORPHOLOGICAL COMPARISON OF THREE SPECIES* OF ESCHSCHOLZIA

	E. parishii (n=6)	*E. covillei* (n=12)	*E. minutiflora* (n=18)
Habit (rosette)	Poorly developed	Well developed	Well developed (Colorado Desert) or lacking (Mohave Desert)
Habit (branching)	Slender, delicate	Much-branched	Much-branched
Length of longest petals (range in mm.)	8–22	7–18	4–10
Length of mature buds (range in mm.)	7–16	6–9	2–7
Bud apex	Acuminate	Acuminate	Blunt (Colorado Desert or acuminate (Mohave Desert)
Number of stamens (range)	16–37	8–15	4–15
Length of longest stamens (range in mm.)	4–7.5	3.5–5	2–4
Number of pollen grooves** (range of means)	5.5–7	7.5–9.1	8.2–10.4
Diameter of pollen (range in microns)	20–32	24–37	25–44

* Only considering plants from which the chromosome number has been determined, 9 of *E. parishii*, 12 of *E. covillei*, and 27 of *E. minutiflora*.

** Mean of each plant based on 10 grains.

tions. One plant (*Axelrod 9170*) which was examined in detail had only 10 stamens per bud, a pollen diameter of 40 to 44 microns and usually 11 rarely 10 grooves per pollen grain. I have examined the pollen of the diploids *E. californica* Cham., *E. caespitosa* Benth., *E. glyptosperma* Greene, and *E. californica* var. *peninsularis* (Greene) Munz, and have found these plants to have a pollen variation comparable to *E. parishii* and out of the range of the pollen of *E. minutiflora*. A comparison of the pollen traits of *E. minutiflora* in the South Coast Range to those of *E. parishii* as shown in table 1 can leave little doubt that these Coast Range plants are hexaploid. The presence of this desert hexaploid in dry areas of the South Coast Ranges is not too surprising for a similar pattern of distribution is known for other desert annuals, e.g. *Linanthus parryae* (Gray) Greene, *Streptanthella longirostris* (Wats.) Rydb., *Erio-*

gonum trichopes Torr., *Chaenactis xantiana* Gray and *Salvia columbariae* Benth.

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ABNORMAL FRUITS AND SEEDS IN ARCEUTHOBIUM[1]

Frank G. Hawksworth

The normal *Arceuthobium* fruit, as described in the literature (Thoday and Johnson 1930, Dowding 1931, Gill 1935, Kuijt 1955, 1960), consists of a single seed containing one embryo. This paper describes abnormal fruits with two seeds and seeds with two embryos and endosperms as found in some specimens of *A. americanum* Nutt. ex Engelm. and *A. vaginatum* f. *cryptopodum* (Engelm.) Gill.

The fruit of *Arceuthobium* and other members of the Loranthaceae differs from other angiosperms in that there are no true ovules. The ovarian cavity becomes nearly filled by an undifferentiated mound of tissue termed the mamelon, nipple, or ovarian papilla. Two embryo sacs are borne within the ovarian papilla. Usually only one embryo sac develops, but occasional diembryonic seeds have been reported in a number of species (Peirce 1905, Weir 1914, and Heinricher 1915). The process of fertilization in *Arceuthobium* has not been precisely described. However, the development of the embryo sac after fertilization is apparently similar to that in most dicotyledonous plants. As the fruit matures, the dominant embryo sac develops into a copious endosperm with a small embryo. The remnants of the ovarian papilla become crushed, and in *A. pusillum* they form a distinct "crest" at the base of the seed (Thoday and Johnson 1930). The crest was not well defined in the mature, normal *A. americanum* (fig. 1A) and *A. vaginatum* f. *cryptopodum* fruits examined. However, a small mass of tissue which is presumed to be analogous to the

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[1] Acknowledgment is expressed to Job Kuijt, Department of Biology and Botany, University of British Columbia, for reviewing the manuscript and to William Schacht, School of Forestry, Duke University, for providing some of the abnormal fruits described.

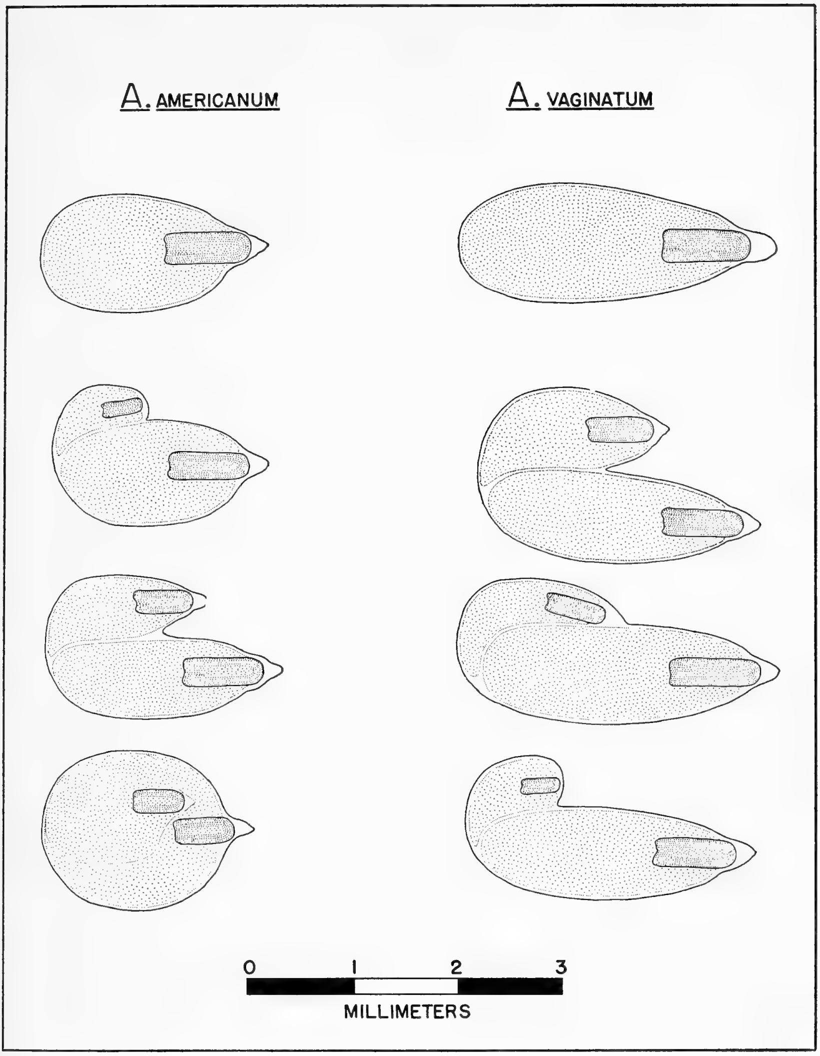

FIG. 1. Semi-diagrammatic drawings of longitudinal sections through *Arceuthobium americanum* fruits. A. Normal fruit with a single seed containing one embryo. The tissues labeled are: *v.c.*, viscin cells; *per.*, pericarp; *e.*, endocarp of the seed; *emb.*, embryo; *end.*, endosperm; *a.l.*, abscission layer; and *ped.*, pedicel. B-F. Abnormal fruits; these are described in the text.

crest in *A. pusillum* was observed in most fruits. At maturity the *Arceuthobium* fruit is severed from its pedicel, and the seed is forcibly ejected.

ABNORMAL FRUITS

Fruits of *A. americanum* with more than one stigma (figs. 1, 2) were noticed from plants in several areas of the Medicine Bow National Forest

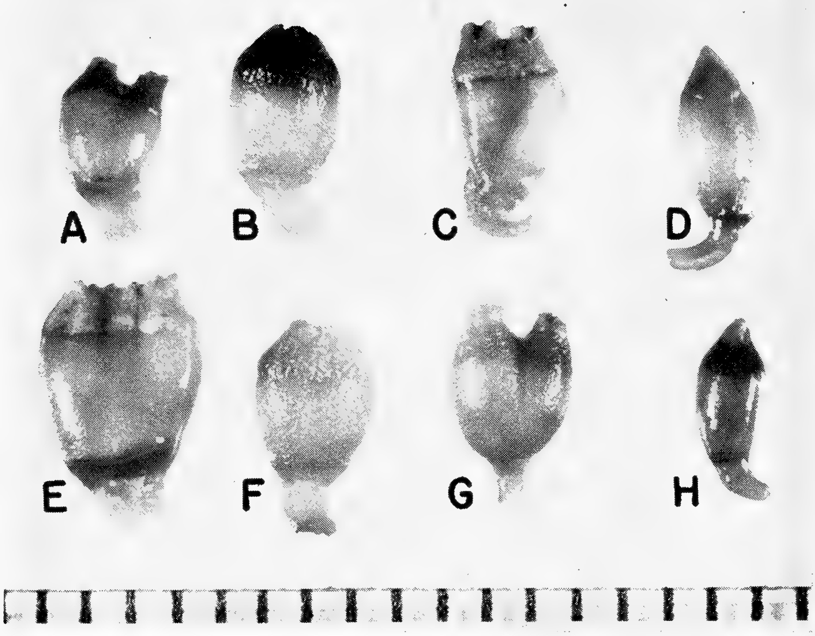

FIG. 2. Fruits of *Arceuthobium americanum*: normal, D and H; abnormal, A-C, E-G. Scale below is millimeter rule.

in southern Wyoming and the Roosevelt National Forest in northern Colorado. In a sample of 803 fruits from one locality in the latter forest, seven, or 0.9 per cent, had two stigmas. Dissection of 16 abnormal fruits collected in August revealed four general types.

TYPE 1. Fruits with two stigmas and two normal seeds (fig. 1B; fig. 2F and 2G). A wall of tissue separating the two seeds was sometimes present (fig. 1F) and sometimes not (fig. 1B). Nine of the sixteen fruits dissected were of this type.

TYPE 2. Fruits with two stigmas, one normal seed and one aborted seed (fig. 1C and 1D; fig. 2A and 2C). Four specimens had a small aborted seed (fig. 1C), but only one was found with two full-sized chambers (fig. 1D).

TYPE 3. Fruit with one stigma but two normal seeds (fig. 1E; fig 2B). Only one such fruit was found.

TYPE 4. Fruit with three stigmas and two normal seeds (fig. 1F; fig. 2E). One of the seeds had two embryos. Only one fruit of this type was found.

The abnormal fruits averaged about the same length as normal ones (3.6 mm.) but were about 50 per cent wider (2.7 compared with 1.9 mm.). The seeds from the multiple fruits measured 0.9 x 2.1 mm. compared with 1.0 x 2.2 mm. for seeds from normal fruits on the same plants.

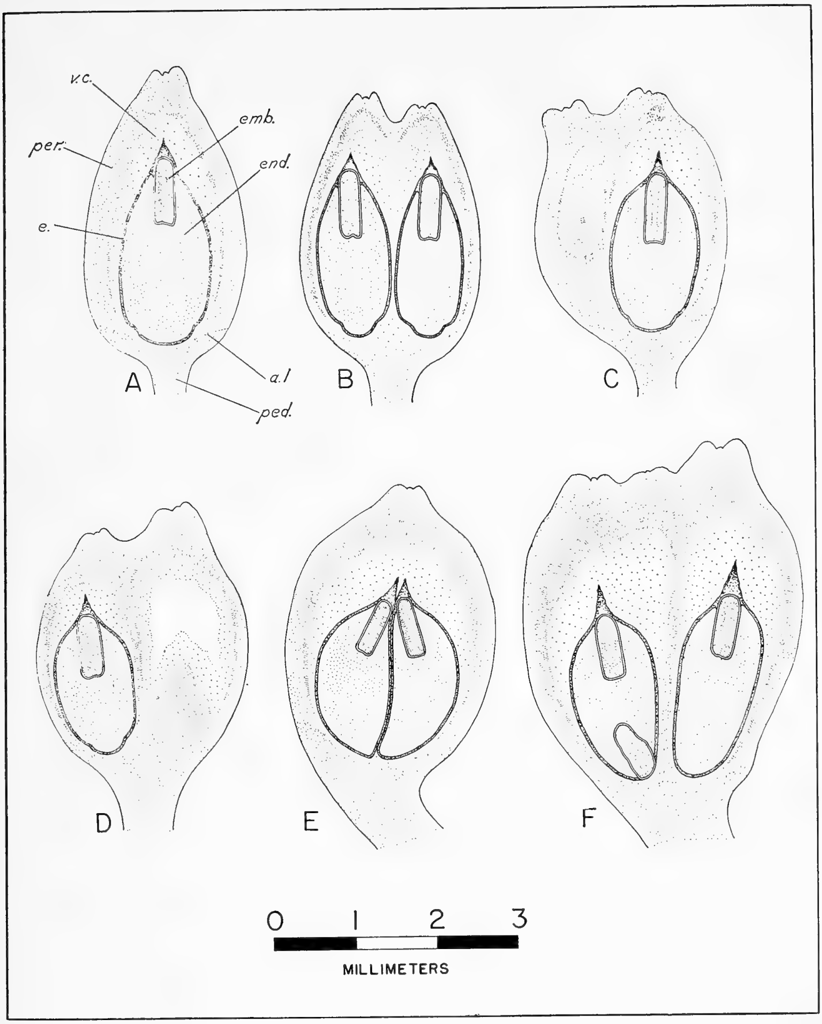

FIG. 3. Seeds of *Arceuthobium americanum* and *A. vaginatum* f. *cryptopodum*. The upper seed in each column is normal and of average size for the species. The lower three seeds in each column represent abnormal forms with two elements, each with an endosperm (light stippling) and embryo (dark stippling) within a common endocarp.

Intensive search yielded only one fruit of *A. vaginatum* f. *cryptopodum* with more than one stigma. This fruit, from near Estes Park, Colorado, had three stigmas and three distinct chambers. Two of these, the outer ones, contained normal seeds, but the central chamber had an apparently aborted seed (similar to that in the right chamber in fig. 1D).

Fruits with multiple stigmas have not been reported previously in *Arceuthobium*. Unfortunately, there has been no opportunity to observe the development of these abnormal fruits. Possibly the double fruits arise as fasciations and each stigma is pollinated separately. The resulting seeds seem to develop more or less independently of each other. The two seeds are enclosed in separate endocarps.

Usually both seeds develop at about the same rate (type 1, fig. 1B), but sometimes one is suppressed (type 2, figs. 1C and 1D). I am unable to explain satisfactorily the development of the fruit bearing a single stigma but containing two normal seeds (type 3, fig. 1E); however, both embryo sacs may have developed as each seed became enclosed in a separate endocarp. The most unusual fruit was that containing three stigmas and two seeds, one with two embryos (type 4, fig. 1F). The diembryonic seed had embryos at opposite ends. Both embryos were about normal size, but the accessory one was somewhat irregular in shape.

ABNORMAL SEEDS

Peirce (1905) described a seed of *A. campylopodum* f. *campylopodum* *(A. occidentale)* that had two embryos (one about normal size and the other one third normal size) but within a single endosperm. Weir (1914) reported diembryonic seeds in *A. vaginatum* f. *cryptopodum* (3 of 20 seeds), *A. douglasii* (4 of 30 seeds), and *A. americanum*, and although he did not describe them in detail, he stated that they were morphologically similar to normal seeds but "occasionally below average size." Heinricher (1915, Plate 1, fig. 6) illustrated an unusual diembryonic seed in the European *A. oxycedri*; the seed itself appears to be similar to normal seeds, but it has two hypocotyls.

Diembryonic seeds have been found by the writer in both *A. americanum* and *A. vaginatum* f. *cryptopodum*. They differ from the diembryonic seeds previously described in the literature (see above) in that they also contain two endosperms (fig. 3). Apparently both embryo sacs develop so that there are two units each of embryo and endosperm, both enclosed within a common endocarp. (These differ from the seeds shown in fig. 1E which are enclosed in separate endocarps.) The two units differ in size, the embryo in the larger unit being about normal size. The embryo in the second unit is smaller, the reduction being approximately proportional to that of the endosperm. No seeds of this type were found in the abnormal fruits dissected, therefore it is assumed that they are formed in normal appearing fruits.

Counts of *Arceuthobium vaginatum* f. *cryptopodum* seeds in various localities showed that 1.0 per cent were of this abnormal type (Table 1).

No counts have been made on the frequency of abnormal seeds in *A. americanum*, but they appear to be about as rare as in *A. vaginatum* f. *cryptopodum*. It has not been determined whether or not these abnormal seeds will produce two hypocotyls. However, Heinricher (1915) and Weir (1914) observed formations of double hypocotyls in the species of *Arceuthobium* which they studied.

TABLE 1. ABNORMAL SEEDS OF ARCEUTHOBIUM VAGINATUM F. CRYPTOPODUM FROM VARIOUS LOCALITIES.

LOCALITY	SEEDS EXAMINED NUMBER	ABNORMAL PERCENT
Sandia Mountains, New Mexico	500	2.4
Manzano Mountains, New Mexico	925	1.7
Flagstaff, Arizona	3,950	0.8
Roosevelt National Forest, Colorado	772	0.7
TOTALS	6,147	1.0

DISCUSSION

The formation of two seeds in the fruit of *Arceuthobium* has the advantage of increased reproductive capacity. However, this is presumably accompanied by decreased efficiency of the seed dispersal mechanism.

Polyembryony is common in the Loranthaceae. Its possible significance in the dioecious mistletoes is discussed by Allard (1943). He suggests that male and female plants may arise from different embryos within a seed. If this is true, it is possible that a mistletoe population could develop in a new area from a single seed.

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TO ALBERT W. C. T. HERRE

Dr. Herre, the California Botanical Society congratulates you on your forthcoming ninety-third birthday, September 16, 1961. This close approach to the century mark in itself excites admiration among us, for few indeed possess the heritage that makes such an accomplishment possible. But attainment of this outstanding age is but one of the attributes that places you high in our esteem, for your accomplishments as a naturalist in the fields of ichthyology, lichenology, and ecology through three quarters of a century set you apart as a scientist extraordinary.

As we realize that lichenology has claimed only a segment of your thought, study, and publishing activities, and that your list of papers dealing with taxonomic ichthyology, ecology, and geographical distribution of fishes includes several hundred titles, we marvel that one man has been able to accomplish so much in his life-time, long and busy though it has been. Nor, we realize, has writing scientific papers, monographs, and textbooks claimed all of your time and energy. Individuals well beyond middle age can recall that their early grade and high school training occurred under your supervision while you served as teacher, principal, and superintendent of schools. Others are equally aware of your administrative and research activities in the Philippines and your promotion of careful work on fishes and other natural resources in that part of the world before you returned to the United States in 1928.

We remember, also, that you accepted a challenging appointment with the Fish and Wildlife Service after you became Curator Emeritus of the Ichthyological Collections at Stanford University in 1947, and spent a strenuous year in your old area of field operations, the Philippine Islands, carrying on extensive collecting activities.

Adding further to your laurels, you followed the Philippine work with a dozen years as Ichthyologist and Curator of Tropical Fishes at the University of Washington, carrying forward work on large collections of lichens during your "spare" time. Then, when Mrs. Herre's health was jeopardized by the cool, damp climate along the Washington coast, and you moved to Santa Cruz, some thought you would be content to reduce your work load and withdraw from active participation in biological research. Others, who knew better your penchant for continuous work, were not greatly surprised that instead, you launched into the final stages of preparing a monograph on the genus *Usnea* as represented in North America. Few, indeed, have the strength, the desire, and the will to take up such an arduous task when nearly ninety years of age. Still fewer successfully apply to the National Science Foundation for a grant to enable them to visit over a score of herbaria and private collections to carry the undertaking to completion!

In celebration of your ninety-third birthday, we congratulate you on your scientific accomplishments, admire your physical stamina and mental alertness, wish we could consistently display your cheerfulness,

Dr. Albert W. C. Herre
on his 85th birthday, Sept. 16, 1953

and hope that one of us may have the privilege of preparing a congratulatory message to you seven years hence. We sincerely hope that you will enjoy yet more years of extraordinary good health and continue your interest in the various phases of natural history that have fascinated you, and to which you have contributed so much during a large portion of a century.—Ira L. Wiggins, Stanford University.

CHROMOSOME COUNTS IN THE GENUS MIMULUS (SCROPHULARIACAE)

Barid B. Mukherjee and Robert K. Vickery, Jr.

Although our long range investigation concerns the evolution of species in sections *Simiolus* and *Erythranthe* of the genus *Mimulus* (Vickery, 1951), we have recently made genetical and cytological studies of several species belonging to other sections of the genus. The crossing results have already been given (Vickery, 1956), and this paper presents the cytological findings.

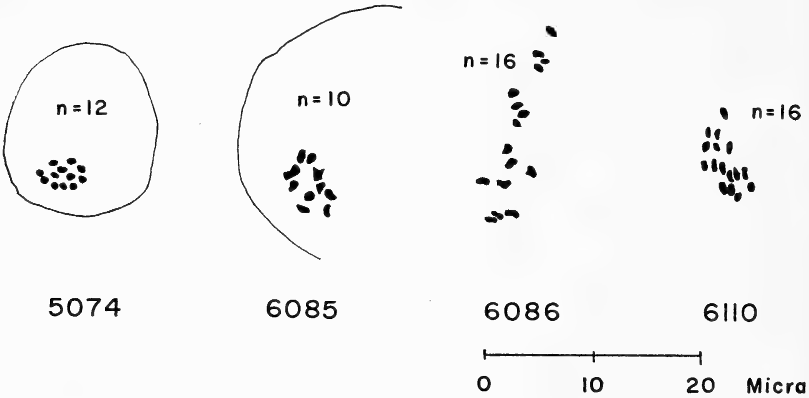

Fig. 1. Meiotic chromosomes of *Mimulus ringens* (5074), *M. aurantiacus* (6085), *M. moschatus* (6086) and *M. floribundus* (6110). All configurations are in or near second metaphase. Camera lucida drawings were made at ×2,520 and reduced to ×1,260 in reproduction.

The same method of bud fixation was employed as in previous investigations (Mukherjee and Vickery, 1959, 1960). Each chromosome number determination was based on counts from an average of nine pollen mother cells. Herbarium specimens of each culture will be deposited in the Garret Herbarium of the University of Utah (UT).

Four species, representing three sections of the genus, were studied: *Mimulus ringens* L. of section *Eumimulus*; *M. aurantiacus* Curt. of section *Diplacus*; and *M. moschatus* Dougl. and *M. floribundus* Dougl., both of section *Paradanthus* (see table 1 and figure 1).

The count of n = 12 for blue flowered *M. ringens* of eastern North America, type species of the genus, differs from any previously reported for the genus (Campbell, 1950; Carlquist, 1953; Darlington and Wylie, 1955; McMinn, 1951; Mukherjee and Vickery, 1959, 1960; Mukherjee, Wiens, and Vickery, 1957a, 1957b; and Vickery, 1955). However, *M. ringens* is the only species so far counted in section *Eumimulus,* and additional counts of n = 12 are possible in this section.

Shrubby *M. aurantiacus* of the chaparral areas of central and northern California was found to have n = 10 chromosomes, as do other

Table 1. Chromosome Counts in the Genus Mimulus.

n = 12	*M. ringens* L., section *Eumimulus.* St.-Jean, St.-Jean County, Province of Quebec, altitude ca. 200 feet, *M. Raymond* and *J. Kucyniak,* summer 1951 (5074).
n = 10	*M. aurantiacus* Curt., section *Diplacus.* Near Round Top, Alameda County, California, altitude 1,200 feet, *Vickery 990* (6085).
n = 16	*M. moschatus* Dougl., section *Paradanthus.* Mill Creek Canyon, Salt Lake County, Utah, altitude 7,400 feet, *Vickery 1036* (6086).
n = 16	*M. floribundus* Dougl., section *Paradanthus.* Hog Ranch, Mather, Tuolumne County, California, altitude 4,600 feet, *Vickery 1372* (6110).

species of section *Diplacus* previously reported by McMinn (1951). McMinn's extensive crossing studies suggest that this number, not found in other sections of the genus, is characteristic of section *Diplacus.*

Mimulus moschatus and *M. floribundus*, both widespread in western North America, were found to have n = 16 chromosomes. Both species have small yellow flowers and are low-growing with viscid-pubescent leaves and stems, but they differ markedly in leaf size and shape and in duration (*M. floribundus* is annual; *M. moschatus* is perennial). The two species hybridized readily in the garden. The F_1 hybrids were vigorous, but completely sterile (Vickery, 1956). Despite the cytological and some morphological similarities, these two entities would appear to be genetically and taxonomically distinct.

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SPHENOPHYLLUM NYMANENSIS SP. NOV. FROM THE UPPER PENNSYLVANIAN[1]

J. F. DAVIDSON

While coal is not found in commercial quantities in Nebraska, there are a number of thin seams exposed in the southeastern counties of the state, and investigation of these has proved to be quite profitable from a paleo-botanical viewpoint. In the majority of sites investigated, a layer of limestone immediately above the coal has precluded the finding of anything but highly coalified fossils. However, in the clay pit of the Western Brick Company at Nebraska City in Otoe County, the exposed Nyman coal shales out, and plant fossils are abundant. Plant material is so abundant in fact that the specimens, frequently with cuticle intact, are almost impossible to separate. It was from this site that representatives of the Pennsylvanian Sphenopsida of the order Sphenophyllales, including the present *Sphenophyllum*, were collected.

According to Condra and Reed (1943), the Nyman coal is found toward the top of the Langdon shale formation of the Richardson Subgroup, Wabaunsee Group, Virgil Series of the Pennsylvanian Sub-system. In part of the clay pit, as in the other sites mentioned above, the Nyman coal lies immediately below the Dover limestone. As the coal begins to shale out, the plant remains are separated by such minute quantities of shale as to be almost impossible to recover. However, as shaling continues, and the amount of shale increases, the plant remains are more readily defined. Preservation is very good in the fine sediment, and, as reported by Barbour (1914), many compressions retain their cuticular coverings which may be floated free, cleared, and mounted for study.

In the deposit, specimens of *Sphenophyllum* are fairly common, although few show more than two or three nodes. *Sphenophyllum cuneifolium* Sternb., *S. emarginatum* Brong. and *S. majus* Brong. are represented, as well as another large-leaved taxon which was at first considered to be a variant of *S. majus*. Closer examination, and a comparison of a number of these large-leaved specimens with specimens of *S. majus* indicate that two taxa are involved, and the name *Sphenophyllum nymanensis* is hereby proposed for the novelty.

Sphenophyllum nymanensis sp. nov. (Fig. 1) Leaves in whorls of 6 per node, 12–17 mm. long, 5–10 mm. wide; veins branching 3–5 times from the base, terminating at the rounded to somewhat truncate apex; stems fairly robust for a *Sphenophyllum*, about 2 mm. in diameter, with nodes swollen to 3 mm.; internodes subequalling the leaf length, 12–17 mm. long.

LOCALITY. Clay pit, Western Brick Company, Nebraska City, Otoe County, Nebraska.

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[1] This work was supported by a grant from the University of Nebraska Research Council.

HORIZON. Nyman coal, and Langdon shale above, Virgil Series, Upper Pennsylvanian.

TYPE. Paleobotanical collection, University of Nebraska State Museum.

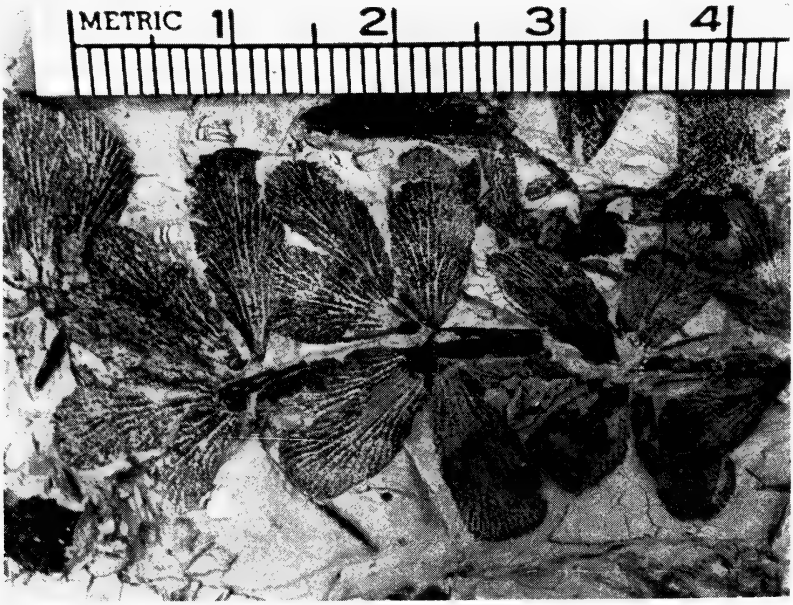

FIG. 1. *Sphenophyllum nymanensis* J. F. Davidson.

Sphenopyllum nymanensis, in terms of size most closely resembles *S. majus* from which it is readily distinguished by the following characters:

S. nymanensis	*S. majus*
6 leaves per node	8–10 leaves per node
leaf apex rounded to slightly truncate	leaf apex truncate
leaf margin entire	leaf margin with each vein terminating in a small deltoid tooth.

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A NEW NAME IN THE ALGAL GENUS PHORMIDIUM

Francis Drouet

Phormidium anabaenoides, nom. nov. *P. thermale* Drouet. Publ. Field Mus. Bot. 20(6):138. 1942. A new name is necessary for this alga of hot springs of Lake and Sonoma counties, California, because of the discovery in the literature of another *P. thermale* described by Professor V. Vouk (Prirod. Istr. Hrvatske i Slavon., Jugosl. Akad., Mat.-Prirod. Razr. 8:9. 1916). The research involved here was supported by the National Science Foundation.

Department of Botany, College of Agriculture
University of Arizona, Tucson

NOTES AND NEWS

Plagiobothrys austinae (Greene) Johnston: A New Addition to the Oregon Flora.—In April, 1959, the distinctive *Plagiobothrys austinae* (Greene) Johnston, formerly believed endemic to the Great Valley of California with a range of distribution from Stanislaus to Shasta counties, was collected in the botanically interesting Agate Desert west of Camp White, Jackson County, Oregon (*Ornduff 5043A*, UC, OSC, WTU). The locality in Oregon where this species occurs is separated from its nearest station in California near Redding, Shasta County, by about 140 miles of the Klamath-Cascade mountain complex. In many aspects of vegetation and topography, the Agate Desert is strongly reminiscent of parts of the northern Sacramento Valley in California; consequently, intensive collecting in the future may be expected to reveal additional Californian floral elements in the Agate Desert.—Francia Chisaki and Robert Ornduff, Department of Botany, University of California, Berkeley.

Stegnosperma cubense and Gossypium klotzschianum davidsonii not known in the Revillagigedos.—On the expedition of the California Academy of Sciences to the Revillagigedo Islands in 1925, plant collections were made not only there but also en route (Proc. Calif. Acad. ser. 4, 18:393–484, 1929). Labels of way specimens, headed "Expedition to the Revillagigedo Islands," have led evidently to one and apparently to two erroneous reports.

Rogers (Ann. Missouri Bot. Gard. 36:476, 1949) reported *Stegnosperma cubense* A. Richard from the Revillagigedos on the basis of *Mason 1846*; but Mason's fieldbook shows that this collection is from Isabel Island, just off the Mexican mainland.

Hutchinson (in Hutchinson, Silow, and Stephens, The evolution of *Gossypium* and the differentiation of the cultivated cottons, 1947, p. 23) reported *Gossypium klotzschianum* var. *davidsonii* (Kellogg) Hutchinson from the Revillagigedos, though without citing a specimen. This report has been repeated elsewhere. Upon inquiry, Dr. Hutchinson wrote that the report appeared to be erroneous, based on a specimen from an expedition to the Revillagigedos but collected in Baja California. Very likely he was misled by the same label heading (*Mason 1936, 1937* from Magdalena Bay).

Since it does not seem feasible at present to square the facts with the reports by introducing these two plants into the Revillagigedos, perhaps the best expedient is this note.—Reid Moran, Natural History Museum, San Diego, California.

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EVOLUTION OF THE GALIUM MULTIFLORUM COMPLEX IN WESTERN NORTH AMERICA

I. DIPLOIDS AND POLYPLOIDS IN THIS DIOECIOUS GROUP

FRIEDRICH EHRENDORFER

The *Galium multiflorum* complex comprises a group of races which are spottily distributed through the interior of western North America. They occupy, for the most part, dry and rocky talus slopes and cliffs, and they range from the *Larrea* desert zone to alpine timberline. Life forms change correspondingly from low xerophytic desert shrubs to reduced alpine hemicryptophytes. All members of this racial complex are dioecious and sexually reproducing. Their mostly rotate, yellowish or greenish flowers are insect pollinated. Long silky hairs on the fruits facilitate wind dispersal.

The *Galium multiflorum* complex belongs to the section *Lopho-Galium* K. Schum. of this rubiaceous genus. Circumscription, differentiation, and first detailed taxonomic treatment along classical lines have been worked out by Ehrendorfer (1956). Further contributions, including a somewhat changed taxonomical evaluation, have been published by Dempster (1959).

Within the frame of a broad scientific project aiming at an understanding of the main evolutionary features of this world-wide genus along comparative lines (for publications available so far, see Ehrendorfer 1958), work on the *Galium multiflorum* complex has been continued and expanded since 1959. This has been made possible by financial support from a Rockefeller grant and especially from National Science Foundation grant number 9825. Under the guidance and extremely stimulating cooperation of Professor G. L. Stebbins, the author carried out intensive research work in 1959; this included study of habitats and accompanying vegetation for nearly all of the chief divisions of the *G. multiflorum* complex, collection of transplant material and extensive population samples for statistical analyses, cytological research, and comparison of practically all herbarium material available. Later this project was joined and continued by Lauramay T. Dempster, whose help in various respects is gratefully acknowledged.

The present research on the *Galium multiflorum* complex aims at a reconstruction of its evolution in time and space as part of the general unfolding of the Great Basin flora and vegetation since the Tertiary and at the demonstration of the main evolutionary mechanisms involved. Results will be published in a series under the general heading of which this is the first contribution. The main questions dealt with here are: (a) basic evolutionary mechanisms as elucidated by cytological behaviour; and (b) distribution of diploids and polyploids within the complex.

MADROÑO, Vol. 16, No. 4, pp. 109–140. October 30, 1961.

MATERIALS AND METHODS

Populations of various races of the *Galium multiflorum* complex studied in the field were designated by collection numbers. The italicized numbers in the text refer to the field collection numbers of the author and his various co-workers. Further data on these collections will be found in the detailed list of collections below. Transplant material was obtained and grown in the greenhouse of the Genetics Department, University of California, Davis, and later also in Orinda, California. Cultivation over long periods seems difficult, however, as requirements are quite specialized as to soil, temperature, etc. Carnoy solution (5 parts of 95 per cent alcohol: 3 parts of chloroform: 1 part of concentrated acetic acid) was used for the fixation of young flower buds in the field and of fresh shoot apices from transplanted material. Fixations were stored in the refrigerator. Saturated aceto-carmine with iron was employed for staining: anther material was squashed after short and gentle heating in the stain, whereas vegetative tissues were boiled in aceto-carmine for two minutes. A Zeiss standard Series GFL microscope was used for cytological work, and the drawings were made with a camera lucida. Herbarium vouchers from plants with known chromosome number will be deposited in principal herbaria after conclusion of the present research project.

GENERAL CYTOLOGY

Mitosis, meiosis and pollen grain mitosis were studied in various races of the *Galium multiflorum* complex. As a main result the existence can be established of a polyploid series with diploids, tetraploids and a local hexaploid (see discussion), all having the base number $x=11$. Apart from determination of chromosome numbers some general cytological observations have been made.

The dioecious sex differentiation in the group led to the question as to whether sex chromosomes were cytologically recognizable. Mitoses of shoot apices from male and female plants of the diploid *G. hallii* were carefully compared. No obvious difference in number or shape of chromosomes could be detected. One has to consider, though, that with relatively small and not very clearly differentiated chromosomes (fig. 1a), minor differences could easily escape notice. In various diploid and polyploid races meioses in pollen mother cells were scrutinized in order to find heteromorphic bivalents of sex chromosomes, but without success. Cytological differentiation of males and females in the *G. multiflorum* complex, therefore, seems to be absent or cryptic.

Comparisons were made of mitoses from shoot apices of very distantly related diploids, like *G. hallii* and *G. hypotrichium* subsp. *tomentellum,* in order to find out whether structural differentiation of chromosome sets had occurred (fig. 1a, b). Results show that there is much similarity. Absolute size differences apparent from the figures 1a and 1b may be due to the developmental stage of the individual cells. In both races the chromosome set consists of: A) one pair of SAT-chromosomes,[1] B) one pair

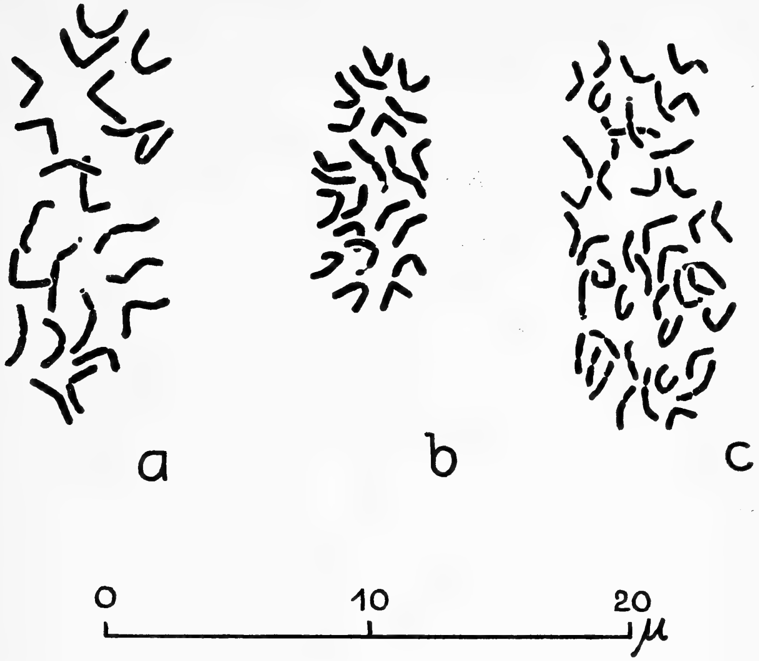

FIG. 1. Somatic mitosis in *Galium*. *a, G. hallii* (*5901*), *b, G. hypotrichium* subsp. *tomentellum* (*5941*), *c, G. grayanum* subsp. *glabrescens* (*5963,* tp. 2).

of long and strongly heterobrachial chromosomes, C) four pairs of chromosomes with less conspicuously different arms, and D) five pairs of chromosomes with median or submedian centromere. Groups C and D are not always clearly separable. This general pattern is also maintained in the allotetraploid *G. grayanum* subsp. *glabrescens* (fig. 1c). In spite of these similarities, indications for some structural differentiation can be found, e.g., in the SAT-chromosomes, where relation between long and short arms as well as satellite size are clearly different in *G. hallii* and *G. hypotrichium* subsp. *tomentellum.*

In spite of some cell-to-cell variability in chromosome size, there is a clear hereditary diminution of chromosome size with polyploidy. This is demonstrated better by comparison of somatic mitoses (fig. 1) from diploids than by comparison of corresponding stages of pollen meioses (fig. 2a, b) or pollen mitoses (fig. 2 l, m). Diminution of chromosome size is less obvious in the probably quite recent local hexaploid (fig. 2c). This reduction of chromosome size (and very likely nuclear size) in polyploids does not fully compensate the cell size increase correlated with

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[1] The satellites often stick to the short arms, making it difficult to recognize the SAT-chromosomes. Such sticking seems to happen nearly always in pollen mitoses fig. 2 l, m).

polyploidy, as is apparent from comparison of PMC's and young pollen grains which are larger in polyploids than in diploids (fig. 2a-c, l, m). Studies to determine the effect of polyploid level upon stomatal size are being carried on by Mrs. Dempster, with promising results for the use of stomatal measurement as an indication of ploidy when cytological evidence is lacking.

In polyploids of the *Galium multiflorum* complex there is occasional intra-individual somatic instability of chromosome number. This has been established for *G. grayanum* subsp. *glabrescens* (*5963*, tp. 1) and it probably occurs in *G. munzii* (*5980*, tp. c.). From excellent fixations resulting in exceptionally clear mitotic pictures, it is evident that the former plant has 2n=45 as the most common number in young buds and shoot apices, but that occasional deviations occur, of which –44 –43 –42 –41 as a reductional series and –47 as an indication for accumulation were actually observed. One plant (*5980*, tp. c.) seems to vary between 2n=42 –44–45. In a number of other polyploids, e.g., *G. grayanum* subsp. *glabrescens* (*5963*, tp. 2) and *G. munzii* var. *kingstonense* (*5969*), counts of numerous mitoses always gave the stable number 2n=44. Intra-individual instability of chromosome number may be due to unbalanced primary number and/or spindle defects. Unstable somatic chromosome numbers have not been found in diploids.

Normal sexual reproduction is highly probable within the group. The course of pollen meiosis is remarkably normal in diploids and polyploids; male and female plants always coexist in the populations, often with an excess of males, and there is obvious morphological variability within the populations.

Chiasma frequency is variable. In the diploids with their relatively large chromosomes, frequency of bivalents with two chiasmata is often higher than 50 per cent, the other bivalents having only one chiasma (fig. 2d, e). Unpaired chromosomes seem to be extremely rare in the diploids. In the tetraploids with reduced chromosome size, the number of chiasmata is decidedly lower. In *G. hypotrichium* from Alpine County, for instance, there are only 15 per cent bivalents with two chiasmata in a plant from the Ebbetts Pass series (*5920*) and 10.9 per cent in a plant from the Sonora Pass series (*5917*) [each calculated from 50 PMC's]. Multivalents (trivalents with univalents and quadrivalents in chains and rings, fig. 2f) are relatively rare. In the above-mentioned plants there were 8 per cent PMC's with III+I and 28 per cent with IV (*5920*) and 8 per cent PMC's with III+I and 22 per cent with IV (*5917*). Univalents lag in anaphase I (fig. 2h), and are prematurely divided, but their halves are unable to divide a second time in anaphase II (fig. 2i); so they are eliminated or finally fuse with some of the telophase nuclei. As a result, pollen grains of polyploids occasionally contain deviating chromosome numbers (fig. 2m). This phenomenon must be basically responsible for some polymorphism of 2n numbers in populations of polyploids.

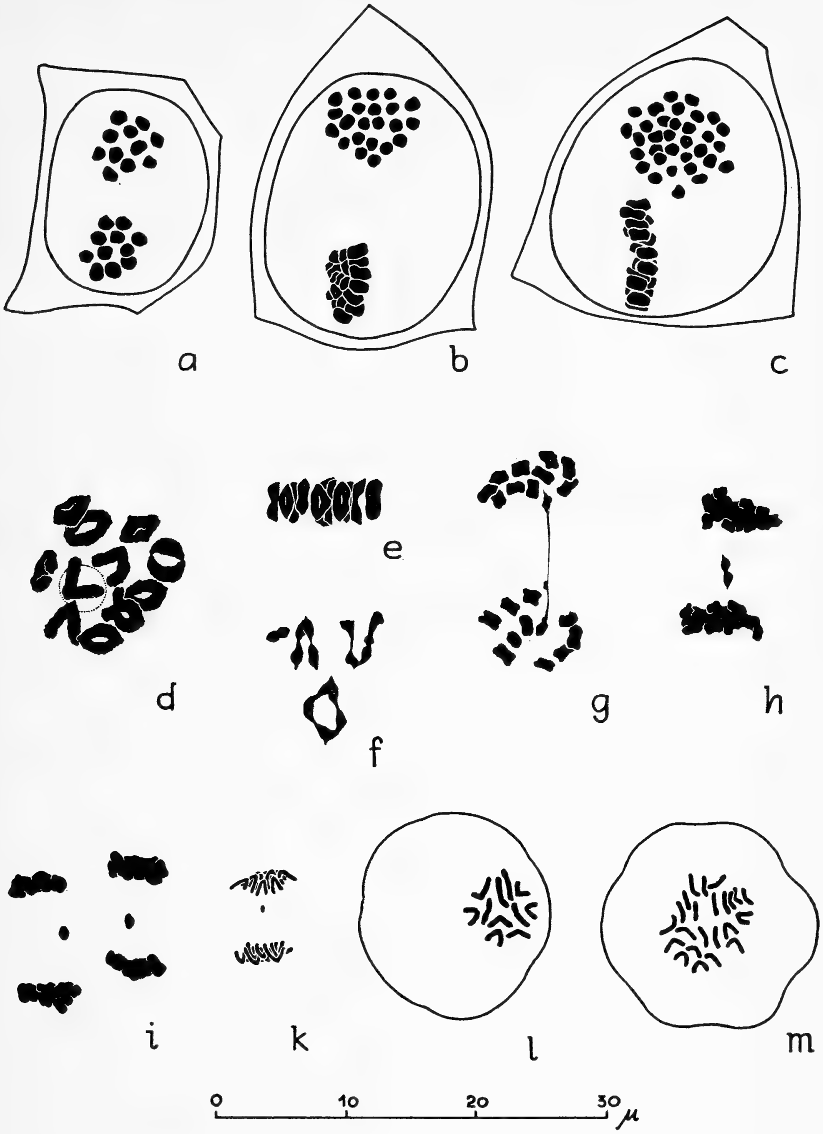

FIG. 2. Division figures in *Galium*. *a-c*, PMC metaphase II in diploid, tetraploid and hexaploid plants: *a, G. serpenticum*–2x (*5911–5913*, fd. IIa); *b, G. munzii*–4x (*5903*, tp.); *c, Galium* (6x race), Warner Mountains (*5909, 5910*). *d-i*, PMC divisions: *d*, diakinesis, *G. grayanum*–2x (*5933–5936*); *e*, metaphase I, side view, *G. serpenticum*–2x (*5914*); *f*, multivalents, III+I, IV chain, IV ring, *G. hypotrichium* subsp. *hypotrichium*–4x (*5920*); *g*, anaphase I with bridge and attached fragment, *G. parishii*–2x (*5902*); *h*, telophase I with lagging univalent, *G. hypotrichium* subsp. *hypotrichium*–4x (*5917*); *i*, telophase II with lagging univalent halves, *G. hypotrichium* subsp. *hypotrichium*–4x (*5920*). *k-m*, first pollen mitosis: *k*, anaphase with free acentric fragment, *G. hypotrichium* subsp. *hypotrichium*–2x (*5916*); *l*, metaphase *G. hypotrichium* subsp. *hypotrichium*–2x (*5916*); *m*, metaphase, aberrant pollen grain with n=23, *G. munzii* × *G. hypotrichium* subsp. *subalpinum*–4x (*5947*).

In 3 diploids, 1 tetraploid and 1 hexaploid, consequences of chromosome aberrations have been seen: bridges with and without fragments in

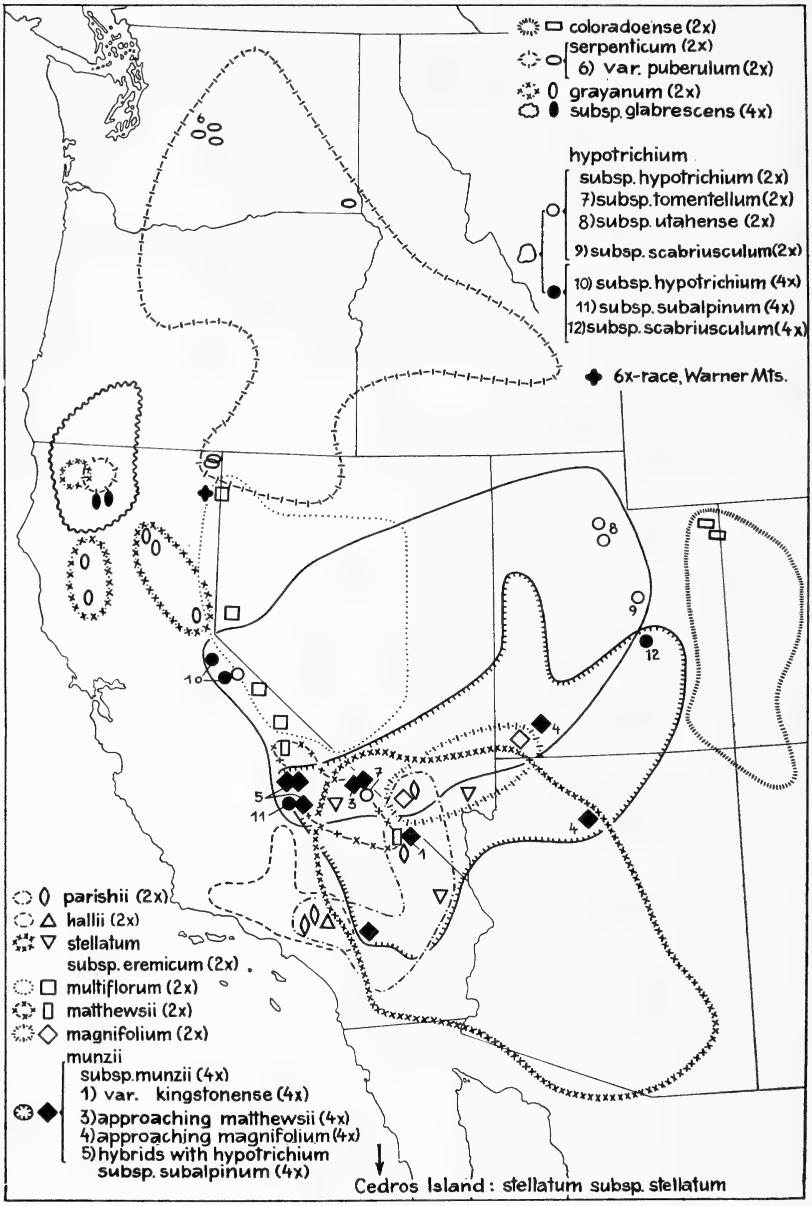

FIG. 3. Distribution of the *Galium multiflorum* complex, shown by outlines. Locations of populations examined cytologically are indicated by individual symbols.

anaphase I (fig. 2g), and liberation of attached fragments in anaphase of pollen mitosis (fig. 2k). In the hexaploid there are occasional spindle defects, restitution nuclei, and formation of resultant dyads.

Male sterility as a result of break-down of pollen development after normal meiosis has been observed in a diploid *G. serpenticum* plant from Mount Bidwell (*5911*).

Distribution of diploids and polyploids

Determination of chromosome numbers and ploidy levels is one of the major prerequisites for the reconstruction of the evolutionary history of the *Galium multiflorum* complex. So far, chromosome counts are available for most of the major species, subspecies, and hybrid populations presently recognized. These counts originate from 51 populations and more than 100 individuals. Populations with known chromosome numbers are shown on the map (fig. 3), as single symbols within the outlines of the total distributional area of their respective taxa.

The following list contains further information on geographical origin and habitat of the populations cytologically studied. The abbreviation "fd." indicates fixations made in the field, mostly comprising several individuals; chromosome counts in such instances usually refer to more than one individual. The abbreviation "tp." indicates fixations from single transplant individuals further designated by numbers or letters. Definite chromosome numbers are given after a minimum of several unquestionable counts per plant; if only one or few counts are available the symbol "±" is used. The abbreviation "ca." refers to approximate counts. Chromosome numbers are indicated in the diploid state (2n). They have been determined from vegetative tissues in flowers and shoot apices. Where counts have been carried out on pollen meiosis or pollen mitosis, 2n numbers have been extrapolated and an asterisk is added.

As is evident from the list, diploid populations are always uniform in respect to chromosome number (2n=22), while certain fluctuations of 2n numbers around straight x multiples have been observed in some polyploid populations: *G. munzii* from Wildrose Canyon (2n=44, 46), Lone Pine Creek (2n=42, 44), Zion National Park (2n=44, 45) and Grand Canyon (2n=42, 44). Polyploids are obviously less sensitive to aneuploidy, addition or loss of chromosomes, than diploids. The origin of aberrant types must be due to meiotic irregularities and deviating chromosome numbers in the gametes, or to intra-individual somatic instability, with similar consequences, situations which have already been referred to.

In the following list of collections, only previously published names have been used, and the taxonomic scheme followed is not necessarily in entire agreement with the author's present views. The taxonomic position of the plants in some of the populations represented is still uncertain, and their placement in the list is conservatively based on published work of the past

GALIUM COLORADOENSE Wight

Utah, Dinosaur National Monument, 1 mile west of campground near Split Mountain, 5150 feet; Shinarump Quartz conglomerate; sandy and gravelly north slope, very open Pinyon-Juniper: *Ehrendorfer* & *Stutz 5950.* tp.: 2n=22

Utah, Uintah County, just south of Brush Creek on Highway 44, ca. 11 miles north northeast of Vernal, ca. 6000 feet; open bushy and herbaceous pioneer growth on steep Jurassic sandstone cliff: *Ehrendorfer* & *Stutz 5951.* tp.: 2n=22

GALIUM GRAYANUM Ehrendf.

subsp. GRAYANUM

California, Tehama County, North Coast Ranges, South Yollo Bolly Mountain, 7700–8080 feet; gentle to steep talus slopes, metamorphic schists; subalpine pioneer vegetation among very open *Abies magnifica*: *Ehrendorfer 5933, 5934, 5935, 5936.*
fd.: 2n=22*

California, Lake-Colusa County, Goat Mountain, North Coast Ranges, 6000 feet: leg. *G. L. Stebbins* fd.: 2n=22

California, Lassen National Park, Brokeoff Mountain, 9000 feet; gentle to steep talus slopes, volcanic andesite; subalpine pioneer vegetation: *Ehrendorfer, Stebbins* & *Dempster 5964, 5965, 5966, 5967.*
tp. 0 : 2n=22
tp. 1 : 2n=22

California, Butte-Plumas County, Summit above Jonesville, ridge east of pass, 6700–7000 feet; rocks and talus slopes, volcanic andesite; pioneer vegetation among subalpine chaparral, *Abies magnifica* and *Pinus monticola*: type locality, *Ehrendorfer 5937, 5938, 5939.* fd.: 2n=22*

California, Placer County, Sierra Nevada, Sugar Bowl resort southwest of Donner Summit, 7200 feet; steep northeast slope, andesite talus and rocky outcrops; pioneer vegetation among *Quercus vaccinifolia, Abies magnifica* and *Pinus monticola*: *Ehrendorfer* & *Stebbins 5905.* fd.: 2n=22*

subsp. GLABRESCENS Ehrendf.

California, Siskiyou-Trinity County, west flank of Scott Mountain, ca. 6300 feet; ultrabasic intrusives; serpentine-peridotite; talus and gravel within very open *Pinus jeffreyi* and *Abies concolor*: *Ehrendorfer* & *Stebbins 5915.* fd.: 2n=44*

California, Siskiyou County, 0.5 mile south-southeast of Castle Lake, southwest of Mount Shasta village, ca. 6000 feet; serpentine talus, pioneer vegetation among *Arctostaphylos nevadensis, Pinus monticola, Abies magnifica*: type locality, *Ehrendorfer, Stebbins* & *Dempster 5963.*
tp. 1 : 2n=41–42–43–44–**45**–47
tp. 2 : 2n=44 (stable)

GALIUM HALLII Munz & Jtn.

California, Los Angeles County, northeast side of San Gabriel Mountains, Sawmill Canyon at west end of Swartout Valley, between Wrightwood and Lone Pine, 6600 feet; on steep north slopes, in mineral soil (schist) among *Quercus Kelloggii* and *Pinus ponderosa*: *Ehrendorfer 5901.* fd.: 2n=22

GALIUM HYPOTRICHIUM Gray

subsp. HYPOTRICHIUM

California, Alpine-Mono County, Sierra Nevada, ca. 0.5 mile south of Sonora Pass, ca. 10,200 feet; wind-exposed talus slope on crest line, volcanic rocks; very scattered pioneers: type locality, *Ehrendorfer 5916.* fd.: 2n=22*
fd.: 2n=22

California, Alpine County, Sierra Nevada, ca. 2 miles west of Sonora Pass, ca. 9500 feet; sheltered west slope, volcanic talus; *Ribes* bushes and herbs: *Ehrendorfer 5917.*
fd.: 2n=44*

California, Alpine County, Sierra Nevada, ca. 0.5 mile southeast of Ebbetts Pass, 8950 feet; northwest slope, volcanic talus; *Symphoricarpos, Artemisia,* herbs: *Ehrendorfer 5920.* fd.: 2n=44*

subsp. SCABRIUSCULUM Ehrendf. (*G. coloradoense* var. *scabriusculum* Dempster)
Utah, Carbon County, Castle Gate, side canyon on southwest of main valley, entrance ca. 1 mile northwest of the town, ca. 6500 feet; gully with steep sandstone slopes; grassy and herbaceous cover among open *Pinus ponderosa* and *Symphoricarpos*: *Ehrendorfer* & *Stutz 5954.* tp.: 2n=22

Utah, Emery County, small side canyons on either side of Buckhorn Wash, ca. 1 mile north of San Rafael River bridge, ca. 4500 feet; dry bottom of gullies with boulders and sand from sandstone; very open Pinyon-Juniper and scrub: near type locality, *Ehrendorfer* & *Stutz 5952, 5953.* tp. a: 2n=44
tp. b: 2n=±44
tp. c: 2n=ca. 44

subsp. SUBALPINUM (Hilend & Howell) Ehrendf.
California, Inyo County, Sierra Nevada, Cottonwood Lake Basin, slopes north and northwest above Muir Lake, ca. 11,200 feet; granitic talus; open *Pinus balfouriana, Holodiscus* and pioneer herbs: *Ehrendorfer 5945, 5946.* tp. 1: 2n=±44
tp. 2: 2n=±44

subsp. TOMENTELLUM Ehrendf.
California, Inyo County, Panamint Mountains, Telescope Peak, below top on north side, ca. 11,000 feet; talus of metamorphic schists; pioneers among very open *Pinus aristata*: type locality, *Ehrendorfer 5941.* fd.: 2n=22

subsp. UTAHENSE Ehrendf.
Utah, Utah County, Wasatch Mountains, American Fork Canyon, steep north slopes along trail to Timpanogos Cave, 6400–6800 feet; limestone rocks and talus; bushes and herbaceous pioneers among scattered *Pseudotsuga* and *Abies*: type locality, *Ehrendorfer* & *Stutz 5949.* tp.: 2n=22

Utah, Salt Lake County, Wasatch Mountains, steep north slopes, ca. 1 mile southwest of Alta, ca. 9000 feet; limestone rocks and crevices; vegetation similar to *5949*; *Ehrendorfer* & *Stutz 5955.* tp.: 2n=22

GALIUM MAGNIFOLIUM (Dempster) Dempster
Nevada, Clark County, Charleston Mountains, southwest of Las Vegas, near Cottonwood Springs, canyon above Bar Nothing Ranch (= Wilson's Ranch), ca. 4200 feet; steep north slope along creek, alluvial material below mesozoic sandstone; open Pinyon with *Artemisia, Yucca* and *Opuntia*: type locality, *Ehrendorfer* & *Dempster 5975.* fd.: 2n=±22
tp.: 2n= 22

Utah, Washington County, ca. 1 mile northeast of Hurricane, steep slope above tributary of Virgin River, ca. 3000 feet; Jurassic sandstone and talus; with *Ephedra, Artemisia,* etc.; *Ehrendorfer* & *Dempster 5979.* fd.: 2n=22

GALIUM MATTHEWSII Gray
California, Inyo County, east side of Sierra Nevada, Big Pine Creek, slopes above the camp site and road head, 8800 feet; loose granitic talus and sand, among *Artemisia*: *Ehrendorfer 5922.* fd.: 2n=22*

California, San Bernardino County, Kingston Mountains, steep slopes south of Kingston Pass, ca. 5500 feet; crevices of granite: *Ehrendorfer* & *Dempster 5974.*
tp. a: 2n=22
tp. b: 2n=22

GALIUM MULTIFLORUM Kell.
California, Modoc County, south of Eagleville, cliff above Lower Alkali Lake, 5000 feet; in crevices and at the base of east-northeast-exposed basalt rocks: *Ehrendorfer* & *Stebbins 5908.* tp.: 2n=22

California, Mono County, northwest shore of Mono Lake, on upper terrace, 6550 feet; among *Artemisia* and *Purshia* on light pumice sand: *Ehrendorfer 5918.*
tp.: 2n=22

Nevada, Storey County, Washoe Mountains, 2.2 miles north of Virginia City on Highway 17 to Reno, ca. 6600 feet; steep north slope, on volcanic talus among *Artemisia,* open Pinyon-Juniper along gully: type locality, *Ehrendorfer* & *Stebbins 5906.* fd.: 2n=22*

forma HIRSUTUM (A. Gray) Ehrendf.

California, Mono County, Sherwin Grade, dry wash southwest of Highway 6, ca. 6600 feet; volcanic rhyolite talus and rocks among *Artemisia,* open Pinyon: *Ehrendorfer* & *Dempster 5921.* tp.: 2n=22

GALIUM MUNZII Hilend & Howell

var. KINGSTONENSE Dempster

California, San Bernardino County, Kingston Mountains, steep slopes south of Kingston Pass, in gullies and toward the top, 5800–6000 feet; rocky ravines and steep slopes with Pinyon, granite: type locality, *Ehrendorfer* & *Dempster 5969, 5971.*
tp. a: 2n=44
tp. b: 2n=44

subsp. MUNZII

California, Inyo County, Lone Pine Creek just above its break-through into Owens Valley, ca. 5000 feet; steep north slopes with Pinyon on granitic sand: *Ehrendorfer 5927.*
tp. a (glabrous form): 2n=42
tp. b (hirsute form): 2n=44

California. Inyo County, Panamint Mountains, Wildrose Canyon, above charcoal kilns, ca. 7200 feet; metamorphic schists and sandstones; open Pinyon and Juniper, talus: *Ehrendorfer* & *Dempster 5968.*
tp. a (hirsute form): 2n=44
tp. b (hirsute form): 2n=44
tp. c (glabrescent form): 2n= ca. 44
tp. d (approaching *G. mathewsii* = var. *carneum* Hilend & Howell, 1934): 2n=46

California, Inyo County, Panamint Mountains, along trail from Mahogany Flat to Telescope Peak, ca. 8500 feet; metamorphic schists; talus, with *Holodiscus, Artemisia,* etc.: *Ehrendorfer 5943.* fd.: 2n=44*

California, San Bernardino County, San Bernardino Mountains, lower portion of Cushenbury Canyon, ca. 5000 feet; granitic talus, northeast slopes just above the wash, among open Pinyon-Juniper: *Ehrendorfer 5903.* fd.: 2n=±44
tp.: 2n=44*

probable hybrids with G. HYPOTRICHIUM subsp. SUBALPINUM

California, Inyo County, east side of Sierra Nevada, Lone Pine Creek, 0.5 mile below Whitney Portal, steep ravine with northwest exposure, ca. 8370 feet; granitic boulders and talus; open *Chrysothamnus* and *Artemisia*: *Ehrendorfer 5929.* fd.: 2n=44*
tp.: 2n=±44

California, Inyo County, east side of Sierra Nevada, Little Cottonwood Creek above Lone Pine, ca. 8800 feet; granitic rock and sand; *Cercocarpus, Holodiscus* and *Artemisia*: *Ehrendorfer 5947.* fd.: 2n=44*

approaching G. MAGNIFOLIUM

Utah, Zion National Park, trail to The Narrows, ca. 4300 feet; sandy and gravelly talus below Navajo sandstone cliffs, eastern exposure; loose cover of herbs and scrub; *Ehrendorfer* & *Dempster 5980.*
tp. a (hirsute form): 2n=44
tp. b (hirsute form): 2n=45
tp. c (glabrous form): 2n=±42–44–45

Arizona, Grand Canyon National Park, south rim, uppermost portion of Grand View

Trail, ca. 7000 feet; arenaceous limestone; steep slope with herbs, among *Cercocarpus, Amelanchier* and *Pinus edulis* in northern exposure: *Ehrendorfer & Dempster 5981.*

tp. a (somewhat hairy form): 2n=44
tp. b (glabrous form): 2n=42

GALIUM PARISHII Hilend & Howell
California, San Bernardino County, San Bernardino Mountains, top of San Gorgonio Mountain, 11,485 feet: leg. *P. Raven 11,152.* fd.: 2n=22*

California, Los Angeles County, San Gabriel Mountains, hills about 2 miles north of Big Pines, ca. 6500 feet; granitic talus in northwest exposure: open *Artemisia* with *Pinus jeffryi*: *Ehrendorfer & Grant 5902.* fd.: 2n=22*

California, San Bernardino County, Kingston Mountains, steep slopes south of Kingston Pass, ca. 5600 feet; granitic talus slopes and shady rock crevices: *Ehrendorfer & Dempster 5972, 5973.* fd.: 2n=22
tp.: 2n=22

Nevada, Clark County, Charleston Mountains, Kyle Canyon, southwest slopes, southeast of Cathedral Rock camp site, ca. 7600 feet; limestone talus and rock crevices among open *Pinus, Abies* and *Cercocarpus*: *Ehrendorfer & Dempster 5976.*
tp.: 2n=22

GALIUM SERPENTICUM Dempster [*G. watsonii* (Gray) Heller sensu Ehrendf.]
Washington, Asotin County, Blue Mountains, below the crest overlooking Indian Tom Creek, 30 miles southwest of Asotin, ca. 5300 feet; basalt, rocks and fine talus below, open bushy and herbaceous pioneer growth: *Ehrendorfer & Ownbey 5956, 5957.*
tp. 1: 2n=22

California, Modoc County, Warner Mountains, Mount Bidwell, southeast side of plateau top, ca. 8000 feet; basalt talus; bushy and herbaceous pioneer vegetation with *Artemisia,* grasses, etc.: *Ehrendorfer & Stebbins 5911, 5912, 5913.*

tp. I: 2n=22
2n=22*
tp. II–1: 2n=22
fd. II: 2n=22*

California, Modoc County, Mount Bidwell, southwest side of plateau top, below rim, ca. 7600 feet; east slope, steep basaltic talus; similar vegetation: *Ehrendorfer & Stebbins 5914.* fd.: 2n=22*

var. PUBERULUM (Piper) Dempster [*G. watsonii* (Gray) Heller subsp. *puberulum* Ehrendf.]
Washington, Kittitas County, Wenatchee Mountains, west-southwest slope in upper Beverley Creek, ca. 4500 feet; serpentine rock and talus, open pioneer vegetation: *Ehrendorfer & Kruckeberg 5958, 5959.* fd.: 2n=22*
tp. 1: 2n=22

Washington, Kittitas County, Liberty, knoll above Boulder Creek, ca. 3500 feet; Eocene sandstone shale; sandy talus slope with pioneers: *Ehrendorfer & Kruckeberg 5960.* tp. 1: 2n=22

Washington, Kittitas-Chelan County, south slope near Blewett Pass, ca. 4000 feet; sandy talus: *Ehrendorfer & Kruckeberg 5962.* tp. 1:2n=22

GALIUM STELLATUM Kell. subsp. EREMICUM (Hilend & Howell) Ehrendf.
California, Inyo County, Darwin Falls, about 3 miles south of Lone Pine-Death Valley highway, 3000 feet; rock crevices in canyon walls, metamorphic schists; desert scrub and some cacti: *Ehrendorfer & Dempster 5940.* fd.: 2n=22

California, San Bernardino County, hills south of Highway 66, 7 miles northeast of Essex, ca. 1000 feet; steep rocky slope, gneiss; desert scrub (*Larrea,* etc.): *Ehrendorfer & Dempster 5982.* tp.: 2n=22

Nevada, Clark County, Valley of Fire State Park, east entrance opposite Elephant Rock, ca. 2000 feet; rocky north slope, Triassic sandstone; desert scrub: *Ehrendorfer & Dempster 5978.* tp.: 2n=22

UNNAMED TAXON (6x race)
California, Modoc County, Warner Mountains, Horse Mountain, south of and toward summit, ca. 8500 feet; basalt talus and rocks; grassy and shrubby pioneers: *Ehrendorfer & Stebbins 5909, 5910.* fd.: 2n=66*

GALIUM ROTHROCKII Gray subsp. ROTHROCKII (a monoecious member of section *Lopho-Galium,* not directly connected with the *G. multiflorum* complex).
Arizona, Grand Canyon National Park, south rim, uppermost portion of Grand View Trail, ca. 7000 feet; arenaceous limestone; steep slope with herbs, among *Cercocarpus, Amelanchier,* and *Pinus edulis* in northern exposure (together with *G. munzii* approaching *G. magnifolium*); *Ehrendorfer & Dempster 5981A.* tp.: 2n=22

DISCUSSION

In spite of general dioecious sex differentiation, an eu-polyploid series 2x–4x–6x with x=11 has developed in the *Galium multiflorum* complex, just as in practically all of the hermaphrodite groups of this genus which have been checked cytologically so far. Polyploidization is less advanced than in some other groups with the majority of the races still diploid and only one very local hexaploid known. In the European section *Lepto-Galium*, for instance, polyploidization has proceeded to the 10x level, with the most widely spread and successful types (*G. pumilum, G. rubrum, G. marchandii*) on the 8x level (Ehrendorfer 1954).

Sexual differentiation in the *G. multiflorum* complex exemplifies an evolutionary trend established in a number of other New World groups of the genus as well. No sex chromosomes have been recognized so far. Sex differentiation in the complex must be similar in character to that in *Rumex* subgenus *Acetosella* or *Melandrium* (Löve and Sarkar 1956, and literature cited there). In these groups genetic sex determiners for the heterogametic sex are so strongly epistatic that polyploidization does not upset the 1:1 segregation mechanism (XY = ♂, XXXY = ♂, XXXXXY = ♂).

The basic evolutionary differentiation of the *G. multiflorum* complex is accompanied by only very slight visible structural changes in chromosomes. Occasional spontaneous aberrations give a clue as to the origin of these.

As a result of the total evolutionary differentiation within this species complex, "marginal" and "extreme" positions in respect to distribution, ecology, and morphology are taken by diploids. Known sympatric contacts between diploids are rare. *Galium matthewsii* and *G. parishii* grow in mixed populations in the Kingston Mountains of southeastern California, but there are no indications of hybridization. This must be owing to the development of internal barriers, possibly involving chromosome structure. In contrast with the diploids, the polyploids are intermediate in distribution, ecology, and many morphological characters. There is some additional evidence that they are of hybrid origin and hybridize much more freely with each other than do the diploids (e.g., *G. munzii* and *G. hypotrichium* subsp. *subalpinum* on the eastern slope of the southern Sierra Nevada). The present cytological findings substantiate the hypothetical racial diagram and interpretation developed by the author in 1956 (fig. 7): therein the polyploid *G. grayanum* subsp. *glabrescens*, *G. munzii*, and the partly polyploid *G. hypotrichium* form central "hot spots" of the complex, while all the marginal racial "cornerstones" are diploid. The general evolutionary situation therefore is very similar to that in other *Galium* groups, e.g. the section *Lepto-Galium* (Ehrendorfer 1954, 1955).

Details of cytological behaviour of the polyploid members of the *G. multiflorum* complex are very much in conformity with facts already known from European species: diminution of chromosome size in polyploid, stabilization of chromosome pairing, possibly via some influence on chiasma frequency, occasional irregularities of chromosome distribution into the gametes caused by formation of multi- and univalents and consequent appearance of biotypes with aberrant chromosome numbers. Intra-individual somatic instability of chromosome number has not been reported for *Galium* before, but the phenomenon seems not to be rare in polyploids (Gottschalk 1958, and literature cited there).

The cytological data here set forth point the way to some revisions in the taxonomic treatment of the *G. multiflorum* complex. The tetraploid *Galium grayanum* subsp. *glabrescens*, for example, should perhaps be accorded specific status, but in other cases specific separation on the basis of different ploidy levels seems imposible and highly impractical as within *G. hypotrichium* where even subspecific separation of the very closely adjacent and very similar 2x and 4x populations on Sonora Pass (Sierra Nevada) is an extreme procedure. Obviously no generalized rules can be applied in diploid-polyploid racial pairs, as has been previously shown with European *Lepto-Galium* and other groups. Taxonomic questions concerning the *Galium multiflorum* complex will be dealt with in other papers of this series.

SUMMARY

1. The western North American *Galium multiflorum* complex consists of sexual, dioecious races. Chromosome numbers have been established for most of the recognized taxa, including counts from 51 populations and more than 100 individuals. Primarily the chromosome numbers form an eu-ployploid series 2x–4x–6x with x=11. The distribution of the various diploids and polyploids is mapped.

2. Cell size (PMC's, pollen) is generally increased in polyploids.

3. Chromosome size and number of chiasmata are generally reduced in polyploids.

4. In two tetraploid plants a certain intra-individual somatic instability of chromosome number has been established; this has not been observed in diploids.

5. In polyploids there is a limited amount of multi- and univalent formation during PMC meiosis, with consequent irregularities of chromosome number in the gametes.
6. In four tetraploid (but never in diploid) populations, individuals with different standard chromosome numbers (2n=42–44–45–46) have been observed.
7. No differences in the chromosome sets of male and female plants could be demonstrated.
8. In PMC meioses and pollen mitoses some consequences of spontaneous chromosome aberrations (bridges, fragments) have been found.
9. Chromosome sets of various diploids and polyploids are quite similar, but there are certain differences (e.g. in the SAT-chromosomes) as a result of structural changes.
10. Cytological findings are briefly discussed from comparative evolutionary and taxonomic viewpoints.

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A NEW SPECIES OF LYCIUM IN NEVADA

Cornelius H. Muller

A unique endemic *Lycium* occurs in Nevada in the area of the Atomic Energy Commission Nevada Test Site on Frenchman Flat. The plant was first discovered by Dr. William H. Rickard who remarked its extremely viscid, 4-merous corolla, and who suspected that it represented an undescribed species. It was collected in quantity by him, V. K. Carpenter, and Janice E. Beatley in the course of ecological investigations and subsequently by Dr. Beatley at my request. Material was submitted almost simultaneously to C. L. Hitchock and to me. Professor Hitchcock concurred in the opinion that the plant was undescribed and offered an analysis of its position in the genus but generously disclaimed any desire to undertake its publication. To him and to Dr. Beatley I am indebted for the opportunity to study this interesting material. Dr. Philip Wells has gathered considerable information on the distribution of the species. He discovered a large population on the southeasterly bajada of the Spotted Range and in northwestern Clark County. I am indebted to him for guidance to these localities.

The species typically grows on gravelly alluvium, predominantly limestone, in association with *Atriplex confertifolia* at the upper limit of *Larrea divaricata* and about the lower limit of *Coleogyne ramosissima*. It extends onto the playa clay on Frenchman Flat and onto quartzite beds on the lower slopes of the Spotted Range.

Lycium rickardii sp. nov. Frutex 0.5 m. altus, glaber; ramis albis spinosis; foliis 3–12 vel 18 mm. longis, 1.5–3 vel 6 mm. latis, 4–8-fasciculatis, obovatis vel spatulatis, floribus solitariis, pedicellis 0.5 mm. longis; calyce campanulato, tubo 6 mm. longo, lobis 4, 3 mm. longis; corolla tubuliformi, tubo 8–14 mm. longo, extra et intra viscido, lobis 4, circa 3 mm. longis; staminibus inclusis, corollae tubi partem supra mediam adhaerentibus, basi corollae intraque villosis; bacca subrotunda, 4–5 mm. longa, 2- vel 3-sperma, in calyce inclusa.

Intricately branched shrub about 0.5 m. tall or less; branchlets spinose, their smooth bark strikingly glaucous, weathering gray and fissuring after 2 or 3 years, the wood very soft and brittle; leaves 3 to 12 or even 18 mm. long, 1.5 to 3 or 6 mm. broad, in fascicles of 4 to 8, spatulate to obovate, the gradually narrowed base scarcely distinguishable from the blade, the apex broadly rounded, very thick and succulent, the midrib scarcely discernible in dried leaves, slightly glaucous green, the epidermal cells almost vescicular, giving the false impression of puberulence upon drying; flowers usually solitary in the leaf fascicles, the pedicels less than 1 mm. long; calyx highly variable, accrescent during and after anthesis, very succulent, the tube 6 mm. long, about 4 mm. broad, the 4 lobes 1 to 3 mm. long, mere teeth or broadly deltate-ovate, obtuse, broadly spreading or rarely erect; corolla white, the throat and veins suffused with purple or green, strictly tubular or narrowly funnel-shaped (the basal portion shrinking strongly upon drying), 8 to 14 mm. long, 2.5 to 3.5 mm. broad, the lobes about 3 mm. long, ovate, apically rounded, rotate or reflexed with age, 4-merous but a fifth lobe sometimes represented by a vascular bundle and an abortive petal, both outer and inner surfaces markedly viscid-glandular (this not apparent in dried material); stamens as many as the corolla lobes, an abortive petal sometimes carrying a full-sized staminode; filaments equal, plain, adnate about ¾ to ⅘ the height of the tube, strikingly pubescent with long hairs in the basal ⅓ or ½ of their length; anthers included by the throat; gynoecium bilocular, glabrous, with thin yellow walls, on a

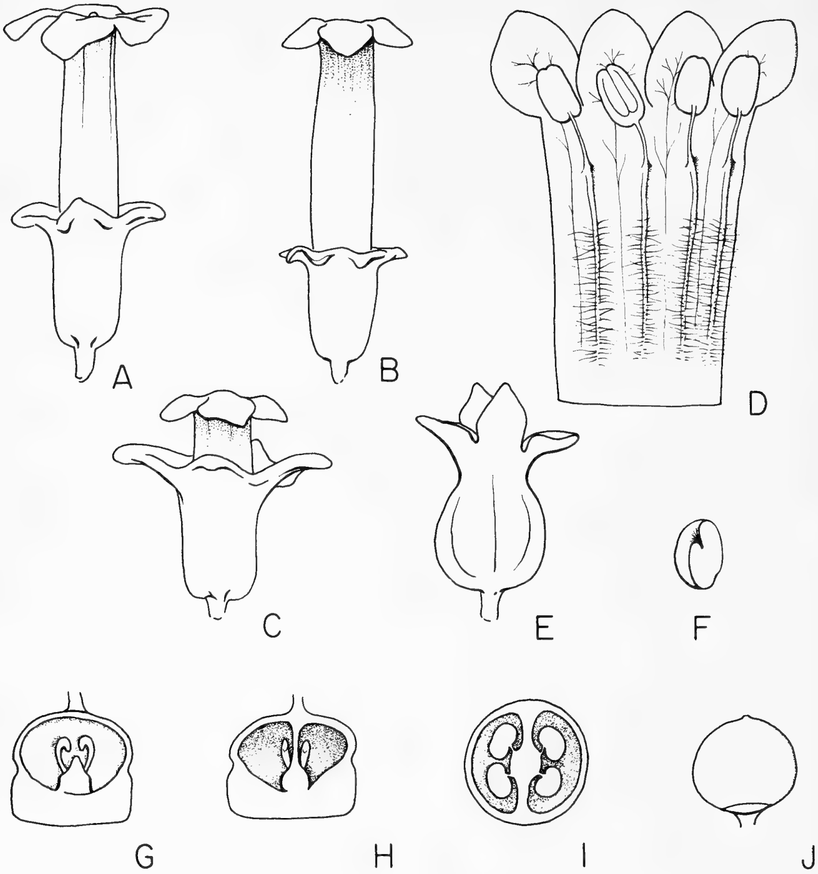

FIG. 1. *Lycium rickardii* sp. nov.: A–C, flowers, × 3; D, interior of corolla, × 3; E, fruiting calyx, × 3; F, mature seed, × 3; G, longitudinal section of ovary at anthesis parallel to the septum showing a pair of ovules on a single placenta, × 9; H, longitudinal section of ovary at anthesis at right angles to the septum showing one of each pair of ovules on each placenta, × 9; I, cross section of ovary, × 9; J, mature fruit, × 3. Drawn by Isabelle Haller from fresh material (*Beatley 2, 3, 4* and *Muller 10945*) except in the instances of F and J which were based on *Rickard* and *Beatley*, 2 May 1959.

thickened bright red disc, each locule 2-ovulate, no abortive ovules and no lower cells developing in the disc; style at anthesis reaching about half the length of the corolla; stigma green, slightly 2-lobed, irregular; fruit subrotund, about 4 or 5 mm. long and broad, completely enclosed in the accrescent, urceolate calyx and surmounted by the constricted throat and divergent sepals, the exocarp cartilaginous, the disc remaining red and slightly fleshy but not enlarging with the fruit, 1 or 2 seeds maturing in each locule of the ovary, thus producing a 2-seeded or, more often, a 3-

seeded fruit, the seeds flattened on the common face, about 3 or 4 mm. long, minutely pitted, the aborted ovule(s) always in the original position.

NEVADA. Nye County: codominant in shadscale scrub at 4100 feet on south-facing bajada of the Spotted Range, 16.6 miles west of Indian Springs, 8 April 1961, *Muller 10940, 10941, 10943, 10944, 10945* (holotype UCSB, sheet no. 8765), *10946, 10947*; codominant in shadscale scrub at 4200 feet in southerly foothills of the Spotted Range, ½ mile above the highway and 16.6 miles west of Indian Springs, 8 April 1961, *Muller 10948, 10949, 10950*; "east of playa" on Frenchman Flat, 2 May 1959, *Rickard* and *Beatley s.n.* (from which the fruit is described); "south of playa, near Lycium Plot 4;" "northwest of playa;" "near playa":[1] all on Frenchman Flat, 2 April 1959, *Rickard, Carpenter,* and *Beatley s.n.*; with *Larrea* and *Atriplex* south of playa at 3100 feet on Frenchman Flat, 11 April 1961, *Beatley 2*; with *Larrea* south of playa at 3100 feet on Frenchman Flat, 11 April 1961, *Beatley 3;* with *Larrea* east of playa at 3100 feet on Frenchman Flat, 11 April 1961, *Beatley 4.* Clark County: rare in shadscale scrub at edge of foothills 1½ miles south of Indian Springs, 8 April 1961, *Muller 10951.*

All specimens cited are deposited in the herbarium of the University of California, Santa Barbara, and duplicates are being distributed.

Lycium rickardii negotiates Hitchcock's key (1932) past *L. pallidum* Miers (p. 202) but fits neither "G. Fruit 2–4-seeded, with 1 or 2 fertile seeds in the top of each carpel, and abortive ovules in compartment below" nor "GG. Fruit not as above, with more than four seeds." Rather, each locule contains two ovules, and there is no division of the locule into compartments as in *L. macrodon* and *L. puberulum.* If one ovule aborts, it appears on the same placenta and in the same locule with the matured seed. In this respect *L. rickardii* agrees with *L. shockleyi* Gray, an emended description of which was published by Muller (1940). The Hitchcock (1932) key may be emended as follows:

G. Fruit 2–4 seeded.
  H. Fruit with each carpel divided into two locules, the upper bearing 1 or 2 seeds and the lower locule bearing aborted ovules; calyx not enclosing fruit. . . . *L. macrodon* and *L. puberulum*
  HH. Fruit with one locule to each carpel, the seeds or abortive ovules totalling 2 in each locule; calyx enclosing fruit.
    I. Fruit with an irregular suture or fold on one or both sides, filaments adnate nearly full length, the anthers appearing almost sessile. . . *L. shockleyi*
    II. Fruit lacking a suture or fold, filaments free in upper ¼ of ⅕ of their lengths . . . . *L. rickardii*
GG. Fruit with more than 4 seeds. . . . . *L. cooperi* et seq.

The relationship of *L. rickardii* to *L. shockleyi* is apparent in the number of ovules in each carpel, the lack of a lower compartment with abortive ovules, and the 4-merous condition. However, the partially free filaments and lack of a suture or fold on the side of the fruit clearly distinguish it from *L. shockleyi.* Its fruit and stamen characters suggest *L. californicum* Nutt. ex Gray, but in the latter species the corolla is much smaller with proportionately shorter lobes and each locule contains a

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[1] The latter two collections bear the following notes: "Corollas 4-merous, shining viscid within and without; shrub less than 2 feet high."

single ovule. Professor Hitchock (personal letter to William H. Rickard, 22 November 1960) pointed out the intermediacy of *L. rickardii* between *L. californicum* and "such species as *L. macrodon* and *L. puberulum*." It might be added that both *L. rickardii* and *L. shockleyi* stand in this position with *L. rickardii* closer to *L. californicum* and *L. shockleyi* more similar to *L. macrodon* Gray, *L. puberulum* Gray, and *L. cooperi* Gray.

It is extremely likely that *L. rickardii* is somewhat more widely distributed than at present known. In the rather copious material at hand there is no evidence that heavy doses of irradiation at the Test Site are in any way responsible for the characters of *L. rickardii*. The longevity of these plants insures their being older than the Test Site, and their essential uniformity with those of the southerly and southeasterly range of the species makes it highly unlikely that the characters here noted might have arisen as a result of somatic mutation.

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SOME RECENT OBSERVATIONS ON PONDEROSA, JEFFREY AND WASHOE PINES IN NORTHEASTERN CALIFORNIA

John R. Haller

In an earlier paper (1959), I suggested that *Pinus jeffreyi* Grev. and Balf. is less susceptible to cold than is *P. ponderosa* Dougl. ex Lawson, and that for this reason *P. jeffreyi* replaces *P. ponderosa* at high altitudes in the mountains of California. Dr. Willis W. Wagener reported recently (1960), however, that established trees of *P. ponderosa* survived at least as well and occasionally better than *P. jeffreyi* following periods of severe cold in northeastern California. The purpose of the present paper is to present additional information on the pines of northeastern California which I believe will show that there is no discrepancy between Wagener's observations and my own, and that, in fact, they even reinforce one another.

In our respective papers, Dr. Wagener and I were discussing examples from different areas—his from northeastern California, mine mostly from cismontane California, that portion of the state lying to the west of the Sierra-Cascade crest. I deliberately omitted a discussion of the northeastern Californian pines because the great bulk of the Ponderosa Pine in California occurs in the cismontane portion of the state, and because northeastern California is climatologically and floristically more closely related to the Great Basin region than to the rest of California. In addition, the ecological, genetic, and taxonomic relationships of the pines in northeastern California appear to be far more complex than in the remainder of the state. I am currently preparing a paper which will attempt to describe their relationships with each other and with the pines farther to the east.

There is considerable evidence available which supports the idea that *Pinus ponderosa* from cismontane California is more susceptible to low temperatures than either *P. jeffreyi* or *P. ponderosa* from more interior localities. The precise altitudinal zonation on the western slope of the Sierra Nevada, with *P. ponderosa* occupying the lower elevations and *P. jeffreyi* occupying the higher, is very suggestive of a difference in cold tolerance (Table 1). As I have indicated previously (1959), in the narrow zone where these species overlap, *P. jeffreyi* nearly always occupies the colder sites, such as canyon bottoms and the margins of low-lying meadows. Pearson (1931) reported that first-year seedlings of *P. ponderosa* from the Sierra National Forest (on the western slope of the Sierra Nevada) planted near Flagstaff, Arizona, were killed by a November freeze,[1] whereas seedlings from several other western states planted at the same locality were not injured. Weidman (1939) reported that young trees of *P. ponderosa* from the vicinity of Weed, California (west of the Cascade crest), planted near Sandpoint in northern Idaho were killed at the age of 12 years when the temperature fell rapidly from 45°F to —12°F. Trees of approximately the same age from 19 localities in Oregon, Washington, Idaho, Montana, South Dakota, Colorado, Utah, New Mexico and Arizona, planted in the same site as the Californian trees, survived the cold. Temperatures lower than —12°F occasionally occur within the range of *P. jeffreyi* in the western Sierra Nevada and within the range of both *P. ponderosa* and *P. jeffreyi* in transmontane northeastern California, but virtually never within the cismontane range of *P. ponderosa* (Table 1). The temperatures shown in Table 1 are the lowest that occurred in 1949, which was a year of record-breaking cold for many of the stations. This is the same year that Wagener observed fairly extensive damage to both *P. ponderosa* and *P. jeffreyi* in California. Table 1 shows that *P. ponderosa* occurs in the warmer cismontane localities and *P. jeffreyi* in the colder, but in transmontane California the two species grow in equally cold localities which are frequently colder than the coldest cismontane *P. jeffreyi* localities.

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[1] Neither the temperature nor the year of its occurrence were given by Pearson. However, the coldest November temperature on record for Flagstaff for the years 1906–1930 is —4°F. This is probably not sufficiently cold to kill mature *P. ponderosa* from cismontane California (see Table 1), but was cold enough to be fatal to the more susceptible seedlings.

TABLE 1. MINIMUM TEMPERATURES IN 1949 IN CALIFORNIA.
Based on official records of the United States Weather Bureau*

A. Cismontane Localities

LOCALITY	COUNTY	ELEV.	TEMP.
Ponderosa Zone			
Placerville	Eldorado	1900 ft.	14°F
Sierra City	Sierra	4200	5°
Calaveras Grove	Calaveras	4800	5°
Yosemite Valley	Mariposa	4000	2°
Mt. Shasta (town)	Siskiyou	3500	1°
South Entrance, Yosemite N. P.	Mariposa	5100	—3°
Ponderosa-Jeffrey Zone			
Giant Forest	Tulare	6400	—4°
Grant Grove	Tulare	6700	—6°
Lake Spaulding	Nevada	5000	—8°
Jeffrey Zone			
Manzanita Lake	Shasta	5800	—3°
Huntington Lake	Fresno	7000	—10°
Twin Lakes	Alpine	7900	—24°
Soda Springs	Nevada	6700	—27°

B. Transmontane Localities

LOCALITY	COUNTY	ELEV.	TEMP.
Ponderosa Zone			
Cedarville	Modoc	4700 ft.	—20°F
Mount Hebron	Siskiyou	4200	—22°
Alturas	Modoc	4300	—31°
Ponderosa-Jeffrey Zone			
Truckee	Nevada	6000	—19°
Sierraville	Sierra	5000	—25°
Boca	Nevada	5500	—41°
Jeffrey Zone			
Woodfords	Alpine	5600	—10°
Bridgeport	Mono	6400	—31°

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* In some of the localities listed above, the species concerned does not occur in the immediate vicinity of the weather station. However, discrepancies between weather station temperatures and those in the adjacent pine localities have been kept to a minimum by selecting stations in situations that are ecologically similar to the pine localities and never more than a few miles removed from them. Stations have also been selected to show the maximum temperature variation within each zone.

The evidence given above indicates that *Pinus ponderosa* from northeastern California is different physiologically from that on the cismontane slopes, since it survives temperatures lower than those that have killed cismontane *P. ponderosa* in experiments. This physiological difference is reflected in the relative distribution of *P. ponderosa* and *P. jeffreyi* in northeastern California, where these two species occur together over much more extensive areas than on the western slopes of the mountains. Furthermore, there is no tendency for *P. jeffreyi* to occupy the colder sites within these extensive mixed stands, as occurs on the cismontane slopes.

In addition to the physiological—distributional differences between cis- and transmontane *Pinus ponderosa,* there are morphological differences. To begin with, the *P. ponderosa* from northeastern California is far more variable than that in the western Sierra Nevada, ranging from essentially identical to that farther west to something strikingly different. Because of this high variability, it is difficult to generalize about particular character differences. However, one character, needle thickness, shows relatively consistent differences between the west and east sides of the Sierra-Cascade crest. In all of the cismontane localities where I have measured needle thickness in mixed stands of *P. ponderosa* and *P. jeffreyi,* the mean thickness is greater in *P. jeffreyi.* In the typical examples given in Table 2A, the needles of *P. jeffreyi* average 0.19 mm. thicker than those of *P. ponderosa,* and the difference between the two species is highly significant at each of the three localities shown. Just the reverse is true on the east side of the Sierra-Cascade crest, where the needles of *P. ponderosa* average 0.12 mm. thicker than those of *P. jeffreyi* (Table 2B). However, east of the crest the differences between the species range from essentially nil at Sierraville to very pronounced at Hobart Mills. It is noteworthy that at Sierraville, where the needles of *P. ponderosa* are thinnest, the population is not unusually variable and is in most respects very similar to cismontane *P. ponderosa.* On the other hand, the *P. ponderosa* near Hobart Mills, which has much thicker needles than *P. jeffreyi,* is tremendously variable and for the most part very different from cismontane *P. ponderosa* (Haller, 1957). This thick-needled Hobart Mills population is located just three miles from Boca, which frequently has the lowest winter temperatures of any station in California (Table 1), suggesting that thick needles may be adaptively advantageous in cold climates.

There are at least three possible causes for the physiological and morphological differences between the cis- and transmontane *Pinus ponderosa* in northern California: environmental modification, differential selection from a heterozygous gene pool, and introgressive hybridization. A certain amount of environmental modification no doubt occurs in all populations of *P. ponderosa,* as the experiments of Weidman, the Institute of Forest Genetics, and my own observations (1957 and in press) have shown. However, these same experiments and observations show that the greater proportion of all physiological and morphological traits is genetically determined and cannot be ascribed solely to modification. Selection from a heterozygous gene pool has probably been the principal mechanism that has enabled *P. ponderosa* to occupy so many diverse habitats in western North America and to differentiate into a number of geographical races or subspecies. The geographical pattern of variation shown by these races is, however, a subtle one, and I have found that the

TABLE 2. MEAN NEEDLE THICKNESS IN PONDEROSA, JEFFREY AND WASHOE PINE POPULATIONS

A. Cismontane Localities

LOCALITY	COUNTY	ELEVATION (feet)	SAMPLE SIZE	MEAN NEEDLE WIDTH		SIGNIFICANCE OF DIFFERENCE
				PONDEROSA	JEFFREY	
Silver Fork, American River	Eldorado	6400	10	1.32 mm.	1.54 mm.	.004
Ebbetts Pass Highway	Calaveras	6300	24	1.60	1.75	.005
Shasta Valley	Siskiyou	4500	25	1.65	1.83	<.001
Mean of cismontane Ponderosa and Jeffrey populations:				1.52	1.71	

B. Transmontane Localities

LOCALITY	COUNTY	ELEVATION (feet)	SAMPLE SIZE	MEAN NEEDLE WIDTH		SIGNIFICANCE OF DIFFERENCE
Sierraville	Sierra	5000	25	1.78	1.78	......
Dixie Mtn. Game Refuge	Plumas	5700	10	2.01	1.88	.075
Hobart Mills	Nevada	5800	50	2.10	1.87	<.00003
Mean of transmontane Ponderosa and Jeffrey populations:				1.96	1.84	
				WASHOE	JEFFREY	
Mt. Rose, Nev.	Washoe	7200	25	2.05 mm.	1.88	.0006
Warner Mtns.	Modoc	7500	14	2.13	2.02*	.10
Mean of transmontane Washoe and Jeffrey populations:				2.09	1.95	

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* The Warner Mountain Jeffrey Pine population is not sympatric with the Washoe Pine population, but is located a few miles away.

overall variability of the populations is usually about the same from one locality to the next. As already stated, many of the *P. ponderosa* populations in northeastern California differ strikingly from nearby populations and also display great variability. Such a pattern would be expected if hybridization were taking place.

The probable introgressant of *Pinus ponderosa* in northeastern California is *P. washoensis* Mason and Stockwell. One of the more outstanding characters of *P. washoensis* is its thick needles, which also characterize the variable *P. ponderosa* populations at Hobart Mills and Dixie Mountain Game Refuge (Table 2B). In addition there are other characters of *P. washoensis*, such as compact cones and short needles, which are prevalent in these variable *P. ponderosa* populations. I am still in the process of analyzing data from *P. ponderosa, P. washoensis,* and *P. jeffreyi* in northeastern California, but I am reasonably certain that the hybridization suggested here will be confirmed by further investigation.

The only published record of *Pinus washoensis* is from the type locality, on the watershed of Galena Creek, Mount Rose, Washoe County, Nevada (Mason and Stockwell, 1945). This locality is about 14 miles east of the Hobart Mills *P. ponderosa* population. A much more extensive stand of *P. washoensis* occurs in the Warner Mountains, Modoc County, California. The best stands, which include many trees that are four feet in diameter, are located in the southern part of the range, in the general vicinity of the Patterson Ranger Station. Specimens from this area have been deposited in the herbarium of the University of California at Santa Barbara. Both the Mount Rose and Warner Mountain stands of *P. washoensis* occur above the 7000 foot elevation, apparently too high for *P. ponderosa.* The Mount Rose stand occurs sympatrically with *P. jeffreyi,* whereas the Warner Mountain stand occurs almost entirely above a narrow zone of *P. jeffreyi.* Additional stands of typical *P. washoensis* might well occur on other sufficiently high peaks in northeastern California. *Pinus washoensis* also occurs sporadically at lower elevations, for example in the variable *"P. ponderosa"* population near Hobart Mills. Very few individuals at this locality are "good" *P. washoensis,* but many of the trees in this apparent hybrid swarm are more similar to *P. washoensis* than they are to typical *P. ponderosa* (Haller, 1957).

The factors which limit the distribution of individuals of taxa such as *Pinus ponderosa, P. jeffreyi,* and *P. washoensis* are extremely difficult to circumscribe exactly. However, some idea of the relative cold susceptibilities of members of these taxa might be obtained from a series of experiments. For example, seeds of *P. ponderosa* and *P. jeffreyi* from the same site in the western Sierra Nevada and from northeastern California could be grown under uniform conditions, and the seedlings subjected to increasing intensities of cold. If a sufficient number of experiments were made, it would be apparent whether *P. ponderosa* is ever more susceptible to cold than *P. jeffreyi,* or if either or both species vary from one locality to another in their relative susceptibility. The results of any such experiments would have to be interpreted with caution, however. For example, *P. ponderosa* and *P. jeffreyi* from the same site in the western Sierra Nevada (near the upper altitudinal limit of the former and the lower limit of the latter) might be found to have an identical tolerance for cold. The upward migration of *P. ponderosa* could nonetheless be checked at this point by cold, because the species has exhausted its genetic potential for cold tolerance. *Pinus jeffreyi,* on the other hand, could have a much greater potential cold tolerance, which might be expressed only at higher altitudes, where it would be favored by natural selection.

The possibility also exists that the upward migration of *Pinus ponderosa* is not checked by low winter temperatures, but by insufficiently high temperatures during the growing season. Pearson (1931) stated that low summer temperatures are the principal deterrent to the success of *P. ponderosa* when it is planted at elevations above its normal range in the San Francisco Mountains of Arizona. In this region, *P. ponderosa* is limited to the valleys and lower slopes of the mountains where summer maximum temperatures are higher but winter minima are lower than in the Douglas Fir zone immediately above.

Evidence has been submitted in this paper that *Pinus ponderosa* from cismontane California is more susceptible to cold than is *P. jeffreyi,* that *P. ponderosa* from northeastern California is at least as tolerant of cold as is *P. jeffreyi* and that the spread of *P. ponderosa* to higher elevations is checked in Arizona by low summer temperatures rather than by extremes of cold in winter. Most of this evidence is indirect, and a more precise determination as to the factor or factors which limit *P. ponderosa* in its many different habitats will have to await the outcome of future experiments. For the present, it appears reasonable to postulate that low temperatures, whether in the form of low winter minima or low summer maxima, play an important role in limiting the distribution of *P. ponderosa.*

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INFLUENCE OF TEMPERATURE AND OTHER FACTORS ON CEANOTHUS MEGACARPUS SEED GERMINATION

ELMER BURTON HADLEY[1]

One of the striking characteristics of chaparral is the absence of any kind of seedlings beneath mature, undisturbed stands. After such disturbances as bulldozing or fire, however, an abundance of seedlings appears, suggesting that scarification or heat make the germination possible (Cooper 1922, Went *et al.* 1952, Horton & Kraebel 1955, Quick 1959).

The density and dryness of this chaparral brush cover in California, the accumulation of large quantities of dry litter beneath the brush, and the Mediterranean type climate, all combine to create an extreme fire

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[1] The author wishes to express his thanks to the University of California at Santa Barbara for extending the full use of its facilities and to Dr. L. C. Bliss and Dr. C. H. Muller for generous aid and advice in the course of this study.

hazard during the long summer droughts. Many chaparral species are so specifically adapted to the resulting periodic fires as to indicate a long history of subjection to recurrent fires in the geologic past (Jepson 1925). Horton (1945) found that *Ceanothus* species in general have a life span of about forty years. In areas unburned for a period of at least forty years, however, other species have, to a large extent, replaced *Ceanothus* because there has been no regeneration by *Ceanothus*.

Two fire responses are very common among chaparral species: resprouting from burls (underground root crowns) that are not killed by fire, and heat induced seed germination due to cracking of impervious seed coats. *Arctostaphylos glandulosa*[2] is an example of a species that shows the first type of fire response. Almost no seedlings of this "stump sprouting" species are found following fires. *Ceanothus megacarpus*, wherein the entire shrub is usually killed outright by fires, represents the second type of response—regeneration by seed following fire. Other shrubs, such as *Adenostoma fasciculatum*, exhibit both types of fire responses.

In addition to the resprouting shrubs and seedlings of chaparral species, a recently burned-over area contains many annuals and short-lived perennial herbs and subshrubs as well as weeds. Eventually the chaparral vegetation dominates and the under vegetation perishes.

Fire or heat induced increases in germination were first investigated by Wright (1931), who found that oven heating greatly increased the germination of a number of chaparral species, including *Ceanothus megacarpus*. Sampson (1944), and Went *et al.* (1952) have also investigated increased germination of chaparral species due to fire. Stone & Juhren (1951), investigating germination of seeds of *Rhus ovata*, found that temperatures of 80°C induced the rupturing of impervious seed coats and thus permitted water to reach the embryos. Quick (1935), using seeds of several species of *Ceanothus*, also found that heat cracked the impervious seed coats. Stratification, following the heat treatment, resulted in further germination increases in these species.

In none of these investigations, however, were the possible modifying effects of natural field conditions on heat induced germination considered. In the present investigation an attempt was made to determine the effect of temperature, of mechanical injury, and of accumulated litter on the germination of seed of *Ceanothus megacarpus*.

METHODS

Except for field observations and collecting the seeds, all other phases of this investigation were carried out in the greenhouse of the University of California at Santa Barbara. All results obtained must, therefore, be considered no more than suggestive of what might occur under field conditions.

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[2] Nomenclature is that of Munz (1959).

Large quantities of *Ceanothus megacarpus* seeds were gathered from the Santa Ynez Mountains above Santa Barbara, California, in June, 1959, and air dried for two months in the laboratory. Voucher specimens are on deposit at the herbarium of the University of California at Santa Barbara.

All experiments were conducted in controlled temperature boxes, using sterilized petri dishes with moistened filter paper. All seeds were treated with the fungicide, Semesan. Seeds were germinated at a temperature regime of 26°C and 17°C (alternating 12-hour periods at each temperature). Each experiment was conducted for a thirty-day period, and germination in all cases was defined as emergence of the radicle.

In order to determine the effect of heating or cutting of the seed coat on *Ceanothus megacarpus* seed germination, a first experiment was run using three lots of seeds. The first lot was subjected to a temperature of 100°C for 5 minutes in an electric oven, the second to mechanical rupturing of the seed coat at the micropilar end with a razor blade, and the third lot served as controls (no heating or cutting). Each of the above three treatments consisted of three replicates using 25 seeds per dish. These seeds were moistened with distilled water and germinated as described in the previous paragraph.

In order to determine the possible effects of leaf litter on germination, a second series of experiments was set up using actual leaf material on top of the seeds in the petri dishes. Sets of seeds were prepared, each with three replicates as in the previous experiment, i.e., heated seeds, cut seeds, and controls. Fresh leaves, duff (dead fallen leaves not yet decayed beyond recognition), and ashed duff (7 grams of duff ashed at 700°C in a muffle furnace for 45 minutes) of *Adenostoma fasciculatum* were used in equal quantities on each of the first three sets of seeds, while a fourth set of three petri dishes of seeds was left as a control. *Adenostoma fasciculatum* was chosen because it is one of the most abundant and cosmopolitan species comprising the chaparral community. Except for the presence of leaf material, the seeds were germinated with distilled water as in the previous experiment. To test the hypothesis that any stimulation of seed germination due to duff is really a mineral effect, another part of this second experiment was run using a modified Hoagland's solution containing trace elements (Hoagland and Arnon 1950) in place of the distilled water.

In the third experiment, the effect of using leached duff (partial removal of minerals) was investigated. The duff was leached in eight changes of distilled water for 96 hours before being placed over the seeds.

All data were subjected to an analysis of variance using the individual degrees of freedom technique (Snedecor 1956). Space does not permit its inclusion, but a complete analysis of variance for the data may be found in Hadley (1960).

TABLE 1. EFFECT OF TEMPERATURE, MECHANICAL RUPTURING OF SEED COAT, AND ADENOSTOMA FASCICULATUM LEAF LITTER ON CEANOTHUS MEGACARPUS SEED GERMINATION.

		Percentage Germination*		
	Treatment	Cut seed	Heated seed (100°C for 5 min.)	Untreated seed
I.	Distilled water	86	23	0
II.	Distilled water +			
	Adenostoma duff	87	75	1
	Adenostoma duff ashed	41	24	0
	Adenostoma fresh leaves	24	13	0
	Control	83	25	0
	Hoaglands solution +			
	Adenostoma duff	95	57	0
	Adenostoma duff ashed	31	29	0
	Adenostoma fresh leaves	21	21	0
	Control	88	77	1
III.	Leached duff	85	41	1
	Unleached duff	87	80	4

* All experiments run in replicates of 3 with 25 seeds in each replicate.

Experiment I—Effect of heating and cutting of seed coat on *Ceanothus megacarpus* seed germination.

Experiment II—Influence of *Adenostoma fasciculatum* leaf litter and/or Hoagland's solution on the germination percentage of *Ceanothus megacarpus* seeds.

Experiment III—Effectiveness of leached *Adenostoma fasciculatum* duff vs. unleached duff in stimulating *C. megacarpus* seed germination.

RESULTS

Under the conditions of this investigation, germination of *Ceanothus megacarpus* seeds is facilitated by either heating or cutting the seed coats. As shown in Table 1, however, mechanical rupturing is the more effective treatment.

Presence of the various *Adenostoma* leaf material did not significantly affect the germination of the untreated controls, but did significantly affect the germination of the heated and cut seed (Table 1). Presence of duff over the heat treated seeds significantly stimulated the germination percentage of these seeds, resulting in a four-fold increase over the controls. This increase was shown by later experiments to be attributable to increased minerals made available by the decayed duff. Since cut seeds displayed maximum germination with or without duff being added, the effect of adding duff could not be measured accurately in the case of the cut seed.

Presence of fresh leaf material resulted in a significant reduction of cut seed germination, possibly due to the presence of an inhibitor in the fresh leaves (Naveh 1960). Application of ashed duff also caused a significant reduction in the germination of cut seed.

Substitution of Hoagland's solution in place of distilled water resulted in little change in the germination per cent of seed treated with either ashed duff or fresh leaves (Table 1). These results show that fresh leaf material or ashed duff have the same inhibiting effect, whether distilled water or Hoagland's solution is used. Germination per cent of heated seeds is very similar, whether treated with distilled water plus *Adenostoma* duff or only with Hoagland's solution. Leaching of this duff (partial removal of minerals) significantly reduced the effectiveness of duff in stimulating germination of the heat treated seeds (Table 1).

Discussion and Conclusions

Ceanothus megacarpus seed germination percentage was increased by heating these seeds for 5 minutes at 100°C. Mechanical rupturing of the seed coat was found to have an effect similar to heating, but to a greater degree. This would suggest that the stimulatory effect of heating involved in this species is primarily one of rupturing a previously impervious seed coat, thus allowing water to reach the embryo. The smaller increases in germination in the case of the heated seed may be due to injury to some of the embryos due to heat, to a random cracking of the seed coat away from the micropilar end which might hamper radicle emergence, or to the variability in seed coat thickness (some of the seed coats may not be cracked by this particular temperature).

Application of leaf material of another chaparral species, *Adenostoma fasciculatum*, has a definite effect on the germination percentage of *Ceanothus megacarpus. Adenostoma* duff enhances the germination of heat treated *C. megacarpus* seeds. Since a similar effect was obtained when Hoagland's solution was substituted in place of the distilled water and duff, this stimulation of germination can possibly be attributed to increasing mineral concentration provided by the decaying duff. The conclusion that germination was stimulated by available minerals in the duff is supported by the fact that there was marked reduction in percentage of seed germination when the seeds were topped by leached duff.

The apparent inhibition of germination by fresh leaves of *Adenostoma* may be due to the presence of an inhibitor or inhibitor complex in these leaves (Naveh 1960). The reduced germination of cut seed in the presence of ashed duff may be due to increased pH. Sampson (1944), using several grass species, has noted this ash inhibition, which was attributed to increased pH. The germination percentage of heated seeds in the presence of ashed duff, remained similar to that of non-treated heated seeds. This would suggest that ashed duff did not have an inhibitory effect on heated seed.

What part heating, mechanical rupturing, and plant litter actually play in the field can only be suggested, for in the field the situation created in the laboratory does not exist. Obviously, rupturing of the seed coat due to mechanical injury can be of only minor ecological significance in the field except where bulldozing, sharp deer hoofs, or some other agent may crack the seed coats. Accidental rupturing may therefore account for at least a portion of the few young seedlings that are sometimes found in disturbed but unburned areas.

The extremely low percentage of germination noted for untreated seed may serve to explain the field observation that young seedlings of *Ceanothus megacarpus* are not found under undisturbed, mature chaparral in which this species is a constituent. Heat treatment of *Ceanothus megacarpus* seeds by fires should be of tremendous importance in the repopulation of burned areas. This increase in germination percentage due to cracking of the seed coat by heat could account for the abundance of *Ceanothus* seedlings found immediately following a fire.

It must be remembered that all chaparral fires are not alike; they differ in intensity, duration, and temperatures reached during the fire. Some fires consume both shrub crowns and litter; others are principally confined to the shrub crowns leaving pockets of litter unconsumed. Therefore a differential destruction of duff by fire is noted in the field. Some fires could easily provide the required temperatures for the duration of time necessary to crack the seed coats and yet not burn away all of the duff that would be present. Other fires, even though they might burn away most or all of the duff and seeds, would still provide temperatures necessary to crack the seed coats of those seeds which were buried in and therefore protected by the soil. Thus breaking of the seed coat by heat would account for the *Ceanothus* seedlings that Quick (1959) and others have encountered after fires in the chaparral.

Only *Adenostoma fasciculatum* leaf litter was used in these experiments. It is possible that the duff and fresh leaves of many of the other chaparral species might exhibit similar effects on *Ceanothus megacarpus* seeds and those of several other chaparral species. This is a subject that would indeed be worth further investigation.

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REVIEWS

Flora of the Santa Cruz Mountains of California. A manual of the vascular plants. By John Hunter Thomas. viii + 434 pages, 249 figs. and 16 photos, 1 map. Stanford University Press, Stanford, California. 1961. $8.50.

The first impression, upon taking up the "Flora of the Santa Cruz Mountains," is of an attractive, well-designed book with clear typography, generous spacing, indented keys, good illustrations, and with an adequate binding. The Stanford University Press is to be congratulated upon producing a volume of exceptionally fine appearance.

Although the book is entitled "Flora of the Santa Cruz Mountains," it encompasses the whole San Francisco peninsula, and thence southward to the Pajaro River and from the ocean east to the middle of the Santa Clara Valley. Coverage is comprehensive, including both native and introduced plants. The number of kinds of introduced plants occurring spontaneously is amazing; 31 per cent of the 1799 taxa listed fall into this category.

For each of the species listed, Thomas gives the scientific name, common name, habitat, localities in the area, time of blooming, and place of origin for introduced species. Sometimes elevation is given and, occasionally, associated species. Brief comments, often on taxonomic problems, are made for some species. Synonyms are included only for convenience in referring to the same taxon in other regional and sectional floras. Specimens are not cited except in a few instances. There are no new names or combinations.

The flora is written for the serious beginner as well as the trained botanist. The beginner, especially, will appreciate the 250 line drawings which are from the "Illustrated Flora of the Pacific States." As a result of better spacing and better paper they are clearer and more attractive than many of the original reproductions in the Illustrated Flora. The common names also appear to correspond to those used by Abrams. Possibly the influence of the latter flora may be responsible in part for the recognition of certain families, for example, Melanthaceae, Parnassiaceae, Hydrangeaceae, Grossulariaceae, Amygdalaceae, Malaceae, Mimosaceae, Caesalpinaceae, Monotropaceae, Pyrolaceae, Vacciniaceae, Convallariaceae, Amaryllidaceae, all of these segregated from the Liliaceae, Saxifragaceae, Rosaceae, Fabaceae, and Ericaceae. Nevertheless, Thomas' taxonomic concepts are, in general, conservative. For example, *Berberis* rather than *Mahonia* is recognized; *Montia exigua* is considered as synonymous with *M. spathulata*; ssp. *decurrens* of *Eriogonum nudum* is not recognized. However, *Dudleya* (not *Echeveria*) and *Horkelia* are used; *Allium breweri* is considered distinct from *A. falcifolium*; and all the forms of *Arctostaphylos* in the Santa Cruz Mountains are accorded specific status. The varietal designation is usually employed rather than the subspecific except when the latter designation has been used in a recent monograph. The arrangement of families in general follows the sequence proposed by Engler and Prantl.

Part I consists of 33 pages of introductory material and 13 pages of keys to the divisions, classes, subclasses, and families. A map shows place names and supplements the description of the area. The geology (4 pages including a stratigraphic profile) is discussed by Dr. Earl E. Brabb. Monthly and yearly average temperatures and average rainfall are given for seven stations. Classification of the vegetation follows Munz and Keck insofar as it may be applied to the Santa Cruz Mountains. The more characteristic plants are listed for each of the plant communities, and photographs illustrate most of them.

Ten pages are devoted to a discussion of the composition and relationships of the flora. The number of native species is approximately 1246 in the Santa Cruz Mountain area of 1386 square miles, compared to 1004 in Marin County (529 square miles), 700 in the Mount Hamilton Range (1500 square miles), and 530 on Mount Diablo (55 square miles). Five distributional patterns are recognized, whereas Campbell and Wiggins recognized 16 for the whole state. Endemic in the area are 10 species, 3 subspecies, 11 varieties, 2 forms, and 1 hybrid. Some are closely restricted to certain geological formations.

Lists, together with localities, are given: 1) of taxa reaching their southern limits of distribution in the area, 2) of taxa reaching their northern limit, 3) of those with affinities with the inner Coast Ranges, 4) of the more obligate serpentine taxa, and 5) of plants with a disjunct distribution to the north. Plants of sandhills and marshes are also discussed. The list of taxa with "their northern limits of distribution in the Coast Range in the Santa Cruz Mountains" applies to the "Outer Coast Ranges" only, as seven species are included which occur somewhat farther north in the Inner Coast Range, on Mount Diablo. These are *Anemopsis californica, Malacothamnus hallii* (*Sphaeralcea fasciculata*), *Osmorrhiza brachypoda*, *Linanthus ambiguus*, *Pholistoma membranaceum*, and *Salvia mellifera.*

Of the 34 taxa occurring in the Santa Cruz Mountains, but regarded by Thomas as being typically species of the Inner Coast Ranges, 24 grow in the Mount Hamilton Range. Only 19 are on Mount Diablo, 13 of which are common to Mount Diablo and the Mount Hamilton Range. Whether *Helianthella castanea* should be considered a plant of the inner ranges is debatable.

Thomas' list of "the more obligate local serpentine plants" (p. 31) caused the writer considerable surprise, as a number of plants which are common and widespread on Mount Diablo are included. The following species are not associated in the writer's mind with serpentine although the records indicate that they may, at times, grow on serpentine: *Festuca pacifica, F. reflexa, Koeleria macrantha* (*K. gracilis, K. cristata*), *Calochortus venustus*, *Allium serratum*, *Lewisia rediviva*, *Astragalus gambellianus*, *Sanicula bipinnatifida*, and *Rigiopappus leptocladus.* Of the remaining taxa, more than half commonly or often grow on serpentine, but are by no means limited to it. Ten or fewer may be truly obligate serpentine plants. Perhaps there is here a difference of opinion as to the interpretation of the phrase "more obligate." However, the list does include species of rather widely differing ranges of tolerance with respect to the substratum and soils. Further observations on the relation of serpentine tolerant species to their substratum need to be stimulated.

Part I closes with a brief résumé of the history of botanical collecting in the area. Photographs of six collectors are presented. The annotated catalogue of vascular plants comprises Part II. Part III consists of a list of 34 general references and a glossary of technical terms. Part IV consists of an index of place names, an index of common names, and an index of scientific names.

The "Flora of the Santa Cruz Mountains of California" presents a synthesis of the present knowledge of the flora of the Santa Cruz Mountain area based on many collections by others as well as by Dr. Thomas. It represents a great deal of work and is a worthy volume which does credit to its author and will be useful to many. In conclusion, we will all, I am sure, concur wholeheartedly with the author's wish that, by acquainting more people with the plants around them, this volume will serve as "a stimulus, however slight, toward more permanent protection of our environment."—MARY L. BOWERMAN, Department of Botany, University of California, Berkeley, California.

Principles of Plant Breeding. By R. W. ALLARD. xi + 485 pp. John Wiley & Sons, Inc. New York and London. 1960. $9.00.

In the Preface, the author states that "Principles of Plant Breeding" is designed primarily to serve as an undergraduate text for students in agriculture. The aim of the book is to stress principles, and to illustrate them with appropriate examples. This task has been accomplished with a high degree of competence. Allard writes with clarity, precision and force. For this reason it should not be difficult for an undergraduate with some training in biometry, and a semester course in genetics, to follow his closely reasoned explanations and interpretations. The entire book is arranged to serve as a text for a two-semester course, but it is conveniently segmented so it can be adapted to the needs of a one-semester or one-quarter course. In addition to its pedagogical function, this book can be studied with profit by the professional plant breeder. It will serve to broaden his outlook and invigorate his research.

The material used to illustrate the principles is slanted to some extent towards cereal and forage crops, but this is not unnatural. More thorough information about plant breeding techniques and procedures is available for this group of crops than for fruit, vegetable, fiber or ornamental crops. A few more examples could, however, have been drawn from cotton and possibly other crops.

As one could anticipate, knowing his interests, the author is particularly surefooted and lucid in chapters concerned with quantitative genetics, population genetics, systems of mating and heterosis. But other sections, for example, "Breeding methods with cross-pollinated crops," "Breeding for disease resistance," and "Polyploidy," are also discussed with equal skill.

This reviewer can suggest only one feature that would perhaps increase the usefulness of the book. A set of carefully composed questions and problems at the end of each chapter might serve as a source of understanding and stimulation. This has been done to some extent by inserting questions in the legends of a few figures. More complete development of this aspect might add to the teaching value of the book.

The references are not copious, but adequate for the purpose. The book is notable for an unusually low incidence of typographical errors. A glossary of terms used in plant breeding and a good index add to its serviceability.

It has taken time for plant breeding to bridge the gap between art and science. "Principles of Plant Breeding" is likely to be marked as a significant milestone in establishing plant breeding as a full-fledged scientific discipline.—THOMAS W. WHITAKER, U. S. Horticultural Field Station, La Jolla, California.

NOTES AND NEWS

The Smithsonian Institution is reprinting Paul C. Standley's *Trees and Shrubs of Mexico,* Contr. U. S. National Herbarium, vol. 23, 1920–26, Parts 1 (pp. xviii + 1–169), 2 (xxxvii + 171–515), 3 (pp. xxviii + 517–848), and 5 (ii + 1313–1721), in 2 paper-bound volumes containing pts. 1–3 and pt. 5, respectively. The price of these 4 parts is $20, postpaid. Part 4 (pp. xxxiv + 849–1312), which is available in the original 1924 edition published by the U. S. National Museum, will be enclosed free of charge. Orders should be accompanied by check and should be addressed to: Publications Distribution Section, Smithsonian Institution, Washington 25, D.C.

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CHROMOSOME COUNTS IN THE SECTION SIMIOLUS OF THE GENUS MIMULUS (SCROPHULARIACEAE). V. THE CHROMOSOMAL HOMOLOGIES OF M. GUTTATUS AND ITS ALLIED SPECIES AND VARIETIES

Barid B. Mukherjee and Robert K. Vickery, Jr.

The purpose of this study[1] was to investigate the chromosomal homologies of *Mimulus guttatus* and its allied species and varieties. This was done by observing the pairing behavior of the chromosomes in the pollen mother cells of F_1 and a few F_2 hybrid plants obtained from crossing various members of the *M. guttatus* complex and its related taxa. This large, highly polymorphic group (Grant, 1924; Pennell, 1951) of gay-looking, yellow-flowered plants consists of a vast number of typically isolated populations of various sizes, of differing combinations of morphological characteristics, and of assorted taxonomic ranks. Its populations grow by springs and streams from the Aleutian Islands to southern Mexico and from the Pacific coast to the Mississippi River in North America, and in the Andes and their foothills in South America.

Of these populations, thirty-seven which exhibited much of the morphological variation and much of the diversity of geographical origin of the entire group were sampled for this investigation. The thirty-seven cultures which were grown from these populations represented at least eighteen different species and varieties (table 1). They included all of the most common forms of the group as well as several rare ones. These representative cultures were crossed in all possible combinations (Vickery, 1956a, 1956b) and most of the resulting seeds were sown. Some of the combinations failed to produce flowering hybrids due to the presence of crossing barriers of various strengths (Vickery, 1956a, 1956b, 1959). Consequently the cytological analysis was limited to the successful hybrids (table 2), which were chiefly combinations of *M. guttatus* with each of the related species plus a few combinations among the latter.

The method of fixing the buds was the same as that employed in the previous investigations (Mukherjee and Vickery, 1959, 1960); i.e., fixation in 2 parts absolute ethanol to 1 part glacial acetic acid saturated with ferric acetate. After 24 hours in the fixative, the buds were transferred to 70% ethanol if they were to be stored for later study. In preparing the slides, the anthers were dissected from the buds and then squashed in a drop of iron-aceto-carmine stain. In many cases the most interesting hybrids produced only one to several flowers which in turn might or might not yield one or more cells suitable for cytological examination. Conse-

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[1] This investigation was supported by the National Science Foundation and the University of Utah Research Fund. Most of these results form a portion of the dissertation of the senior author submitted to the Faculty of the University of Utah in partial fulfillment of the Ph.D. requirements.

Madroño, Vol. 16, No. 5, pp. 141–172. January 31, 1962.

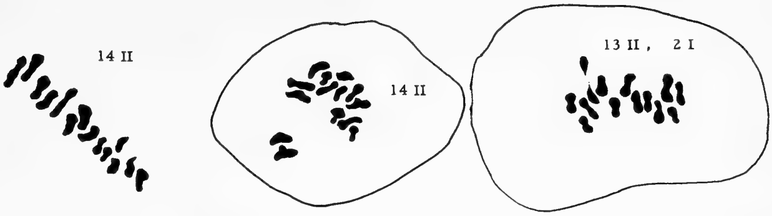
quently many of our counts are based on suboptimum numbers of cells. Nevertheless certain trends are clearly apparent in the results. Most of the cells analyzed were drawn with the aid of a camera lucida and many were photographed. In addition, numerous F_1 hybrid plants were pressed, mounted, and deposited for future reference in the Garrett Herbarium of the University of Utah.

The chromosomes of the different species and varieties ranged in size from dots as small as one-half micron in diameter to ovals as large as one micron wide by two micra long (see figure 1 and the previous papers of this series). Despite this variation in size, which probably was due in part to differing orientations of the chromosomes in the cells, the chromosomes were so similar in general appearance that rarely could we identify the individual chromosomes contributed by each parent to a particular F_1 hybrid. Therefore, our analysis of chromosomal homologies was carried out at the genome level rather than at that of the individual chromosomes. We observed the amount and regularity of chromosome pairing in as many pollen mother cells as possible in over 60 different interspecific and intervarietal hybrids (table 2).

In our cytological examinations of the parental species and varieties (Vickery, 1955; Mukherjee, Wiens, and Vickery, 1957; Mukherjee and Vickery, 1959, 1960), we found no indication of true autosyndesis in any of the cultures. However, under the fixation schedule employed, several of the annual races of *M. guttatus* exhibited chromosome stickiness which simulated autosyndesis and secondary chromosome associations (Vickery, 1959). This difficulty was overcome by techniques suggested by Doctors Harlan Lewis and Henry J. Thompson of the University of California at Los Angeles.

According to our findings, the basic genome in the group appears to be that of the diploid species, specifically, of the type of *M. guttatus* with its $n=14$ chromosomes. Possibly *M. guttatus* and/or the other diploid species such as *M. nasutus, M. glabratus* var. *utahensis, M. tilingii,* etc. (see table 1) may be ancient tetraploids inasmuch as a distantly related species, *M. mohavensis* Lemmon, has $n=7$ chromosomes (Carlquist, 1953). However, at the present time there is no evidence for this hypothesis. Therefore, tentatively we may consider the whole group, *M. guttatus* and its relatives, to consist of species and varieties at the diploid ($n=13$, 14, 15), tetraploid ($n=26, 30, 31, 32$), and hexaploid ($n=45, 46$) chromosomal levels, with one to several examples of aneuploidy at each level. The data at hand suggest to us that this polyploid series is built up on a base number of $x=15$ which presumably is an aneuploid derivative of the basic genome of $n=14$ chromosomes so commonly found in this group of species.

Despite the tremendous range of morphological and physiological variation within *M. guttatus* itself (Grant, 1924), all of its populations thus far counted have $n=14$ chromosomes. The chromosomes of the interpopulation F_1 hybrids exhibited normal chromosome pairing (table 2)



5001, M. guttatus, n = 14
(subsp. guttatus),

X

5004, M. guttatus, n = 14
(subsp. guttatus).

5001, M. guttatus, n = 14
(subsp. guttatus).

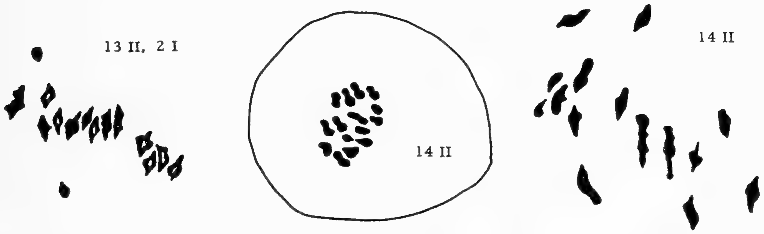
X

5003, M. guttatus, n = 14
(subsp. litoralis).

5001, M. guttatus, n = 14
(subsp. guttatus).

X

5834, M. guttatus, n = 14
(var. puberulus).



5001, M. guttatus, n = 14
(subsp. guttatus).

X

5007, M. guttatus, n = 14
(M. lyratus).

5004, M. guttatus, n = 14
(subsp. guttatus).

X

5010, M. guttatus, n = 14 ± 1, 2
(M. laxus).

5001, M. guttatus, n = 14
(subsp. guttatus).

X

5346, M. guttatus, n = 14
(M. arvensis).

5017, M. guttatus, n = 14
(M. cordatus).

X

5064, M. laciniatus, n = 14

5052, M. guttatus, n = 14
(subsp. guttatus).

X

5339, M. laciniatus, n = 14

5017, M. guttatus, n = 14
(M. cordatus).

X

5044, M. nasutus, n = 14

FIG. 1. Meiotic chromosomes of intraspecific F_1 hybrids of the *Mimulus guttatus* complex as defined in this article. All configurations at or near first metaphase. Camera lucida drawings at an original magnification of × 2,520, reduced to × 1,260.

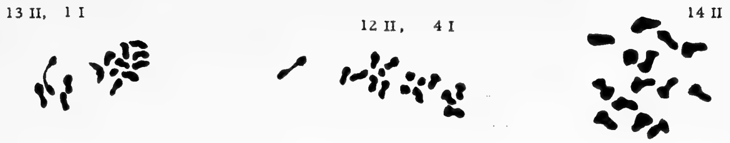
except in a few cases which were probably the result of factors of technique. One exception turned up in the lone intra-*guttatus* F_2 hybrid plant analyzed (5346 × 5839), which had an extra chromosome.

Due in part to this generally pervasive cytological homogeneity, *M. guttatus* has been treated in this article in the broad sense of Grant (1924). Except for *M. platycalyx*, the various species segregated from *M. guttatus* by Pennell (1951) have been included in it (table 1). Several of our cultures could be assigned to these segregate species, specifically, culture 5007 to *M. lyratus*, 5017 to *M. cordatus* [so identified by F. W. Pennell (see *Alexander & Kellogg 2844*, UC 696,020, from which our seeds came)], 5010 to *M. laxus*, and 5346 to *M. arvensis* (table 1.) However, these species intergrade morphologically with each other and with *M. guttatus*. Cytologically, they all appear to possess the same genome (figure 1). Genetically, they are fully interfertile or else separated by no stronger barriers than those that occur within *M. guttatus* in the strict sense (Vickery, 1959). Therefore, with these facts in mind, we have treated *M. lyratus, M. cordatus, M. laxus,* and *M. arvensis* as synonyms of *M. guttatus*.

Two of the *M. guttatus* cultures, 5009 and 5010, from Mather, California, were known to be aberrant in that they occasionally produced microspores with n=13, 15, or 16 chromosomes instead of the usual n=14 (Mukherjee and Vickery, 1959). The present investigation showed that at least some of these aneuploid microspores were functional as can be observed in the chromosome complements of their F_1 hybrids (figure 2 and table 2). A comparable situation was observed in *M. luteus* (table 2) and in *M. glabratus* var. *fremontii* (figure 4). These facts are significant because they indicate a likely mechanism for the production of aneuploid plants. Possibly the already-mentioned intra-*guttatus* F_2 plant (5346 × 5839) with the extra chromosome arose in this manner. Such aneuploid plants might in turn lead to the establishment of aneuploid populations and even, eventually, of aneuploid varieties and species such as commonly occur in the *M. guttatus* complex and its relatives (table 1).

Mimulus guttatus hybridized readily with *M. laciniatus*, with the n=14 form of *M. nasutus*, and with *M. glaucescens*. In the first two cases the hybrids were fertile and their pollen mother cells exhibited regular chromosome pairing, although the regularity of chromosome pairing was considerably decreased in the F_2 individuals studied. The F_1 hybrids of *M. guttatus* × *M. glaucescens* were nearly sterile, and their chromosomes showed reduced pairing (figure 2 and table 2). Probably *M. laciniatus* and *M. nasutus* should be considered simply as well-marked varieties of *M. guttatus*, whereas *M. glaucescens* should be treated as a nearly distinct species.

Mimulus platycalyx (n=15) and the n=13 form of *M. nasutus* both hybridized with *M. guttatus*, but the F_1 hybrids produced were partially sterile (Vickery, 1956b). The chromosomes in the pollen mother cells of the hybrids showed regular pairing of 13II and 1I for *M. guttatus*



5327, M. nasutus, n = 13. x 5003, M. guttatus, n = 14.

5014, M. guttatus, n = 14. x 5653, M. glaucescens, n = 14.

5017, M. guttatus, n = 14. x 5653, M. glaucescens, n = 14.

5752, M. platycalyx, n = 15. x 5010, M. guttatus, n = 14 ± 1, 2.

5339, M. laciniatus, n = 14. x 5327, M. nasutus, n = 13.

FIG. 2. Meiotic chromosomes of interspecific F_1 hybrids of *Mimulus guttatus* complex. All configurations at or near first metaphase. Camera lucida drawings at an original magnification of × 2,520, reduced to × 1,260.

× *M. nasutus* and 14II and 1I for *M. guttatus* × *platycalyx* except where the aberrant culture 5010 was a parent (figure 2 and table 2). Despite the aneuploidy and genetic differentiation of these species, both their genomes appear to be basically homologous to that of *M. guttatus*, just as the genomes of the various aneuploid species of section *Alatae* of *Nicotiana* are homologous (Goodspeed, 1954). Clearly, both species are an integral part of the *M. guttatus* complex although their accurate specific designation must await a detailed study of the relevant literature and type specimens.

One of the F_1 hybrids of *M. nasutus* (5751; $n = 14$), × *M. nasutus* (5327; $n = 13$), which would be expected from the foregoing results to show marked sterility was highly fertile instead (Vickery, 1956b). It set an average of 50 seeds per capsule whereas the hybrid resulting from the reciprocal combination averaged only 3 seeds per capsule. The cytological analysis of several pollen mother cells of one of the F_2 hybrids of the highly fertile cross provided the explanation. The fertile hybrid was an amphiploid with $n = 27$ chromosomes (table 2).

The alpine species *M. tilingii* did not hybridize readily with *M. guttatus*. The hybrids that were formed with the exception of two possible amphiploids, produced sterile flowers if they flowered at all. However, the pollen mother cells of these F_1 hybrids of *M. guttatus* × *M. tilingii* exhibited regular chromosome pairing in three of the four cells available for study (figure 3 and table 2). These cells came from hybrids involving both the n=14 and n=15 races of *M. tilingii* var. *tilingii*. Therefore, the basic, or what we may call the *M. guttatus* genome of chromosomes, probably is present in both the chromosomal races of *M. tilingii* var. *tilingii* also, although the crossing barriers between this species and the *M. guttatus* complex are so nearly complete as to warrant its exclusion from the complex. In fact, *M. tilingii* is itself the main species of another complex of related species and varieties.

Mimulus tilingii var. *corallinus* (n=24) forms completely sterile hybrids with *M. guttatus* and with *M. tilingii* var. *tilingii*. In the majority of the pollen mother cells examined in the F_1 hybrids of *M. guttatus* × *M. tilingii* var. *corallinus*, the chromosomes showed 14II and 10I (figure 3 and table 2). In a few cases trivalent chromosome associations were observed which suggest the presence of at least a few residual homologies between some of the additional ten chromosomes of *M. tilingii* var. *corallinus* and the basic genome. The extra ten chromosomes constitute a second genome which appears to be incomplete on the basis of the other known chromosome numbers in the group (table 1). Possibly it is a highly modified derivative of the basic genome. However, its origin and relationships have yet to be determined precisely. *Mimulus tilingii* var. *corallinus* warrants specific rank, but its accurate designation must also, as with the members of the *M. guttatus* complex, await an opportunity to study the literature and type specimens involved.

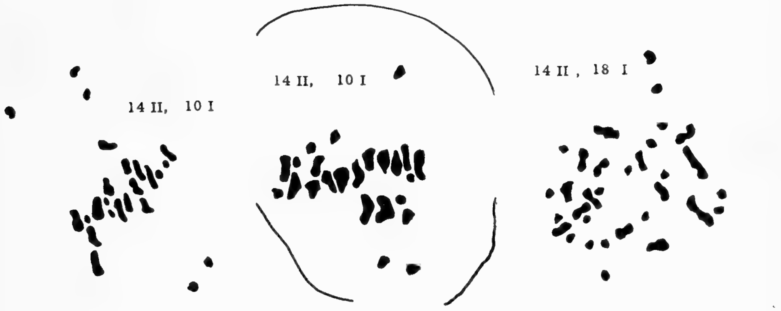
Mimulus guttatus will hybridize with South American *M. luteus* (n=30, 31, or 32), but the hybrids are completely sterile. The chromosomes in the pollen mother cells of the hybrids show considerable pairing (figure 3 and table 2). In some cases the number of pairs exceeds that of the basic genome, which must mean that *M. luteus* chromosomes are, at least occasionally, pairing with each other. However, inasmuch as there was no indication of autosyndesis in *M. luteus* itself (Mukherjee and Vickery, 1960), probably most of the paired chromosomes are homologues coming from *M. guttatus* or *M. tilingii* on the one hand and from *M. luteus* on the other. Therefore the basic genome appears to be present in *M. luteus* though in slightly modified form. The second genome of *M. luteus* may be a drastically modified form of the basic genome, but its true origin and relationship is not clearly demonstrated by the available data.

Mimulus guttatus formed nearly sterile hybrids with *M. glabratus* var. *utahensis* (n=14). Typically the chromosomes of the pollen mother cells of these hybrids exhibited 13 bivalent and 2 univalent chromosome configurations at the first metaphase stage of meiosis (figure 4 and table 2). Apparently the two genomes are essentially homologous, but one pair of chromosomes has become so modified as to synapse only rarely. Therefore, in view of the sterility of the F_1 hybrids and the slight cytological differentiation of these species and despite the morphological similarity, *M. glabratus* var. *utahensis* should not be included in the *M. guttatus* complex of species. It is an integral part of the large, widespread, and varied *M. glabratus* complex.

5017, M. guttatus, n = 14.
x
5012, M. tilingii var. tilingii, n = 14.

5967, M. tilingii var. tilingii, n = 15.
x
5052, M. guttatus, n = 14.

5689, M. tilingii var. tilingii, n = 14.
x
5012, M. tilingii var. tilingii, n = 14.



5011, M. tilingii var. corallinus, n = 24.
x
5052, M. guttatus, n = 14.

5011, M. tilingii var. corallinus, n = 24.
x
5007, M. guttatus, n = 14.

5052, M. guttatus, n = 14.
x
5043, M. luteus, n = 32.

5012, M. tilingii, n = 14.
x
5043, M. luteus, n = 32.

FIG. 3. Meiotic chromosomes of interspecific F_1 hybrids of *Mimulus guttatus* complex with *M. tilingii* and *M. luteus* complexes, etc. All configurations at or near first metaphase. Camera lucida drawings at an original magnification of × 2,520, reduced to × 1,260.

The pollen mother cells of the F_1 hybrids of *M. tilingii* var. *tilingii* × *M. glabratus* var. *utahensis* (5012 × 5747) frequently exhibited a small extra chromosome and hence were n=15. The extra chromosome was probably a B chromosome from culture 5747, because it was not observed in culture 5012 (culture 5747 has yet to be studied cytologically). Furthermore, both parental forms are known to contain other populations with n=15 chromosomes (Mukherjee, Wiens, and Vickery, 1957; Mukherjee and Vickery, 1959).

As with the preceding variety, *M. guttatus* formed nearly completely sterile F_1 hybrids with *M. glabratus* var. *fremontii* (n=30, 31). However, the pollen mother cells of these hybrids displayed much variation in the pairing behavior of their chromosomes (table 2). They showed the least amount of consistent pairing of any of the hybrids studied. They averaged

TABLE 1. ORIGIN OF CULTURES USED IN THE CYTOGENETIC INVESTIGATION OF THE RELATIONSHIP OF MIMULUS GUTTATUS AND ITS SPECIES

Species, culture, and chromosome number	**Origin and Collector**
M. guttatus DC.	
(*M. guttatus* DC. subsp. *guttatus*)	
5001, n=14	Pacific Grove, Monterey County, California, altitude 5 feet, *Vickery 1* (UT).
5004, n=14	Chew's Ridge, Monterey County, California, altitude 4,500 feet, *Vickery 3* (UT).
5015, n=14	Mono Inn, Mono County, California, altitude 6,450 feet, *Clausen 2043* (UT).
5052, n=14	Mt. Diablo, Contra Costa County, California, altitude 1,000 feet, *Stebbins 703* (UT).
(*M. guttatus* subsp. *litoralis* Pennell)	
5003, n=14	Pescadero, San Mateo County, California, altitude 30 feet, *Clausen 2083* (UT).
(*M. guttatus* var. *puberulus* [Greene] Grant)	
5006, n=14	Yosemite Junction (rocky creek), Tuolumne County, California, altitude 1,300 feet, *Hiesey 560* (UT).
5009, n=14 ± 1 or 2	Mather (Hog Ranch meadow), Tuolumne County, California, altitude 4,600 feet, *Hiesey 571* (UT).
5014, n=14	Lee Vining Canyon, Mono County, California, altitude 8,000 feet, *Clausen 2039* (UT).
5753, n=14	Stanislaus River, Tuolumne County, California, altitude and collector uncertain.
5834, n=14	Salt Lake City, Salt Lake County, Utah, altitude 4,400 feet, *Vickery 330* (UT).
5835, n=14	Centerville, Davis County, Utah, altitude 4,360 feet, *Vickery 331* (UT).
5837, n=14	Fish Haven, Bear Lake County, Idaho, altitude 6,100 feet, *Vickery 322* (UT).
5839, n=14	Big Cottonwood Canyon, Salt Lake County, Utah, altitude 7,100 feet, *Vickery 334* (UT).
5864, n=14	Skaggs Springs, Sonoma County, California, altitude ca. 50 feet, *R. W. Holm*, Spring 1951, unmounted.

Species, culture, and chromosome number	Origin and Collector
(*M. lyratus* Bentham)	
5007, n=14	Yosemite Junction (marsh), Tuolumne County, California, altitude 1,350 feet, *Hiesey 559* (UT).
(*M. laxus* Pennell)	
5010, n=14 ± 1 or 2	Mather (Hog Ranch spring area), Tuolumne County, California, altitude 4,800 feet, *Hiesey 569* (UT).
(*M. cordatus* Greene)	
5017, n=14	Darwin Falls, Inyo County, California, altitude 2,500 feet, *Alexander* & *Kellogg 2844* (UC).
(*M. arvensis* Greene)	
5346, n=14	Mount Oso, Stanislaus County, California, altitude 1,000 feet, *Vickery 190* (UT).
M. laciniatus Gray	
5064, n=14	The Dardanelles, Tuolumne County, California, altitude 5,775 feet, *Alexander* & *Kellogg 3746* (UC).
5339, n=14	Lake Eleanor Road, Tuolumne County, California, altitude 4,200 feet, *Vickery 179* (UT).
M. glaucescens Greene	
5653, n=14	Richardson Springs, Butte County, California, altitude 600 feet, *Pennell* & *Heller 25,667* (UT).
M. platycalyx Pennell	
5752, n=15	Crystal Lakes Reservoir, San Mateo County, California, altitude 800 feet, *G. T. Oberlander,* April 1951 (UT).
M. nasutus Greene	
5044, n=14	Hastings Reservation, Monterey County, California, altitude 1,500 feet, *Stebbins 701* (UT).
5327, n=13	West of Yosemite Junction, Tuolumne County, California, altitude 475 feet, *Vickery 168* (UT).
M. tilingii Regel var. *tilingii*	
5012, n=14	Slate Creek, Mono County, California, altitude 10,000 feet, *Clausen 2075* (UT).
5689, n=14	Dana Plateau, Mono County, California, altitude 11,300 feet, *C. W. Sharsmith,* Aug. 21, 1950.
5690, n=14	Budd Lake, Tuolumne County, California, altitude 10,250 feet, *C. W. Sharsmith,* Sept. 13, 1950.
5967, n=15	Mount Timpanogos, Utah County, Utah, altitude 7,800 feet, *Del Wiens,* Aug. 6, 1956 (UT).
M. tilingii var. *corallinus* (Greene) Grant	
5011, n=25	Porcupine Flat, Tuolumne County, California, altitude 8,000 feet, *Hiesey 576* (UT).

Species, culture, and chromosome number	Origin and Collector
M. luteus L.	
5042, n=32	Illapel, Coquimbo, Chile, altitude 6,200 feet, *U.S.D.A. Plant Introduction number 144,535* (UT).
5043, n=30 + 0, 1 or 2	Illapel, Coquimbo, Chile, altitude 2,000 feet, *U.S.D.A. Plant Introduction number 144,536* (UT).
M. glabratus var. *utahensis* Pennell	
5048, n=14	Mono Lake, Mono County, California, altitude 6,440 feet, *Stebbins 714* (UT).
5747, n=14 + 0, or 1 B chromosome*	Pilot Cone, Mineral County, Nevada, altitude 5,550 feet, *J. Figg-Hoblein,* July 4, 1950.
M. glabratus var. *fremontii* (Bentham) Grant	
5063, n=30	Black Meadow, Black Metal Wash, Whipple Mountains, San Bernardino County, California, altitude ca. 1,200 feet, ? collector (UC).
5373, n=30, (31*)	Kakernot Springs, Alpine Creek, Brewster County, Texas, *Cory 53,186* (UT).
M. glabratus var. *parviflorus* (Lindley) Grant	
5041, n=45	Illapel, Coquimbo, Chile, altitude 4,000 feet, *U.S.D.A. Plant Introduction number 144,534* (UT).
M. pilosiusculus HBK.	
5320, n=46	Botanic Garden, Copenhagen, Denmark (Wild in Argentina, Chile, and Peru). *U.S.D.A. Plant Introduction number 181,130* (UT).

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* Chromosome number based on counts in F_1 hybrids involving this culture (see table 2).

about 9 pairs per cell. Probably *M. glabratus* var. *fremontii* contains the basic genome, but in definitely modified form.

Mimulus guttatus forms nearly sterile hybrids with *M. glabratus* var. *parviflorus* (n=45) and its closely allied species *M. pilosiusculus* (n=46). The chromosomes of the pollen mother cells of these F_1 hybrids exhibited essentially regular pairing of 14II, 30I and 14II and 31I, respectively. These forms contain the basic genome plus two additional genomes. One of the additional genomes is probably homologous to the second genome of *M. glabratus* var. *fremontii* as shown by three somewhat ambiguous counts (see table 2). This hybrid, *M. glabratus* var. *parviflorus* (5041) × *M. glabratus* var. *fremontii* (5373), was hard to

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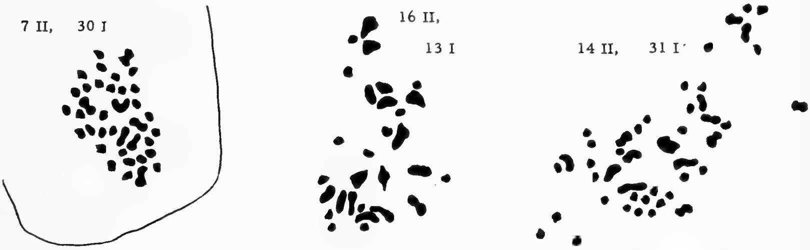
EXPLANATION OF FIGURE 4

Meiotic chromosomes of interspecific F_1 hybrids of *Mimulus guttatus* complex with the *M. glabratus* complex, etc. All configurations at or near first metaphase. Camera lucida drawings at an original magnification of × 2,520, reduced to × 1,260.

5004, M. guttatus, n = 14.
X
5747, M. glabratus var. utahensis, n = 14.

5010, M. guttatus, n = 14.
X
5048, M. glabratus var. utahensis, n = 14.

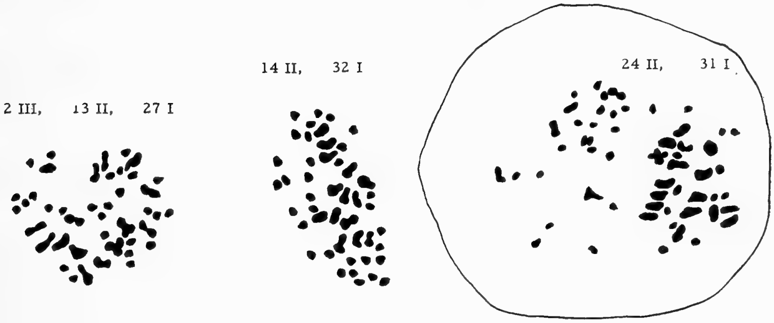
5747, M. glabratus var. utahensis, n = 14 ± 0, 1
X
5012, M. tilingii var. tilingii, n = 14



5346, M. guttatus, n = 14.
X
5063, M. glabratus var. fremontii, n = 30.

5015, M. guttatus, n = 14.
X
5373, M. glabratus var. fremontii, n = 30, 31.

5041, M. glabratus var. parviflorus, n = 45.
X
5010, M. guttatus, n = 14.



5041, M. glabratus var. parviflorus, n = 45.
X
5339, M. laciniatus, n = 14.

5320, M. pilosiusculus, n = 46.
X
5052, M. guttatus, n = 14.

5041, M. glabratus var. parviflorus, n = 45
X
5373, M. glabratus var. fremontii, n = 30, 31

Fig. 4. Meiotic chromosomes, *Mimulus guttatus* complex and relatives, F_1 hybrids.

make and even harder to analyze cytologically. The chromosome numbers are too low for it to be a spontaneous autododecaploid instead of the true hybrid which it appeared to be on morphological grounds. We do not know how to explain the extra chromosomes, but the large number of pairs suggests to us that *M. glabratus* var. *fremontii* and *M. glabratus* var. *parviflorus* have two genomes in common. The affinities of the third genome in the South American form are not apparent from the data at hand.

The basic *M. guttatus* genome appears to be little modified in these South American forms, whereas it was slightly modified in *M. glabratus* var. *utahensis* from the Great Basin and greatly modified in *M. glabratus* var. *fremontii* from the southwestern United States. These North and South American entities of the *M. glabratus* complex probably are not as closely related as their current taxonomic status suggests (Grant, 1924; Fassett, 1939; Pennell, 1947).

In conclusion, despite the low number of pollen mother cells analyzed, the basic or *M. guttatus* genome of 14 chromosomes appears to be present

TABLE 2. PAIRING BEHAVIOR OF MEIOTIC CHROMOSOMES IN F_1 AND A FEW F_2 HYBRIDS OF MIMULUS GUTTATUS AND ITS RELATIVES.

Combinations of parental species and varieties	**Culture numbers of the parents**	**Number of PMC's examined and pairing behavior**
F_1 HYBRIDS		
guttatus × *guttatus*	5001 × 5003	1-14II
n=14 n=14	5001 × 5004	4–14II
	5001 × 5006	12–14II*
	5001 × 5007	2–14II; 1–13II, 2I
	5001 × 5009	2–14II†
	5001 × 5010	5–14II†
	5001 × 5052	1–14II
	5001 × 5346	3–14II
	5001 × 5753	4–14II
	5001 × 5834	1–14II; 1–13II, 2I 1–12II,, 4I 1–11II, 6I
	5003 × 5839	3-14II
	5004 × 5006	8–14II*
	5004 × 5010	1–14II†
	5006 × 5834	3–14II*
	5009 × 5010	1–14II†
	5014 × 5834	2–14II
	5052 × 5006	10–14II*
	5052 × 5837	1–14II
	5753 × 5001	7–14II
	5835 × 5834	3-14II
guttatus × *laciniatus*	5017 × 5064	3–14II
n=14 n=14	5017 × 5339	2–14II
	5052 × 5339	4–14II
	5064 × 5017	2–14II

Combinations of parental species and varieties	Culture numbers of the parents	Number of PMC's examined and pairing behavior
guttatus × *glaucescens*	5014 × 5653	1–12II, 4I
n=14 n=14		2–11II, 6I
	5017 × 5653	4–14II
	5837 × 5653	4–14II, 1–11II, 6I
guttatus × *platycalyx*	5017 ×5752	3–14II, 1I
n=14 n=15	5752 × 5010	1–14II; 1–13II, 2I;
		1–12II, 4I†
guttatus × *nasutus*	5017 × 5044	3–14II
n=14 n=14		
guttatus × *nasutus*	5017 × 5327	2–13II, 1I
n=14 n=13	5327 × 5003	2–13II, 1I
guttatus × *tillingii* var. *tilingii*	5012 × 5052	1–3II, 22I
n=14 n=14	5017 × 5012	1–14II
guttatus × *tilingii* var. *corallinus*	5010 × 5011	1–14II, 10I†
n=14 n=24	5011 × 5007	7–14II,10I
	5011 × 5052	1–4III, 10II, 6I;
		2–3III, 12II, 5I;
		1–14II, 10I
guttatus × *luteus*	5017 × 5043	1–1III, 11II, 19I;
n=14 n=30, 31, 32		1–10II, 25I
	5052 × 5043	1–16II, 12I;
		1–15II, 14I;
		3–14II, 18I
guttatus × *glabratus* var. *utahensis*	5004 × 5747	2–14II
n=14 n=14	5010 × 5048	11–13II, 2I†
	5017 × 5747	3–13II, 2I
	5837 × 5747	4–14II
guttatus × *glabratus* var. *fremontii*	5014 × 5373	1–44I
n=14 n=30, 31	5015 × 5373	1–16II, 13I;
		1–9II, 26I
	5346 × 5063	1–15II, 14I;
		1–7II, 30I
laciniatus × *nasutus*	5339 × 5327	3-13II, 1I
n=14 n=13		
glaucescens × *platycalyx*	5653 × 5752	6–14II, 1I
n=14 n=15		
tilingii var. *tilingii* × *guttatus*	5967 × 5052	2–14II, 1I
n=15 n=14		
tilingii var. *tilingii* × *tilingii* var.	5689 × 5012	3–14II
n=14 *tilingii*	5690 × 5012	1–14II
n=14		
luteus × *tilingii* var. *tilingii*	5043 × 5012	1–17II, 10I;
n=30, 31, 32 n=14		2–15II, 14I;
		1–14II, 16I
luteus × *tilingii* var. *tilingii*	5042 × 5690	2–14II, 18I
n=32 n=14		

Combinations of parental species and varieties	Culture numbers of the parents	Number of PMC's examined and pairing behavior
glabratus var. *utahensis* × *tilingii* var. *tilingii* n=14 + 0, 1 n=14	5747 × 5012	7–14II, 1I; 1–14II
glabratus var. *parviflorus* × *guttatus* n=45 n=14	5041 × 5010	3–14II, 31I†
glabratus var. *parviflorus* × *laciniatus* n=45 n=14	5041 × 5339	1–2III, 13II, 27I; 1–14II, 31I
glabratus var. *parviflorus* × *glabratus* var. *fremontii* n=45 n=30, 31	5041 × 5373	1–24II, 31I; 1–30II, 23I (and one M_{II} cell containing configuration of 31 and 40+chromosomes)
pilosiusculus × *guttatus* n=46 n=14	5320 × 5052 5320 × 5864	2–14II, 32I 2–15II, 30I*
F$_2$ HYBRIDS		
guttatus × *guttatus* n=14 n=14	5346 × 5839	7–14II, 1I
guttatus × *laciniatus* n=14 n=14	5052 × 5339	1–14II; 2–13II, 2I; 1–12II, 4I; 1–9II, 10I
nasutus × *nasutus* n=14 n=13	5751 × 5327	1–12II,30I

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[*] Culture 5006 and 5864 and their hybrids were subject to chromosome stickiness due to too slow fixation.

[†] In culture 5009 and 5010, n=14 ± 1 or 2.

in all 18 species and varieties of the *M. guttatus* complex and its relatives in section *Simiolus* studied in this investigation. In several cases, e.g., *M. nasutus, M. platycalyx, M. tilingii,* the basic genome has been changed in number by aneuploidy. In other cases, e.g., *M. glaucescens, M. luteus, M. glabratus* var. *utahensis* and particularly in *M. glabratus* var. *fremontii,* it has been modified by mutations, as indicated by a decrease in the regularity of chromosome pairing in the F$_1$ hybrids. The second genome of *M. glabratus* var. *fremontii* (n=30, 31) appears to be homologous to the second genome of *M. glabratus* var. *parviflorus* (n=45), but its further relationships are not known. The homologies of the additional genomes present in the various tetraploid and hexaploid species have yet to be fully determined.

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MILO S. BAKER (1868–1961)

On January 4, 1961, the career of Milo S. Baker came to an end in his 92nd year. His was a role that closes the second dynasty of California botanists, namely those botanists who were direct career descendants of the colorful pioneers, many of whom he knew personally. His career as a plant collector of the California flora opened with the close of the last century and continued well over half of the current century, for he was very active to the end.

Born in Strawberry Point in Iowa on July 19, 1868, he came to California with his parents in 1875 to settle in Oak Run, Tehama County. At the age of twelve he was taken to San Jose, where he completed high school and entered what was then San Jose Normal School. At the end of one year he was admitted by examination to the teaching profession in the public schools of Santa Clara County. In 1887 he went to Modoc County to teach in the elementary schools. To reach his school, he walked from Redding to Bieber, a distance of almost 100 miles. He collected plants in this general area, and corresponded about them with Professor E. L. Greene of the University of California. Much of the flora of eastern Shasta and Lassen counties was first made known through his work. Noteworthy is *Cupressus Bakeri,* discovered by him in the lava beds and named in his honor by Professor Willis Linn Jepson in the first volume of the Flora of California. In 1894, Milo Baker and F. P. Nutting, a like-minded field botanist, spent six weeks collecting together in Lassen and Modoc counties. Their collections were widely distributed in herbaria. At the close of the century he came to the University of California, where he majored in chemistry and took courses in botany. On completion of his work he taught at Lowell High School in San Francisco from 1901 to 1906. Somewhere in his travels he contracted malaria and decided to leave the teaching profession in the interests of his health. He purchased a ranch in Kenwood, Sonoma County, which he named "The Maples," a name which appears on some of his collections; it is situated at the entrance of Adobe Canyon, where Sonoma Creek enters Sonoma Valley. I suspect he was led to this particular ranch because of its botanical assets rather than its agricultural promise. Its rocks are of basalt, Sonoma tuff, and serpentine, and they selected their flora accordingly. His career as a rancher was not a great success, and it is not surprising that in 1922 he began teaching in Santa Rosa High School and later in Santa Rosa Junior College, where he had a distinguished career. Few high school or junior college teachers of botany have inspired so many students to follow plant science in some form as a career. Few teachers have aroused a greater interest in botany among the laymen of their community. Under his generalship, the annual wild flower shows in Sonoma County attracted the attention of all of central California. They were outstanding in their representation of the flora as well as in the inspired participation of the community in making them a success. As a result Santa Rosa is outstanding in its botanically informed populace.

His research interests were twofold. First and foremost was the genus *Viola,* upon which he published several dissertations and which he studied through a living collection at his home. Second was his interest in the flora of the North Coast Ranges of California. He published an annotated list of the plants of this area in mimeograph form and kept it up-to-date in several editions.

Baker was a man whose scientific ambition was always afire. Although a robust man, in his later years his ambition far exceeded his physical capacity. He literally refused to accept old age and at the age of 91 he spoke frequently of his plan to collect violets on Mt. McKinley in Alaska and sought companions to accompany him. He was not easily dissuaded.

He built an excellent herbarium of the North Coast Range counties. It is now fittingly housed at Santa Rosa Junior College and stands as a monument to his inspired teaching. His collection of violets is now housed at the University of California at Berkeley and is a marvelous research collection of this group of plants.

A photograph of Milo S. Baker and a dedication to him form the frontispiece of Volume XIII of MADROÑO.

I wish to express my appreciation to Mrs. Avis Stopple, Librarian at Santa Rosa Junior College, for assistance in the preparation of the annotated bibliography which follows—HERBERT L. MASON, Department of Botany, University of California, Berkeley.

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CYTOLOGICAL OBSERVATIONS ON ADIANTUM × TRACYI C. C. HALL[1]

Warren H. Wagner, Jr.

The California maidenhair fern, *Adiantum jordanii* C. Muell. (syn. *A. emarginatum* D. C. Eaton) is one of the endemic pteridophytes of the California Floral Province (Howell 1960). In the North Coast Ranges where it comes into association with the wide-ranging *A. pedatum* L., there has occasionally been found an intermediate plant, *A.* × *tracyi* C. C. Hall, which combines the characteristics of these sharply different species (Wagner 1956). A single plant of the intermediate fern was discovered as early as 1895 along the Eel River near Pepperwood, Humboldt County, by Mr. J. P. Tracy, and the observations to be recorded here are based on a propagated descendant of that plant. Other naturally occurring specimens of *A.* × *tracyi* have been found in Sonoma and Marin counties. Easily propagated from rhizomes, this fern has proved a decorative and hardy garden plant.

Adiantum × *tracyi* has been interpreted as an interspecific hybrid because of its morphological intermediacy in a number of obvious features; its sporadic distribution, and occurrence where the putative parents grow nearby; and the irregularity of its spores (Wagner, *ibid.*). The facts to be reported below tend to supply additional evidence for considering that this fern is a natural hybrid. To obtain cytological observations, the immature sori of *Adiantum* × *tracyi* were fixed in Newcomer's Fixing Fluid (Newcomer, 1953). Collections were made in May, June, and July 1960 from plants growing at the University of Michigan Botanical Gardens.

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[1] Research in connection with National Science Foundation Grant G10846.

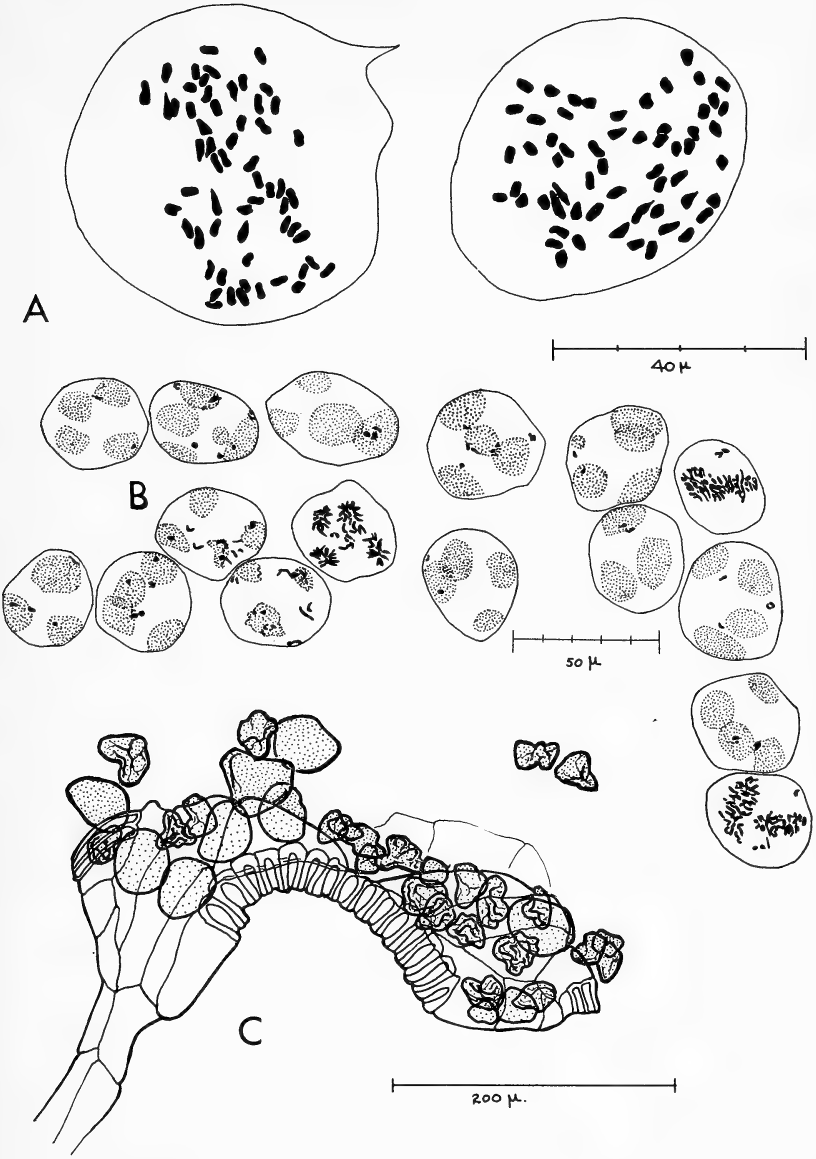

FIG. 1. *Adiantum* × *tracyi*: A, meiotic metaphase showing 59 univalents; B, sporocytes extruded from a single sporangium and squashed, showing different stages and unassimilated chromosomes; and C, sporangium forced open with alcohol and diaphane, showing part of spore complement; note small wrinkled spores and large smooth spores. (Camera lucida drawings, based on material obtained from descendant of the original plant.)

The proper stages of meiotic division were found by selecting pinnules which had reached full size and upon which the sori were of approximately mature dimensions but pale greenish-white in color. Because of the leathery false indusium it was difficult to scrape out the young sporangia. The entire indusium was removed, therefore, placed on a microscope slide in acetocarmine stain, and broken apart, after heating, by tapping briskly with the point of a dissecting needle on the cover-slip. This broke apart the false indusium and the sporangia (and sometimes, unfortunately, the cover-slip), but the spore mother cells became sufficiently separated so that they could be properly squashed and studied under the microscope. Camera lucida drawings were made of good preparations, and the slides were made permanent.

The observations of meiosis were interesting for two reasons. First, there was no pairing at all between the chromosomes. At metaphase, the chromosomes become very short and oblong in outline, and in not one of the numerous figures observed were there any indications of pairing. This fact suggests that there is a lack of homology between the two genomes that make up the chromosome complement, and that they very likely came from different species.

The second interesting observation was that the number of chromosomes is 59. Such a number seems at first unusual for a presumably diploid plant, and it suggests at least two explanations: either the plant is one in which there has been the loss or addition of a chromosome, or it is a hybrid between parents with different chromosome numbers, one of them with an odd number and the other with an even number.

The distribution of chromosomes at metaphase is irregular, and tetrad formation is characterized by three to five daughter nuclei plus a varying number of excluded chromosomes, as shown in figure 1, B. There is some lack of synchrony in the meiotic divisions of the sixteen spore mother cells, so that at one time it is possible to find several different stages in tetrad formation in the same sporangium. This is unlike the situation ordinarily observed in normal leptosporangiate fern species, where sporogenesis proceeds approximately simultaneously in all sixteen spore mother cells of a sporangium. As would be expected and as was reported earlier (Wagner, 1956), the spores are abortive and irregular. Even at an early stage in the spore maturation their irregularity is evident. Many of them are small and become corrugated or folded, and in the same sporangia others are very large and smooth. Figure 1, C, shows a mature sporangium forced open by alcohol and diaphane and with part of the variable spore complement present.

That *Adiantum* × *tracyi* may actually have arisen from parents with different chromosome numbers is suggested by the fact that in four genera of Adiantaceae (*Adiantum, Cheilanthes, Aleuritopteris,* and *Saffordia*) two numbers are known, viz. $n = 29$ and $n = 30$, among the species of each. The other adiantaceous genera, so far as is known at present, have only single numbers among their species, the number of each genus being either n = 29 or n = 30 (Manton 1959). *Adiantum pedatum,* which is one of the presumed parents of *A.* × *tracyi,* has been observed in material from two regions (Vancouver: Manton 1959; and Ontario: Britton 1953) to have n = 29. If it can be assumed that this number is characteristic of *A. pedatum* everywhere, then we may suggest that the other presumed parent, the endemic Californian *A. jordanii,* which has not yet been examined cytologically, will probably prove to have n = 30 chromosomes.

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TAXONOMIC AND NOMENCLATURAL NOTES ON PLATYDESMA (HAWAII) AND A NEW NAME FOR A MELICOPE (SOLOMON ISLANDS)[1]

BENJAMIN C. STONE [2]

The genus *Platydesma* was proposed by Horace Mann, Jr. (1866) to include one species, *P. campanulatum* (*–a*), which had been collected by Mann and W. T. Brigham "on the mountains behind Honolulu." A slightly expanded description is found in Mann (1869). Two species were added to the genus by Hillebrand (1888) in his "Flora of the Hawaiian Islands": *P. cornutum* (*–a*), from the island of Oahu, and *P. rostratum* (*–a*), from the island of Kauai. Hillebrand (*op. cit.*) also transferred to *Platydesma* a species described by Asa Gray as *Pelea auriculaefolia* (1854, p. 343; 1857, pl. 36), but this was an error, as Rock (1913, 1918) has shown, for Gray's original placement is correct. Although Hillebrand

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[1] Studies in the Hawaiian Rutaceae, I. This paper is the first in a series of studies concerned primarily with the Hawaiian Rutaceae, of which the second and third papers are now in press.

[2] This work was carried out while the writer was Research Assistant, Botany Department, University of Hawaii, Honolulu. It is an outgrowth of studies for a monograph of the genus *Platydesma,* now in press.

FIG. 1. *Platydesma spathulatum* (Gray) B. C. Stone. Holotype of *Melicope spathulata* Gray (US), collected by United States Exploring Expedition of 1838–42 on mountains of Kauai. (Photo courtesy U. S. Nat. Herb.)

cited the type specimens of *Pelea auriculaefolia* Gray (United States Exploring Expedition of 1838–1842, Mauna Kea, Hawaii), it was perhaps not seen by him. He apparently based his conclusion for the transfer of this species to *Platydesma* upon specimens collected by himself in the Kohala Mountains and on the island of Hawaii and also on a specimen collected by Reverend John Lydgate near Laupahoehoe, Hawaii. These Hillebrand and Lydgate specimens are in fact representatives of *Platydesma* and not of *Pelea,* and may be referred to the distinct species *Platydesma Remyi* (Sherff) Degener, Sherff, & Stone (Degener, 1961), to which *P. campanulatum* var. *sessifolium* (*–a*) Rock (1913) may also be referred. Rock's description is typified by one of his collections (*Rock 4222*). *Platydesma Remyi* is based on a collection in the Museum d'Histoire Naturelle of Paris collected by Jules Remy in 1853.

Hector Léveillé (1911) described two species of *Platydesma, P. oahuense* (*–is*) and *P. Fauriei,* but both names are later homonyms, as pointed out by Rock (1914). The first is referable to Mann's original species; the second is not *Platydesma* and is not even rutaceous, but is referable to the solanaceous *Nothocestrum longifolium* Gray.

The species which has been known as *Platydesma campanulatum* is relatively common in the Hawaiian rain-forest, and is met with much more frequently than are the other two species, *P. cornutum* and *P. rostratum.* It is also of wider distribution, at least as presently known, since *P. cornutum* is endemic to Oahu, while *P. rostratum* is found only on Kauai. It is always or nearly always accompanied by such characteristic rain-forest plants as species of *Pelea, Fagara, Straussia,* and *Gouldia.* It is reasonably well represented in herbaria (much better than the other two species), and thus it is rather unfortunate that the specific epithet must be changed.

The name *Platydesma campanulatum* (*–a*) Mann was not the first for this species. Some years earlier, Asa Gray (1854) had described it as two different species, *Melicope spathulata* (p. 352) and *M. grandifolia* (p. 354). This fact, suspected by Rock (1918) and later by Skottsberg (1936, although he still used the name *Platydesma campanulatum* in 1944), has not received the formal recognition it requires under the International Code of Botanical Nomenclature. It is necessary, therefore, to choose between Gray's two specific names. The type specimens of both of Gray's species are sterile or nearly sterile. The first, *Melicope spathulata,* is a specimen from Kauai which is in bud (fig. 1). The second, *M. grandifolia,* is a specimen from Hawaii which is altogether sterile (fig. 2). Although the foliage in this second specimen is sufficient for specific placement, it is not entirely reliable for infraspecific placement; nonetheless, this specimen certainly belongs to the same species as the first (*M. spathulata*). Because the type specimen of *M. spathulata* is at least not entirely sterile, being in bud, it seems preferable to use *M. spathulata* rather than *M. grandifolia* as the basionym in the following combination:

FIG. 2. *Platydesma spathulatum* (Gray) B. C. Stone. Holotype of *Melicope? grandifolia* A. Gray (US), collected by United States Exploring Expedition of 1838–42 on Mauna Kea, Hawaii. (Photo courtesy U. S. Nat. Herb.)

Platydesma spathulatum (A. Gray) B. C. Stone, comb. nov.[3] *Melicope spathulata* A. Gray, Bot. U. S. Expl. Exped. 15:354. 1854. *M.*? *grandifolia* A. Gray, *loc. cit. Platydesma campanulata* H. Mann, Proc. Boston Soc. Nat. Hist. 10:317. 1866. Hillebrand, Fl. Haw. Ids. 71 (as *companulata*). 1888. Rock Indig. Trees Haw Ids. 241. 1913. Heller, Minn. Bot. Stud. 1(9):841. 1897. Skottsberg, Acta Horti Gothob. 10:120. 1935; 15:388. 1944. *P. campanulata* var. *macrophylla* Hillebrand, Fl. Haw. Ids. 72. 1888. *P. campanulatum f. coriaceum* Rock. Indig. Trees Haw. Ids. 243. 1913. *P. oahuensis* Léveillé in Fedde, Rep. Sp. Nov. 10:153. 1911.

In addition to the above transfer of specific epithet, there are two varieties requiring transfer, as follows:

Platydesma spathulatum var. **pallidum** (Hillebr.) B. C. Stone, comb. nov. *P. campanulata* var. *pallida* Hillebrand, *op. cit.*

Platydesma spathulatum var. **pubescens** (Skottsb.) B. C. Stone, comb. nov. *P. campanulata* var. *pubescens* Skottsberg, Acta Horti Gothob. 15:388. 1944.

The type of the genus is now to be called *Platydesma spathulatum,* and *P. campanulata* becomes a synonym. However, the ultimate type of the genus is the type specimen of *P. campanulata* (*Mann & Brigham 94,* CU; isotypes, *94* or *94–bis,* at K, BISH), rather than the type of Gray's *Melicope spathulata* (US).

A species from Bougainville, Solomon Islands, given the name *Melicope grandifolia* by B. L. Burtt in 1935, bears a later homonym since Gray's *M. grandifolia* preēmpts that epithet. It is thus necessary to propose the following new name:

Melicope Burttiana B. C. Stone, nom. nov. *M. grandifolia* B. L. Burtt, Kew Bull. 1935: 300, *non* A. Gray, 1854.

Type. Solomon Islands: Bougainville, *Waterhouse B.227* in 1930–31 (US).

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[3] Mann used the generic name *Platydesma* as if it were of feminine gender, and was followed in this by several later authors, but the name is one of several in Greek (such as *Geniostoma*) which, though ending in –a, takes a neuter modifier.

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A NEW SPECIES OF GALIUM IN CALIFORNIA

LAURAMAY T. DEMPSTER [1]

A completely new and radically different species of *Galium* has been discovered by Mrs. Clare Hardham of Paso Robles. Mrs. Hardham, who has been making a study of the flora of the Santa Lucia Mountains, has found the new *Galium* in six separate localities, almost invariably associated with *Cupressus sargentii* Jepson, which is a well-known indicator of serpentine soils. The new species is diploid ($2n = 22$), highly uniform, and almost certainly primitive and residual.

Its nearest relative would seem to be *Galium clementis* Eastwood, which is another endemic occurring a little farther north on Cone and Junipero Serra (Santa Lucia) peaks. More distantly, the new species is certainly related to *G. californicum* H. & A., *G. nuttallii* Gray, *G. bolanderi* Gray, *G. sparsiflorum* Wight, etc., all of which it resembles in its dioecism and in the possession of fleshy fruits. It differs sharply from all of those species, however, in having six leaves to a node instead of four. *Galium clementis* has generally four leaves to a node, but occasionally six, and stands uniquely, therefore, in an intermediate position between the new species, described herein as *G. hardhamae,* and all of our other berry-fruited species. *Galium hardhamae* differs additionally from *G. clementis* in having a less compact habit, fewer shorter hairs (being consequently of a much darker green), slightly smaller leaves and flowers, and in the succulence of its leaves.

Galium hardhamae is a dioecious perennial growing usually under or near *Cupressus sargentii,* on humous serpentine soil. The plants are low and matted, rooting at the nodes, the flowering branches ascending or weakly clambering, the hispid internodes ½ to 2½ cm. long, mostly much longer than the leaves. The leaves (invariably 6 to a node) are bright green, sparsely hispid, lanceolate, acute, and each tipped with a stout hair. When living, they are fleshy, round above and plane beneath. In the

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[1] Contributions from the Jepson Herbarium, number 5.

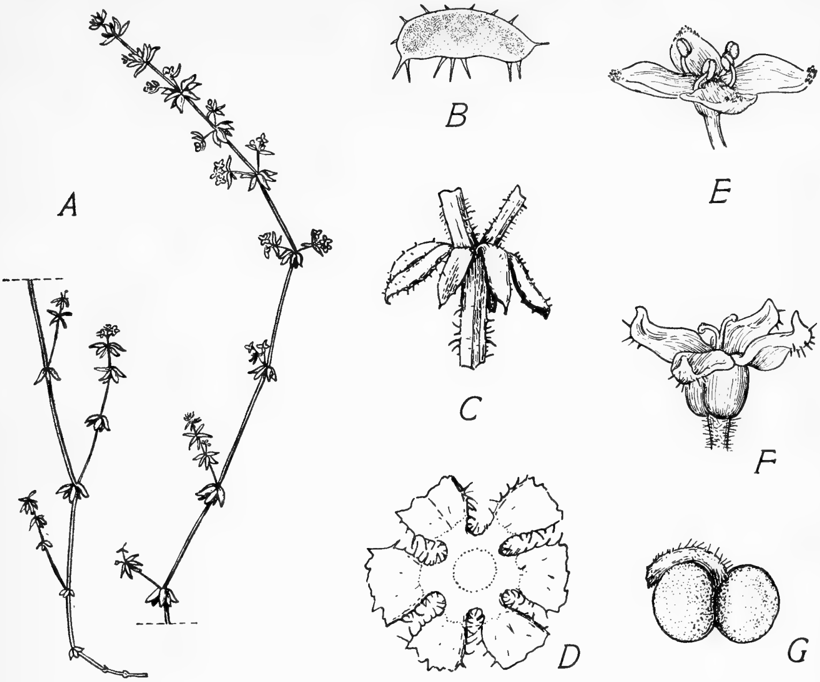

FIG. 1. A, single flowering branch (staminate) × ¾; B, cross section of leaf blade, × 15; C, single node with leaves, × 2½; D, leaf bases of a single whorl, × 15; E, staminate flower, × 10; F, pistillate flower, × 10; G, nearly ripe fruit, × 2½. The difference in the hairs of the two flowers illustrated is not a sexual, but an individual difference.

desiccated condition, however, they curl downward laterally, owing to shrinkage of the spongy parenchyma. Apart from this lateral curling, the leaves are more reflexed or less, depending upon the condition of moisture, being sharply turned back when dried naturally, and spreading horizontally when wet. This activity is apparently a function of the colorless petioles, the green leaf-blades being quite rigid because of their succulence. The inflorescence is long and slender, the branchlets being mostly less than 1 cm. long. The corollas are rotate, about 2 mm. across, yellow or green, sparsely hispid externally. The ovaries are glabrous or nearly so, and the fruit is a didymous berry, or sometimes it is globose because of the abortion of one seed. Fully ripe and dehydrated fruits are black and wrinkled.

Galium hardhamae Dempster, sp. nov. Herba dioica perennis, ramis decumbentibus vel rare scandentibus. Caules hispidi, internodiis longis cm. ½–2½, quam foliis saepe multo longioribus. Folia sena plus minusve reflexa, mm. 2–4 longa, ovata, acuta, ambis paginis hispida, in vita plano-convexa, in herbario deorsum lateraliter volvata. Inflorescentia longa angustaque, ramis brevibus plus minusve 1 mm. Corollae rotatae, diametro circa mm. 2, flavae vel virides, extra sparse hispidae. Ovaria glabra. Fructus carnosi didymi vel saepe orbiculares, laeves.

Type. Seaward slope of Santa Lucia Mountains in grove of Sargent Cypress, south ultimate fork of Alder Creek, southwestern Monterey County, California, at 2200–2500 feet, *Clare Hardham 5650* (JEPS).

Other collections. Monterey County: upper reaches of Alder Creek, *Dempster & Hardham 1406* (JEPS); Villa Creek south of Lion Den Spring, *Hardham 6065*. San Luis Obispo County: Waterdog Creek, *Hardham 6380* (JEPS); Cypress Swamp just northeast of Cypress Mountain, *Hardham & Dempster 5703* (JEPS), *Hardham 3962* (JEPS); Spanish Cabin Creek, *Hardham 5963;* Tobacco Creek, *Hardham 5967;* headwaters of Chris Flood Creek (San Carpoforo), *Hardman 6145.* Numbers otherwise undesignated are in the private collection of Mrs. Hardham at Paso Robles, California.

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A NEW SPECIES OF CRYPTANTHA (SECTION CIRCUMSCISSAE) FROM CALIFORNIA AND TWO RECOMBINATIONS (SECTION CIRCUMSCISSAE AND SECTION ANGUSTIFOLIAE)[1]

Kunjamma Mathew and Peter H. Raven

Cryptantha circumscissa (H. & A.) I. Johnston is an annual herb that occurs over a wide area of western North America, from Wyoming and central Washington to Arizona and northern Baja California. In one population, supposed to be referable to this species and located north of Adelanto on the Mojave Desert of San Bernardino County, California, three distinct entities were found, differing modally from one another in corolla size. The largest-flowered group of plants had corollas 4–6 mm. in diameter and pollen grains 5.5–6.5 μ long. These measurements are beyond the range of variation characteristic of *C. circumscissa*. With further exploration it was found that plants with such measurements comprised a distinctive series of populations from a limited area in southern California, and they are described below as a new species.

Cryptantha similis Mathew & Raven, sp. nov. Herba annua sectionis *Circumscissae*, a *C. circumscissa* persimilie, at differt: corolla 4–6 mm. lato; granis pollinis 5.5–6.5 μ longo.

Slender or bushy, bristly-pubescent annual herb, cymosely branched from the base, with ascending branches to 10 cm. long; leaves linear to narrowly oblanceolate, 3–10 mm. long, inconspicuously pustulate, with

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[1] Thanks are due Professor Harlan Lewis for pointing out the variation pattern leading to this study and for a critical review of this manuscript, and to the curators of the following herbaria for permission to examine material in their care: British Museum (Natural History), California Academy of Sciences, University of California (Berkeley), Dudley Herbarium (Stanford University), Pomona College, Rancho Santa Ana Botanic Garden, and Royal Botanic Gardens (Kew).

no apparent veins, well distributed but congested just below the short inflorescences; inflorescences to 1.5 cm. long, the flowers axillary and very crowded; corollas conspicuous, 4–6 mm. in diameter, white, yellowish at throat; pollen 5.5–6.5 µ long, oblong; fruiting calyx 2.5–4 mm. long, bristly pubescent, the sepals united to near the middle, with a circumscission just below the sinuses, the upper half falling away at maturity, the persistent portion cupulate; pedicels less than 0.5 mm. long; nutlets 4, homomorphous, lance-ovate, 1.2–1.5 mm. long; gynobase about two-thirds the height of the nutlets, slender-pyramidal; style equal to or barely exceeded by the nutlets. Gametic chromosome number, n=6.

Type. 8.7 miles north of Adelanto on United States Highway 395, San Bernardino County, California, *Lewis & Mathew 1113A* (RSA).

Additional specimens examined. California. Kern County: Red Rock Canyon, *Howell 4925* (with *C. circumscissa*); Mojave, *Lemmon in 1881* (with *C. circumscissa*); 12 miles southeast of Mojave, *Crum 1798*. San Bernardino County: Hesperia, *Spencer 387* (with *C. circumscissa*); north of Hinkley, *Anderson 6853*; near Victorville, *Jones in 1926* (with *C. circumscissa*), *Lee 8545, Wilson 31*; Randsburg road, *Weston 621*; 10 miles north of Adelanto, *Kirby 1116*; Barstow, *Munz 2544* (with *C. circumscissa*); between Hesperia and Adelanto, *Munz 4474*; 1.7 miles northeast of Helendale, *Raven 11951*; Swartout Canyon, *Hall 1537*; Swartout Valley, *Munz 4618*; Cajon Pass, *Johnston in 1920, Munz et al. 4672, Parish 11832*. Los Angeles County: above Littlerock, *Ray 931*; between Big Rock Creek and Little Rock Creek on State Highway 138, *Abrams 13946*; Arraster Creek, San Gabriel Mountains, *Peirson 1001*.

Cryptantha similis and *C. circumscissa* comprise the section *Circumscissae* I. Johnston (Contr. Gray Herb. 74:40. 1925). *Cryptantha similis* has both larger corollas and larger pollen grains, the corollas of *C. circumscissa* being only from 1–4 mm. in diameter and the pollen grains from 7–9 µ in length (these measurements based on an examination of more than 100 collections from throughout the range of *C. circumscissa* and including the type: Snake Country, "California," *Tolmie*, K).

The gametic chromosome number of *C. similis* is n=6, whereas that of *C. circumscissa* is usually n=12, although one plant of *C. circumscissa* from the locality north of Adelanto had n=18 (table 1). As already stated, three distinct morphological entities were found at the location north of Adelanto. One of these was the large-flowered *C. similis* just described. The remaining plants at this locality fell into two groups with respect to corolla size, both conforming, however, to the size limits given above for *C. circumscissa*. One of the plants of the smaller-flowered group was counted and was found to have a chromosome number of n=18 (hexaploid; table 1), whereas the plant which was counted from the group with medium-sized flowers had n=12 (tetraploid), the same chromosome number that was found in plants of *C. circumscissa* from other populations. The difference in pollen size between these two groups was not significant. The n=18 plant from north of Adelanto might have had an allohexaplaid origin, with tetraploid *C. circumscissa* (n=12) and diploid *C. similis* (n=6) as the probable parents. Some tetraploid plants of *C. circumscissa* that were examined from other localities, however, had

TABLE 1. CHROMOSOME NUMBERS OF CRYPTANTHA SPECIES*

C. circumscissa (H. & A.) I. Johnston subsp. *circumscissa*
  $n=12$. Nevada. Washoe County: 6.1 miles north-east of Sparks, *Raven 14287.* Esmeralda County: Lida Pass, *Raven 15476.*
    California. Mono County: Sherwin Grade, *Raven 14295, 14296*; Paradise Camp, *Raven 14262.* Inyo County: Bishop Creek, *Raven 14302, 14303.* Kern County: Walker Pass, *Raven 13992.* San Bernardino County: Lenwood, *Raven 13902*; 8.7 miles north of Adelanto, *Lewis & Mathew 1113B.*
  $n=18$. California. San Bernardino County: 8.7 miles north of Adelanto, *Lewis & Mathew 1113C.*
C. micrantha (Torr.) I. Johnston subsp. *lepida* (Gray) Mathew & Raven
  $n=12$. California. Riverside County: San Jacinto Mountains, *Raven 14241.*
C. micrantha subsp. *micrantha*
  $n=12$. California. San Diego County: Borrego Valley, *Raven 14847.*
C. similis Mathew & Raven
  $n=6$. California. San Bernardino County: 8.7 miles north of Adelanto, *Lewis & Mathew 1113A.*

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* Vouchers deposited at Rancho Santa Ana Botanic Garden, Claremont, California.

corollas as small as those of the Adelanto hexaploid. For example, at two California localities outside the range of *C. similis* (Sherwin Creek, Mono County; Bishop Creek, Inyo County), two groups of plants were found growing together that corresponded in corolla size with the tetraploid and the hexaploid ($n=18$) from north of Adelanto. In both of these latter cases, however, all plants examined were tetraploid ($n=12$). Thus there appears to be no basis for the taxonomic segregation of the hexaploid. As for the difference in corolla size between the diploid and tetraploid, it is possible that the diploid may be allogamous to a greater extent than is the teraploid, and thus follow the sort of correlation between polyploidy and autogamy discussed in some detail by Grant (Am. Nat. 90:319–322. 1956). Although the chromosomes are small and difficult to observe, there is no suggestion of multivalent formation in the tetraploid, and hence it may have had an alloploid origin. *Cryptantha similis*, however, appears to be the only diploid closely enough related to *C. circumscissa* to have participated in its origin.

In view of these results, it is pertinent to discuss the patterns of morphological variation of *C. circumscissa.* In the southern Sierra Nevada of California at high elevations there occurs a distinctive geographical entity, *Cryptantha circumscissa* subsp. **rosulata** Mathew & Raven, comb. nov. (*C. circumscissa* var. *rosulata* J. T. Howell, Leafl. West. Bot. 6:104. 1951). Based on measurements of its pollen, *C. circumscissa* subsp. *rosulata* is probably tetraploid like subsp. *circumscissa.* Another variant involves hispid plants from the eastern slopes of the Sierra Nevada which have been separated as *Krynitzkia dichotoma* Greene or as *Cryptantha circumscissa* var. *hispida* (Macbride) I. Johnston (Contr. Gray Herb. 74:1–114. 1925), but inasmuch as they occur intermingled with plants typical of subsp. *circumscissa* in this area and less commonly elsewhere and do not appear to be sharply distinct morphologically, we prefer not to recognize them taxonomically. These patterns of variability in *C. circumscissa* are apparently analogous with that concerned with corolla size, which has already been discussed, and, like it, they are doubtless reinforced by autogamy.

Since the detection of *Cryptantha similis* became possible following the determination of its chromosome number, we also investigated an apparently analogous pair of taxa in the related section *Angustifoliae, Cryptantha micrantha* (Torr.) I. Johnston subsp. *micrantha,* with very small flowers, and another entity with larger flowers, *Cryptantha micrantha* subsp. **lepida** Mathew & Raven, comb. nov. (*Eritrichium micrantha* var. *lepidum* Gray, Syn. Fl. 2:193. 1878). In this case, however, both taxa were found to have the same gametic chromosome number, n = 12 (table 1). It should also be noted that the large- and small-flowered taxa have not been found growing together. They appear to be largely geographical entities best recognized as subspecies.

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REVIEW

Taxonomy of Flowering Plants. By C. L. Porter. viii + 452 pp., W. H. Freeman San Francisco. 1959. $6.75.

"Taxonomy of Flowering Plants" is one in the series of high-quality biology texts published by Freeman and Company. Dr. Porter states that he hopes it will help to fill the gap he sees existing between "texts that are really reference books for advanced students and much abbreviated texts that have had much of the meat of the subject deleted from them." This rather effective compromise is a work of some 450 pages, suitable for introductory courses of either one or two semester's length. It is divided into three principal parts: History, Principles, and Methods; Selected Orders and Families of Monocotyledons; and Selected Orders and Families of Dicotyledons. A 16-page glossary precedes the Index.

Part I, History, Principles, and Methods, is rather abbreviated. It should be entirely satisfactory for many introductory courses, but will require some supplementation in courses where a substantial portion of the students requires more detailed information. An exposition of aims, history, literature, field and herbarium methods, nomenclature, concepts of taxa, construction and use of keys, phytography and terminology, and phylogeny and classification of angiosperms which can be encompassed within 140 pages and yet prove entirely satisfactory for a wide variety of taxonomy courses is probably impossible. Dr. Porter intended to produce a concise treatment, and he is no doubt aware that some will find his work excessively synoptic in places. The reviewer believes that the material on field methods and the chapter entitled "Concepts of Taxa" are cases in point. In addition, instructors who stress nomenclature will find his chapter of the same name very brief indeed. However, the author generally has been remarkably successful within his self-imposed space limitations. The chapter on phytography and terminology is a good one. It is four times as long as the average chapter in this section, and replete with illustrations.

The student will appreciate the detail in this chapter, and the instructor will find that the drawings can eliminate many blackboard drawings or pencil sketches on his part. The illustrations are excellent. The drawings are mainly the work of Evan Gillespie, but a few are from Gray's "Lessons." This chapter also introduces the symbols for floral parts which are used extensively in the last two portions of the book. These symbols are simple ones that make it possible to portray the characteristics of a family in an easily grasped floral diagram. Every chapter in Part I except the one on the construction and use of keys has a list of references pertaining to the subject matter of the chapter. Some of these lists are more than two pages long. These references add considerably to the merits of the book. They should encourage the student to follow up subjects that especially interest him.

Parts II and III, dealing with slightly more than one hundred families of flowering plants frequently encountered in the North American flora, are very good. Porter's treatment should help the student to see the classificatory function of taxonomy as other than an arbitrary system of pigeon-holing. He has maintained a balance between convenience and progress toward more truly phylogenetic systems. His treatment of the monocots (Part II) is basically that of Hutchinson, whereas that of the dicots (Part III) is a modified Englerian sequence. These classes are divided into subclasses, and these in turn into orders and families. A few of the families are further divided into sub-families or tribes. The intent here is not to construct an elaborate system of hierarchies, but rather to show in a natural way that taxonomy is a science that categorizes living things upon the basis of similarities in form and function. Porter's treatment of the identificatory function of taxonomy is excellent. There is a succinct description, a mention of representative genera, a floral diagram, and drawings for almost all of the families treated. In addition, there are many good photographs of representatives of the larger families. These illustrations are designed to teach the student to recognize, without recourse to a book, the important families of flowering plants. The floral diagrams accurately symbolize the characteristics of a given family, yet are easy to comprehend. The drawings, in addition to their sight-recognition function, frequently show (and label) features that elicit questions from students using dichotomous keys. For example, the involucre, bracts, glands, and unisexual flowers of the Euphorbiaceae are labeled, as are the involucre, involucel, carpophore, mericarp, ribs, oil tubes, and stylopodium of the Umbelliferae. The specialized structures characteristic of the Cyperaceae, Gramineae, and Compositae are treated in the same way. The advantages of these drawings over verbal descriptions or blackboard sketches or projected slides are obvious. It is difficult to imagine a more teachable method than Porter's combination of text, floral diagrams, drawings, and photographs.

"Taxonomy of Flowering Plants" impresses this reviewer as being the best available text for many introductory taxonomy courses, especially one-semester or one-quarter ones. It is generally free from errors and objectionable features. However, it should be noted that the tuft of hair on *Epilobium* seeds is better described as comose, rather than comatose (p. 342). Also, from a realistic point of view, conserved family names probably should be used in an elementary text rather than the permissible but relatively unused Apiaceae, Lamiaceae, etc. Gillespie's illustrations are, as usual, very good, and Porter's prose makes the text a readable one. The relative brevity of Part I (History, Principles, and Methods) poses certain difficulties, but this material can be supplemented by the instructor if he feels this is necessary. However, the feature that distinguishes this book from other contemporary texts is the material on plant structures and family characteristics. These sections are perhaps the nearest approach to a do-it-yourself method of instruction in plant identification that can be devised. It should be welcomed by instructors and students in the classroom, and also by persons who wish to learn how to identify plants without having to take a course to do so. John Mooring, Department of Botany, Washington State University, Pullman, Washington.

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THE SANTA LUCIA CUPRESSUS SARGENTII GROVES AND THEIR ASSOCIATED NORTHERN HYDROPHILOUS AND ENDEMIC SPECIES

Clare B. Hardham

Cupressus sargentii Jepson occurs in the Coast Ranges of California from extreme northern Mendocino County in the North Coast Ranges to Santa Barbara County in the South Coast Ranges, where its most southern locality is an isolated outpost in the San Rafael Mountains. Throughout its range it is known as a species which is almost always restricted to soils of serpentine content. It is common over large areas in the North Coast Ranges, but occurs much more sparingly and interruptedly in the South Coast Ranges. In the Santa Lucia Mountains of the South Coast Ranges, it is restricted to a few small areas in Monterey and San Luis Obispo counties. Several local endemics, with only minor exceptions, are restricted to the same habitat. In addition, the dampest and most shaded groves provide ecological niches where several northern hydrophilous species persist.

The groves of *C. sargentii* in the Santa Lucia Mountains occur on metamorphosed serpentine which was formed at various times during the Jurassic Age. In the Santa Lucias the exposed serpentine extends for nearly forty miles along the major fault zones of the range from south of the Cuesta Grade in San Luis Obispo County to Plaskett Creek in Monterey County. It is often slightly oxidized and owes much of its red color to superficial deposits of water-borne iron. It is also highly faulted, metamorphosed, and intruded with volcanics. Basalt, rhyolite, radiolarian chert, and local concentrations of various minerals are often found in conjunction with it. Gold, chrome, and quicksilver have all been mined near one or another of the cypress groves, and there may be commercial deposits of manganese present. The cypress grove south of Lion Den Spring is the only grove which occurs on a substratum obviously different from the usual form of serpentine. Here the serpentine is thoroughly impergnated with aluminum, and the resultant soil is white. Although geologists suspect that the cypress groves may indicate the presence of some mineral besides serpentine, no such correlation has yet been established for the Santa Lucia cypress groves.

Actually the cypress groves occupy only a tiny fraction of the total area of serpentine in the Santa Lucia Mountains. The combined areas of the *C. sargentii* groves can scarcely exceed four or five square miles, whereas the serpentine formations of the Santa Lucias have a total area of roughly 400 square miles. The cypress groves are found along either the King City or the Pine Mountain faults, regions of numerous springs,

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and the groves occur at the heads of the streams which are, in all but the very dryest years, permanent or semipermanent. The cypresses extend down the mountains along the streambeds, especially on the northeast slopes of the range, and isolated trees frequently grow in the streambeds below the groves.

Most of the cypress groves are located along the main ridge of the Santa Lucias at altitudes of about 2500 feet. There are also some cypress groves near Bryson on the ridge formed by the King City Fault, the largest of which is on Waterdog Creek at elevations of 2000 to 2500 feet. A few miles south of this grove there used to be "cedars in swamps," but the trees never reached maturity after a fire in 1953, and they were again burned in 1960, so it is doubtful if these cedar swamps will ever again exist. There are many scattered trees on sandstone in the Los Burros Creek drainage at low elevations. Although they are occasionally as much as a mile distant from the serpentine ridges to the west, presumably there are serpentine ions in the groundwater, and, since there are few competing species, the cypresses have succeeded in establishing themselves. I have found only one small grove on the serpentine above these scattered trees in the Los Burros drainage.

As with many other species that occur in mesic habitats, some of the cypresses have established themselves on the rocky ridges that sometimes mark the upper borders of the cypress groves, but if one has the courage to explore, it is apparent that most of the trees are growing in relatively damp places and even, occasionally, in small swamps. A few of the cypress groves, including the easily accessible grove just north of San Luis Obispo, west of the Cuesta Grade, appear to be quite dry. Despite appearances, however, on the foggy morning of September 22, 1958, the ground beneath the cypress trees in this grove was wet down to the zone of permanent moisture.

The only Forest Service station in the entire area that keeps moisture records is on Rocky Butte at 3590 feet, about 1000 feet higher than the cypress groves. On numerous mornings which are described as "clear" on their records, the relative humidity readings are recorded as being as high or higher than they are on mornings when fog is specified at that altitude. This corroborates my impression that the coastal fogs rise to a considerable altitude in the Santa Lucia Mountains and that the cypress groves probably receive an appreciable amount of moisture from summer fogs. In wet years some of the groves must receive a surprising amount of rain. At the 7X Ranch at the foot of Cypress Mountain near the headwaters of Las Tablas Creek, the rainfall varies from 40 to 80 inches annually (San Luis Obispo County Water Survey). The average at the Krenkel Ranch near Alder Creek is 60 inches. In a wet year at the Ocean View Mine near Burnett Peak, the rainfall was 117 inches, and in the dry winter of 1960-61, the total rainfall was more than 36 inches, the rain gauge having overflowed in one storm.

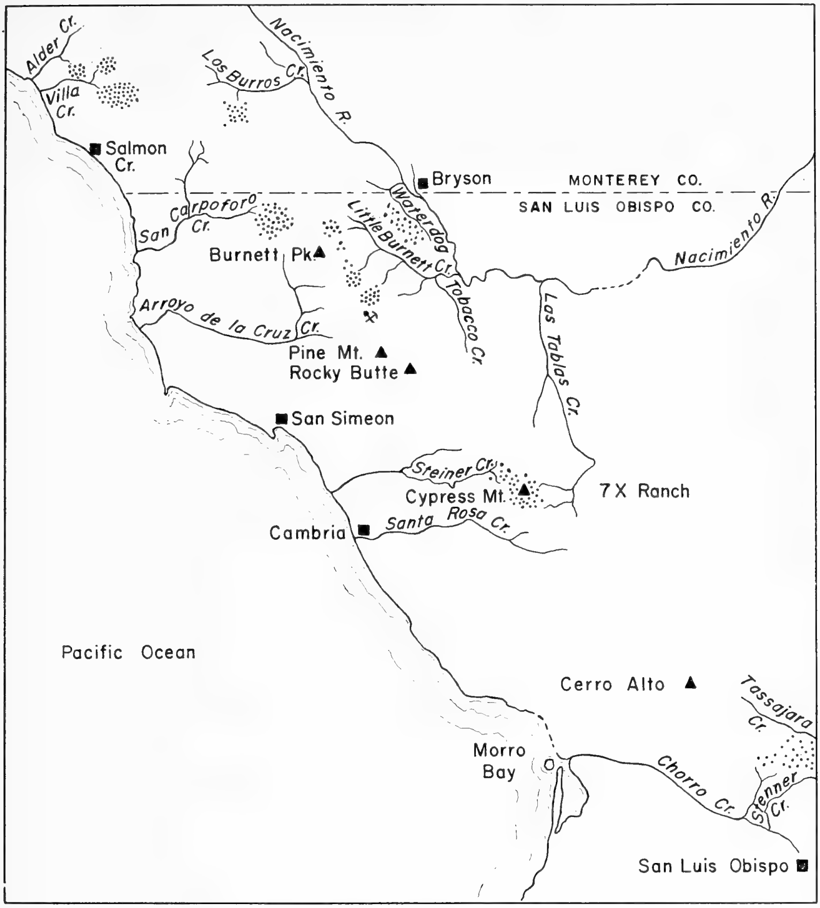

FIG. 1. Distribution map of *Cupressus sargentii* in the Santa Lucia Mountains.

Typically the boundaries of the cypress groves are sharp, with their drier edges bordered in the northern part of the range by mixed *Quercus-Pinus-Pseudotsuga* woodland, and in the southern part by *Quercus-Pinus* woodland.

On the eastern edge of the Santa Lucia Mountains there are two cypress groves, one large grove on a northeast-facing slope at the headwaters of Waterdog Creek and a small grove in a swampy ravine at the head of the main branch of Los Burros Creek. These groves occur along the King City Fault. On the main ridge, along the Pine Mountain Fault, there are approximately fourteen groves. The largest and most southerly grove occurs west of the Cuesta Grade five miles north of San Luis Obispo and includes the Chorro Creek grove described by Carl B. Wolf in "The New World Cypresses" (El Aliso 1:1–444. 1948). The cypresses extend down the north side of the mountain as well as the south, and there are a few trees in Tassajara Creek. The next grove to the north is also large and is located on Cypress Mountain. Cypress Swamp is an area of springs in the extension of this grove down Delaganna Creek, a tributary of Las Tablas Creek. There are many groves near Burnett Peak where the tributaries of Arroyo de la Cruz, San Carpoforo (Chris Flood Creek), Tobacco and Little Burnett creeks have their origins on the main ridge of the Santa Lucias. Many of these groves are small, as well as inaccessible, and I was not able to explore them before they were burned in the fire of 1960 and sprayed with 2-4-D in 1961. I am not sure how much of this area is included in Dr. Wolf's description of the "Pine Mountain Grove." There are actually many small well-defined groves and not one large one as he implies. Also the grove at the head of Chris Flood Creek could not have been included since it was virtually impossible to reach until a few years ago. There are two groves at the head of Villa Creek in Monterey County, one north and one south of Lion Den Spring. The most northerly grove in the Santa Lucia Mountains is on the small tributary of Alder Creek that joins the main stream about half a mile below the public camp ground. North of Alder Creek the serpentine formation dips down and disappears beneath the ocean at Plaskett Creek.

Some of the groves have a thick layer of leaves covering the ground, and in these groves there are few herbaceous species except along the streambeds or rock outcrops. In other groves there has been a great deal of sheet erosion and a number of species grow in crevices in the rocks and on the relatively level areas. In spite of the great diversity in appearance of the different cypress groves, the associated flora is surprisingly uniform, and one can expect to find many or all of the species listed below in any but the smallest cypress groves. Although I have not attempted a complete list of cypress forest endemics and associated northern species, I have included those which are characteristic of the majority of the groves.

PINUS SABINIANA Dougl.

P. COULTERI D. Don

DENDROMECON RIGIDA Benth.

ERIODICTYON CALIFORNICUM (H. & A.) Torr. As far south as Cypress Mountain.

QUERCUS DURATA Jepson

CEANOTHUS spp.

ARCTOSTAPHYLOS spp. Typically *A. obispoensis* Eastw.

LOMATIUM PARVIFOLIUM (H. & A.) Jepson

ZIGADENUS FREMONTII Torr.

BRODIAEA LUTEA (Lindl.) Mort. In the southern Santa Lucias, this species is not common and occurs only near springs and beside streams.

FRITILLARIA LANCEOLATA Pursh

POLYGALA CALIFORNICA Nutt.

ERIOPHYLLUM CONFERTIFLORUM (DC.) Gray var. LAXIFLORUM Gray. Occasional plants of what appears to be *E. lanatum* (Pursh) Forbes as well as hybrids with *E. confertiflorum* occur on nearby serpentine outcrops.

CHEILANTHES SILIQUOSA Maxon. Occasionally *C. californica* (Hook.) Mett. or *C. carlotta-halliae* Wagner & Gilbert also grow in the cypress groves.

CHORIZANTHE VORTREIDII Bdg. As far south as Burnett Peak. This local endemic is rare on serpentine at high altitudes in the Santa Lucias but common on sandstone, especially at lower elevations.

GALIUM HARDHAMAE Dempster. A Santa Lucia cypress forest endemic occurring as far south as Cypress Mountain.

GALIUM CALIFORNICUM H. & A. *Galium nuttallii* Gray and *G. andrewsii* Gray also occur in one cypress grove or another.

MONARDELLA PALMERI Gray. A Santa Lucia cypress forest endemic which occurs occasionally elsewhere on serpentine (Rinconada Mine east of Santa Margarita, *Hoover 6146,* and the west side of Cerro Alto). When it occurs in a cypress grove, the leaves are long, narrow and shiny. Outside the cypress forests the leaves are relatively dull and reminiscent of whatever variety of *M. villosa* Benth. grows nearby. In other characters as well, the plants appear to be intermediate. *Monardella villosa* does not grow in the cypress groves.

In addition to the species in the above list, almost every cypress grove has some species of *Carex.* In groves with much litter covering the soil, the *Carex* is generally *C. globosa* Boott, which also occurs in the nearby oak-conifer woodland. *Carex serratodens* W. Boott grows beside the permanent streams and semipermanent streams. *Carex senta* Boott occurs in Cypress Swamp. Of the other three species of *Carex,* discussed below, one is a local endemic and the other two are northern species.

Carex obispoensis Stacey, a San Luis Obispo County endemic, occurs along the intermittent streams and in low or level places along the top of the ridge in the Cuesta cypress grove and in openings in the surrounding chaparral. It also grows on a rocky east-facing slope almost throughout one of the Burnett Peak groves which has a small semipermanent stream. In the dry year of 1960, only the plants in the obviously much damper lower half of the grove flowered. It is possible that *C. obispoensis* is primarily a plant of moderately dry serpentine soils and that its occasional occurrence at low elevations in boggy spots along streams that drain cyress groves (Stenner Creek,[1] *Eastwood & Howell 2271* and Arroyo de la Cruz, *Hoover 6684, 7951*) should be considered exceptional. It has also been collected on "dry serpentine" outside of a cypress forest at Rinconada Mine (*Hoover 6115, 7208*).

Carex mendocinensis Olney has been found in three cypress groves. At Alder Creek the cypresses occur on several acres of rocky northwest slope as well as along the course of a semipermanent stream. Here *C. mendocinensis* is common, especially beside the stream. It is also common in the Chris Flood grove, where it grows both beside the intermittent streams and the permanent streams and on a northeast-facing slope that is probably covered with hidden springs since the herbaceous cover is unusually luxuriant for a cypress grove. The small swampy grove at the head of Los Burros Creek also has an abundant growth of *C. mendocinensis.* In Cypress Swamp *C. luzulina* Olney grows beside the small permanent

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[1] Stenner Creek, according to the United States Geological Survey maps, is the correct name for this creek, though on many maps it is called Steiner Creek. It is Steiner Creek on the Eastwood and Howell labels. The tributary of San Simeon Creek that has its headwaters on Cypress Mountain is called Steiner Creek.

streams that flow from the springs. I have not found *C. mendocinensis* or *C. luzulina* in the streambeds below the cypress groves.

Many of the usual streamside plants of the Santa Lucias grow in the swampy areas and beside the streams in those cypress groves that have permanent and semipermanent streams, for example, *Mimulus guttatus* DC., *Lilium pardalinum* Kell., and, at Alder Creek, *Epipactis gigantea* Dougl. In Cypress Swamp there are two northern hydrophilous species as well, *Habenaria dilatata* (Pursh) Hook. var. *leucostachys* (Lindl.) Ames and *Parnassia palustris* L. var. *californica* Gray. Both of these plants have been collected elsewhere in this region, the *Parnassia* on Santa Lucia Peak by *M. S. Clemens* in 1921, and the *Habenaria* in a swamp at Arroyo Grande, *Hoover 7338*.

Until recently most of the groves had never been thoroughly explored and it was thought that the cypresses were restricted to the dry serpentine outcrops. In reality they are most abundant on mesic, north-facing slopes where they grow in the vicinity of streams and in swampy areas produced by springs. In several places the cypresses do not occupy the total area of apparently suitable moist habitat. Neither do the associated species extend beyond the sharply delimited boundaries of the groves. It is understandable that the cypress trees may not be able to grow down the beds of streams for any distance below the serpentine to which they are usually restricted, but it is surprising that the associated species are similarly limited. As already mentioned, the two northern species of *Carex, C. mendocinensis* and *C. luzulina,* do not grow in the watercourses below the boundaries of the cypress groves. The cypress groves seem to offer these species a special ecological niche upon which their persistence depends. Although the causal relationships are not fully apparent, it seems probable that the discontinuous occurrence of the cypress groves, their usual sharp delimitation, and the restriction of the associated species to the groves depend both on the influence of the serpentinized soil, which may act by reducing competition from the neighboring chaparral and forest species, and on the obvious need of all these species for a relatively abundant water supply.

It is possible that cypress forests were formerly more extensive in the Santa Lucia Mountains. Typical cypress forest species occur in at least three areas where cypress trees do not grow. *Carex obispoensis* and *Monardella palmeri,* the latter showing evidence of integration with *M. villosa,* have been found in one or two places on serpentine south of the Cuesta cypress grove as well as on Cerro Alto north of that grove. Similarly, near the Burnett Peak cypress groves *Galium hardhamae* and *Monardella palmeri* grow in occasional chaparral openings where there are no cypresses.

Vouchers for all these cypress forest species have been deposited at the Herbarium of the California Academy of Sciences.

Mr. James Collord, geologist for the Madonna Construction Company of San Luis Obispo, described for me the geology of the Pine Mountain fault zone where most of the cypresses occur and helped me to explore the Burnett Peak and Chris Flood Creek groves.

Creston Star Route
Paso Robles, California

CALIFORNIA BOTANICAL EXPLORERS—XII

WILLIS LINN JEPSON

John Milton Bigelow

[The following account of a significant portion of Bigelow's whereabouts and itinerary as a botanical traveler in central California is as pertinent and needful today as it was when Dr. Jepson originally wrote it, pin-pointing as it does the type localities of a number of well-known and more or less widespread species originally collected by Bigelow at the annoyingly elusive "Duffield's Ranch" of the Torrey account in the Pacific Railroad Reports. The first five paragraphs have already been published (in the twice resuscitated journal "Erythea," vol. 3, No. 13, pp. 102–104, Dec., 1938), this initial portion ending with the promise "to be continued." Inasmuch as this number of "Erythea" had a very limited circulation and is not likely to be available to many readers, the entire article, from a typescript copy recently come to light among Dr. Jepson's accumulated papers, is offered herewith.—R. BACIGALUPI, Curator, Jepson Herbarium, Department of Botany, University of California, Berkeley.]

The name of Bigelow is associated with many of the early discovered plant species of California. John Milton Bigelow was born at Peru, Bennington County, Vermont, on June 23, 1804. When he was eleven years old, his family moved to Ohio where he went to the public schools and attended the Medical College of Ohio, at which institution he was graduated March 8, 1832. In November of this same year, he was married to Maria R. Miers of Lancaster, Ohio, where he began the practice of medicine. In 1850 he was appointed surgeon to the Mexican Boundary Commission. While on duty with this survey, he collected and studied the native vegetation of the boundary. His specimens formed part of the material used by John Torrey in the preparation of the Report of the Mexican Boundary Survey (1859), which was under the charge of Major W. H. Emory. Bigelow's name is frequently cited in its pages. In 1853 Dr. Bigelow accepted the position of surgeon and botanist to the expedition of the Pacific Railroad Survey under Lieutenant A. W. Whipple, which left Fort Smith, Arkansas, and proceeded along the Canadian River and across the Llano Estacado to Albuquerque. The Rio Grande was crossed on November 10, 1853 and the expedition, following down the Bill Williams Fork, crossed the Colorado River at the mouth of Williams Fork on February 28, 1854, ferried it about sixty miles above and traversed the Mohave Desert to the Cajon Pass, thence to Los Angeles and San Pedro. Here the survey of Lieutenant Whipple ended; but it was now the most favorable botanizing season in California and Dr. Bigelow in his own interest came north to San Francisco and Marin County to collect more fully the native vegetation of California. His zeal took him across the Great Valley into the Sierra Nevada where he remained until nearly June 1, 1854. He was not the first, but he was amongst the first explorers to botanize at all extensively in the Sierra Nevada. Of Bigelow's entire journey, John Torrey said that "his ample collections," made in 1853 and 1854, "were brought home in perfect order," and adds: "A number of new genera and more than sixty new species have been discovered by Dr. Bigelow, and he has added much valuable information upon many heretofore imperfectly known plants."

In the course of the years the student of California botany needs to consult and study repeatedly the pages of volume four of the Pacific Railroad Reports where, in about one hundred pages, John Torrey has given an account of the Bigelow plants supplemented by twenty-five very fine lithographic engravings. In the citation of localities for California, several extremely local place names occur which are not to be found on maps and which have been difficult to place. One of these is "Duffield's Ranch," which is important as the collecting station for a number of Bigelow plants and especially as the type locality for *Allium tribracteatum* Torr. and other plants then new to science.

To the systematic botanist whose initial or primary interest is in the living plant in its natural state, in its biology, ecological form and associates and habitat conditions, the type locality is vastly a more fruitful quest than the type specimens of early collectors, which are frequently unsatisfactory, fragmentary, or so decadent structurally as to be essentially useless. At the best the type specimen can usually do little more than enable one to make sure that a given binomial belongs to a particular unit; whereas the type locality opens up a new and living world whose potentialities may not be exhausted for years. It was for this reason, as well as for some uncertainties attaching to the identity of *Allium tribracteatum,* that I wished forty years ago to find Duffield ranch which is placed no more definitely in the text than "Sierra Nevada." The name could not be found on any available map or in any index, and constant inquiry amongst pioneers failed in like manner. Resort was then had to a stratagem. I took such dates as are given in Torrey's paper, arranged them in chronological sequence with their localities and I thus made an itinerary for Bigelow. It was soon found that the dates were not always dependable, but where the date agreed with the locality three times or more, it was used on the list. In this manner I obtained the following chronology: From April 4 to April 12, he was in Oakland and the Oakland Hills; April 17 and 18 at Point Reyes; April 20 at Corte Madera; April 25 to 27 in the Napa Valley; May 7 and 8, Stockton to Knights Ferry; May 9 at Sonora; May 10, 11, 12 at "Duffield's Ranch"; May 14, Carson's, Stanislaus River; May 14, Robinson Ferry, Stanislaus River, and

Murphy's Camp; May 15, Washington Mammoth Grove (Calaveras Grove); May 17, Mokelumne Hill; May 18, Ione Valley; May 19 and 20, Grass Valley; May 21, Nevada City and Downieville; May 23, Middle Yuba River; May 25, Marysville and Marysville Buttes.

This list made, it was a natural inference that Duffield ranch was somewhere between Sonora and the Stanislaus River or Murphy's Camp in Calaveras County. Any locality in this region was too low in altitude for the species concerned, so that the inference seemed in some way fallacious.

No systematic effort had been made to find Duffield ranch but for two decades the query had been kept in mind and used on any likely prospect or as a sort of poser to the geographically minded. Now that, in 1916, I had made a Bigelow calendar, a wider appeal was made to local historians and editors of newspapers in the foothill towns, but the effort again proved unavailing.

In 1918, my friend George James Peirce, Professor of Plant Physiology at Stanford University, was in Berkeley as Professor of Botany in the University of California Summer School. At my invitation, he joined in a week-end excursion to Sonora. We arrived in this county-seat town of Tuolumne County in mid-afternoon on the Fourth of July. It seemed that every old-timer on Sonora's High Street was, on this holiday, willing and anxious to tell us about Duffield ranch; it was out near the old Bob Finney place; it was on the Bald Mountain road; it was in this direction and that, in no case more than a few miles away. It developed at once that Duffield was a real character of the 1850's and a dead-shot. Ancient legends regarding him are still spun on the High Street. Finally we found Robert Marshall, a shrewd clear-headed "down-east" Yankee, ninety-one years old, who came to Sonora in the early 1850's, and who recalled with remarkable clearness the local events during the gold days. Said Marshall: "Yes, I knew Duffield. There is a Duffield Mine near Soulsbyville but no Duffield ranch." Then he went on to give an elaborate, particularized and colorful history of Duffield, his activities and associates. In the course of describing the personality of Duffield, he remarked that there was only one man whom Duffield feared, namely Ben Soulsby. "Was Ben Soulsby still living?" "Yes; Ben Soulsby lives in a cabin near Soulsbyville." We went to Soulsbyville, found the cabin a few miles from the village and found Ben Soulsby. When I told my errand he seated himself on a stone step in front of his cabin door. Seventy-eight years of age, he was as utterly distrustful of the stranger and as taciturn as Marshall in Sonora had been hospitable and loquacious. Little could be had from him save that there was no Duffield ranch, but that there was a Duffield mine. It was up the cañon a half-mile; the hole still there, any one could go look at it. Hereupon I played the only valuable card left me and which, it was felt, would be decisive one way or the other. It was obvious that of early events Soulby's memory was clear and sharp. So I took from under my arm a large volume which I had brought along, volume four of the Pacific Railroad Reports. I opened the book to a marked page, placed it in Soulsby's hands and pointed to "Duffield's Ranch" without a syllable of comment. Soulsby looked at the printed words a long, long time without remark. We, his visitors, sat on the ground near him and waited patiently. At length he turned to the title page and noted the date, 1856. Then he went on communing with himself. Finally, he closed the book, ran his rough hand through the enormous shock of iron-gray hair that thatched his head and said very simply and briefly: "Now I bethink myself. There *was* a Duffield ranch. It was up beyant Confidence. Duffield was up there in 1854. The Ward Pike place we call it now."

There was little difficulty finding the Ward Pike place on the Sonora Pass road at about 4800 feet altitude. It seems a plausible inference that Bigelow, coming as a traveler into Sonora, would inevitably meet so showy and ubiquitous a character of the High Street as Duffield, and that Duffield took Bigelow to his mountain ranch. At Duffield ranch, Bigelow spent three days, May 10, 11, and 12, 1854, the year corresponding with the year named by Ben Soulsby. From the ranch as a base he must have made excursions upwards, since some of the species collected by him belong at higher altitudes than Duffield ranch. In his own account of the forest trees of California, it is unmistakable that Bigelow was "high up in the mountains east of Sonora (almost in the snowy regions)" (p. 26) and he further states that he was "fifteen or twenty miles southeast of Sonora, on the headwaters of the Stanislaus and Tuolumne rivers" (p. 24), but the only practicable direction eastward from Sonora he was likely to have traveled is northeast rather than "southeast." The Ward Pike place lies on the top of the ridge between the South Fork Stanislaus River and the North Fork Tuolumne River, truly northeastward from Sonora.

Duffield ranch then, or the region immediately above it, is the type locality for the following new species or varieties collected by Bigelow: *Philadelphus lewisii* var. *parvifolius* Torr., *Potentilla tridentata* (Torr.) Greene (*Horkelia tridentata* Torr.), *Sanicula tuberosa* Torr., *Phlox occidentalis* Durand ex Torr. [today generally considered a phase of *Phlox speciosa* Pursh], and *Allium tribracteatum* Torr. In addition, some nineteen other species are listed as of "Duffield's Ranch" by Torrey. One of these, *Pinus sabiniana,* is perhaps a slip on Torrey's part, since it is not found on the Sonora Pass road at this altitude. It may be noted that Bigelow himself in his account of the forest trees does not list Duffield ranch as a locality for *Pinus sabiniana*. The other species conform altitudinally, or one or two may have been collected a little below the ranch.

Soon after the last date mentioned in the itinerary as given above, Bigelow returned to the eastern United States and reported to his commanding officer in the War Department at Washington for filing his report of the expedition which is dated [but certainly not published in]

August, 1854. This report (in Pacific Railroad Reports, Vol. 4) consists first of a botanical narrative of the expedition from Napoleon on the Mississippi River, by boat up the Arkansas River to Fort Smith, Arkansas, thence overland to Los Angeles and San Pedro (pp. 1–16) and second of a description of the forest trees of the route (pp. 17–21) with a special section on "Descriptions of Valuable or Remarkable California Forest Trees" (pp. 21–26). One of the most interesting contributions made by Bigelow to the Report is a large map giving a botanical profile in color of the forest trees from Fort Smith to San Pedro. He also collaborated with George Engelmann in the preparation of the paper entitled "Description of the Cactaceae" (pp. 27–58, pls. 1–24) in which many of the more commonly known cactus species of our desert regions were first described and named.

In his honor, Asa Gray named the genus *Bigelovia* of the Compositae, a group now covered by other names. There were also dedicated to him *Clematis bigelovii* Torr., *Aster bigelovii* Gray, and *Linosyris bigelovii* Gray of New Mexico, but our commonest cholla, *Opuntia bigelovii*, a widespread cactus of the arid districts of southern California and adjacent areas, named for him by George Engelmann, will perhaps serve most widely to keep in mind a botanical traveler who was so fortunate as to view a considerable part of California while its native vegetation was still in nearly pristine freshness.

In 1860 Dr. Bigelow made his home in Detroit where he was placed in charge of the meteorological work of the Northern and Northwestern Lakes Survey. Some years later he was appointed surgeon to the Marine Hospital in Detroit and Professor of Medical Botany and Materia Medica in the Medical College. He lived in Detroit the remainder of his life and died there July 18, 1878.

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A SUBARBORESCENT NEW ERIODICTYON (HYDROPHYLLACEAE) FROM SAN LUIS OBISPO COUNTY, CALIFORNIA

Philip V. Wells

In June of 1960, the writer encountered colonies of an extremely tall yerba santa, measuring up to thirteen feet in height, on the sandstone ridges of Indian Knob, four miles north of Pismo, San Luis Obispo County, California (fig. 1). In the characters of the inflorescence, there is a close resemblance to *Eriodictyon californicum* (H. & A.) Torr., but the strongly linear and revolute leaves and densely pubescent capsules suggest a relationship to the isolated *E. capitatum* Eastw., which possesses an inflorescence unique for the genus. The combination of characters presented by the San Luis Obispo County *Eriodictyon* clearly sets it apart from the rest of the genus. This was verified by comparison with collections at the California Academy of Sciences and the University of California, Berkeley.

Eriodictyon altissimum P. V. Wells, sp. nov. Frutex glutinosus, 2–4 m. altus; foliis linearibus, 6.0–9.0 cm. longis, 2–4 mm. latis, margine revolutis, supra glabris et glutinosis, infra albo-tomentosis; inflorescentia cymosa-paniculata, ramulis elongatis, 4.0–9.0 cm. longis, glutinosis, floribus secundis in ramulis cymosis; calycis segmentis anguste lanceolatis, 2–3 mm. longis, glabris sed ciliatis et glutinosis; corollis purpurascentibus, infundibuliformibus, 11–15 mm. longis, exteriore villosis, interiore glabris, staminibus inclusis, filamentis basi villosis; stylis purpureis, basi villosis; capsulis pubescentibus.

Tall, straggling shrub to over 4 m. high, averaging ca. 2 m., with a trunk-like main stem up to 12 cm. in basal diameter; growth habit of some individuals excurrent, with falsely whorled lateral branches; suckers freely produced from stout rootstocks, probably serving for propagation when the tops are destroyed by fire; bark of main stems smooth, grayish; branches long and slender, ascending; the branchlets glutinous; leaves alternate, with a tendency to be opposite below, sessile, narrowly linear, 6.0 –9.0 cm. long, 2–4 mm. wide, entire, strongly revolute, glabrous and somewhat glutinous above, densely white-tomentose beneath, with heavy, sweet aroma; inflorescence an open panicle of cymes; flowers on minutely bracteate ramules 1–3 mm. long, secund on the lax, glutinous branches of the inflorescence, the branches ranging from 4–9 cm. in length; sepals lance-linear, 2–3 mm. long, ciliate on the margins, otherwise glabrous but glutinous; corolla infundibuliform, 11–15 mm. long, the limb lavender and the tube pale lavender to whitish below, sparsely villous without, glabrous within; stamens unequal, the filaments villous on the basal half; styles 5–7 mm. long, lavender, sparsely hairy below; ovary ca. 2 mm. long, densely short-pubescent and glutinous; capsule

FIG. 1. *Eriodictyon altissimum,* showing excurrent growth habit present in some individuals. Summit of San Luis Range near Indian Knob, San Luis Obispo County.

glutinous-pubescent, containing numerous polyhedral seeds, the seeds ca. 0.4 mm. long, brown, longitudinally finely striate and reticulate with cross-striations.

Holotype. Sandstone ridges of Indian Knob, elevation 880 feet, four miles north of Pismo, San Luis Obispo County, California, *P. V. Wells 75,* June 30, 1960, OBI. Isotypes at CAS, GH, UC, US.

Eriodictyon altissimum is apparently confined to shallow, sandy soils derived from siliceous sandstone (San Pablo group: upper Miocene) in the eastern part of the San Luis Range at elevations of 650 to 880 feet. It was not found on Franciscan rocks (feldspathic sandstone, radiolarian chert, diabase or serpentine), nor on siliceous Monterey shale, all of which outcrop at comparable elevations in the San Luis Range. The vegetation on the siliceous sandstone to which *E. altissimum* is confined is largely chaparral interspersed with low woodlands of *Quercus agrifolia* Neé, and with one small stand of *Pinus muricata* D. Don. The chaparral matrix is dominated by *Arctostaphylos pilosula* Jeps. & Wies., with associated chamise, toyon, *Ceanothus impressus* Trel., *C. cuneatus* var. *ramulosus* Greene, and the subligneous *Salvia mellifera* Greene. (*Pinus muricata* and *Ceanothus impressus* are conspicuous in the Lompoc endemism area which harbors the linear-leaved *Eriodictyon capitatum*.)

Eriodictyon altissimum, like other members of the genus, has a weedy or pioneer ecology. It is aggressive on roadsides, with numerous young plants invading such disturbed sites. The large production of minute seeds averaging 0.2 mg. in weight provides the necessary mobility. It is apparently a rapidly growing, short-lived shrub, often overtopping by five feet or more the even-statured young manzanitas dating from the last chaparral fire. Thrifty specimens with luxuriant foliage rarely occur in the chaparral, being mainly confined to road sides. By far the greatest number of individuals observed had a senescent appearance, open and straggling with sparse foliage confined to the tips of branches (fig. 1).

Since this *Eriodictyon* combines characters of *E. californicum* and *E. capitatum* (or less possibly *E. angustifolium* Nutt.), one might suppose it to be of recent hybrid origin. However, none of these species occurs in the San Luis Range; in fact, there are no previous records of linear-leaved yerba santas from San Luis Obispo County (R. F. Hoover, unpublished checklist). If hybridization should prove to be involved, the writer sees no reason why a large, apparently stable population evolved in this manner should be given the nomenclatural treatment ordinarily accorded to hybrids of sporadic and ephemeral character.

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A NEW SPECIES OF QUERCUS FROM BAJA CALIFORNIA, MEXICO

Cornelius H. Muller

In a report upon his 1885 collection of the plants of Cedros Island, Baja California, Mexico, Greene (1888) made the following entry:

"66. Quercus. ________. A merely shrubby species of the White Oak series; leaves small, spinose-toothed and persistent; midway up the cañons." Greene's collections (with Geo. W. Dunn) were made in several canyons located on the northeast side of the island. Presumably a specimen of the oak is preserved in his herbarium. In 1922 G. Dallas Hanna collected the same oak at the "north end" of Cedros Island. His specimen is preserved in the herbarium of the California Academy of Sciences.

The plant first came to my notice in the form of a small flowering collection made on the island by A. L. Haines and G. O. Hale in 1939 and submitted to me through the kindness of Dr. Mildred Mathias from the herbarium of the University of California at Los Angeles. Subsequent inquiry concerning additional material brought to light two collections on the mainland in the vicinity of San Vicente some 200 air miles northward from Cedros Island, one near Rancho San Antonio del Mar and the second south of San Vicente. This latter collection was mentioned by Epling and Robinson (1940) under the name, *Quercus dumosa* Nutt.

In February, 1960, I visited the above two mainland localities as well as a stand in Cañon del Río San Ysidro where there is also a hitherto unreported grove of *Pinus muricata.* I am indebted to Mr. Richard Broder for aid in the field on this occasion. In June, 1960, I spent four days in the mountains in the southern half of Cedros Island, principally about Cerro Cedros, which reaches an elevation of 3950 feet.[1] In August, 1960, I encountered typical stands of the species at 3000 feet elevation on the western foot slopes of the Sierra San Pedro Mártir. This locality is characterized by a dry chaparral dominated by *Adenostema fasciculatum* with *A. sparsifolium* and *Arctostaphylos* sp. About the same time Dr. John M. Tucker kindly called to my attention a collection made in 1956 by Mr. John Thomas Howell in San Carlos Canyon above Agua Caliente de San Carlos (the village southeast of Ensenada—not the race track).

Haines and Hale had reported the oak to occur at 1750 feet elevation (according well with Greene's "midway up the cañons"); I found the main body of the Cedros Island population occurring between elevations of 3300 and 3940 feet on north- and west-facing slopes. Here it is associated with *Juniperus californica, Arctostaphylos bicolor, Rhus laurina,* and *Eriogonum fasciculatum.* Adjacent south-facing slopes are dominated by *Pachycormus discolor* var. *veatchiana, Franseria* spp., and only scattered *Juniperus californica.* Very distinct lines separate the mesic and desert slopes. The San Vicente localities, on the other hand, all lie below 300 feet and are usually characterized by *Pinus muricata,* although at the San Antonio del Mar locality *Pinus* is lacking and the community is represented only by *Ribes viburnifolium,* another common associate of the oak.

In spite of a long history, this overlooked species is still sketchily known as to its geographic range. It is safe to assume that far fewer than half its localities are known and that still further unexpected extensions of range will eventually be discovered. It may be found with or without *Pinus muricata* and the common associates of that species, but on the mainland pine groves constitute promising indicators of the oak.

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[1] In this undertaking I incurred extensive obligations for aid without which success would have been impossible: to the U. S. Fish and Wildlife Service for transportation aboard the M. S. *Black Douglas*; to the crew of the *Black Douglas* for unusual courtesy; to Sr. Francisco Amaya, manager of the *Atun-Mex* fish cannery on Cedros Island, for most helpful cooperation and facilities; to Sr. Eduardo Hernandez-Bello of the Mexican fisheries laboratory at Mazatlán for smoothing the way with officials; and especially to Mr. Campbell Grant, my good companion on this and other ventures.

An examination of sterile and flowering materials early suggested that the Cedros oak was not a "white oak" at all but rather was a member of the series *Chrysolepidae* in the subgenus *Protobalanus,* the "intermediate oaks" in which, except for its spinose-toothed leaves, it strongly suggested *Q. vaccinifolia* Kell. An examination of fallen cups and acorns in the San Vicente localities and, more recently, of attached fruit on Cedros Island confirmed this opinion. The presence of tomentum on the inner surface of the acorn shell and the characteristically swollen and puberulent bases of the cup scales are distinctly characters of the series *Chrysolepidae* of *Protobalanus.*

In spite of the superficial resemblance of this species to *Q. vaccinifolia,* it is amply distinct in several basic but scarcely obvious characters. Its position in the subgenus *Protobalanus* is actually fully as anomalous as that of the four previously known species of that group. Each species seems to be a relic and the end point of its own ancient line within the subgenus.

Quercus cedrosensis sp. nov. Arbor parva vel frutex; ramuli 1 mm. diametro, sparse vel dense stellato-pubescentes; folia sempervirentia, coriacea, 6–20 (35) mm. longa, 4–14 (20) mm. lata, integra vel dentata, dentis spinosis, ovata vel lanceolata, acuminata vel obtusata, basi rotundata vel cordata, supra sparse pubescentia vel glabrata, nitida, subtus glaucescentia; venis utrinque 4–8, haud prominentibus; petioli 1.5–2.5 mm. longi; fructus biennis, brevipedunculatus; cupula 5–6 mm. alta, 7–12 mm. lata; glans 15–22 mm. longa, 6–10 mm. lata, angusto-ovoidea vel fusiformis, ad basim tantum cincta.

Small trees to 15 ft. tall with a trunk 2 dm. in diameter with flaky gray bark or, on windswept sites, the trunk decumbent forming a large shrub 2 or 3 m. high and 6 or 8 m. broad, or the shrub quite prostrate and forming a mat as little as 2 dm. high, the stumps sprouting vigorously following fire and prostrate branches rooting freely or the underground parts rhizomatous; twigs about 1 mm. thick, the internodes very short, smooth, brown becoming dark gray, sparsely or densely pubescent with short stellate hairs which persist into the second year; buds about 1 mm. long, broadly ovoid or subrotund, light brown, sparsely pubescent; stipules

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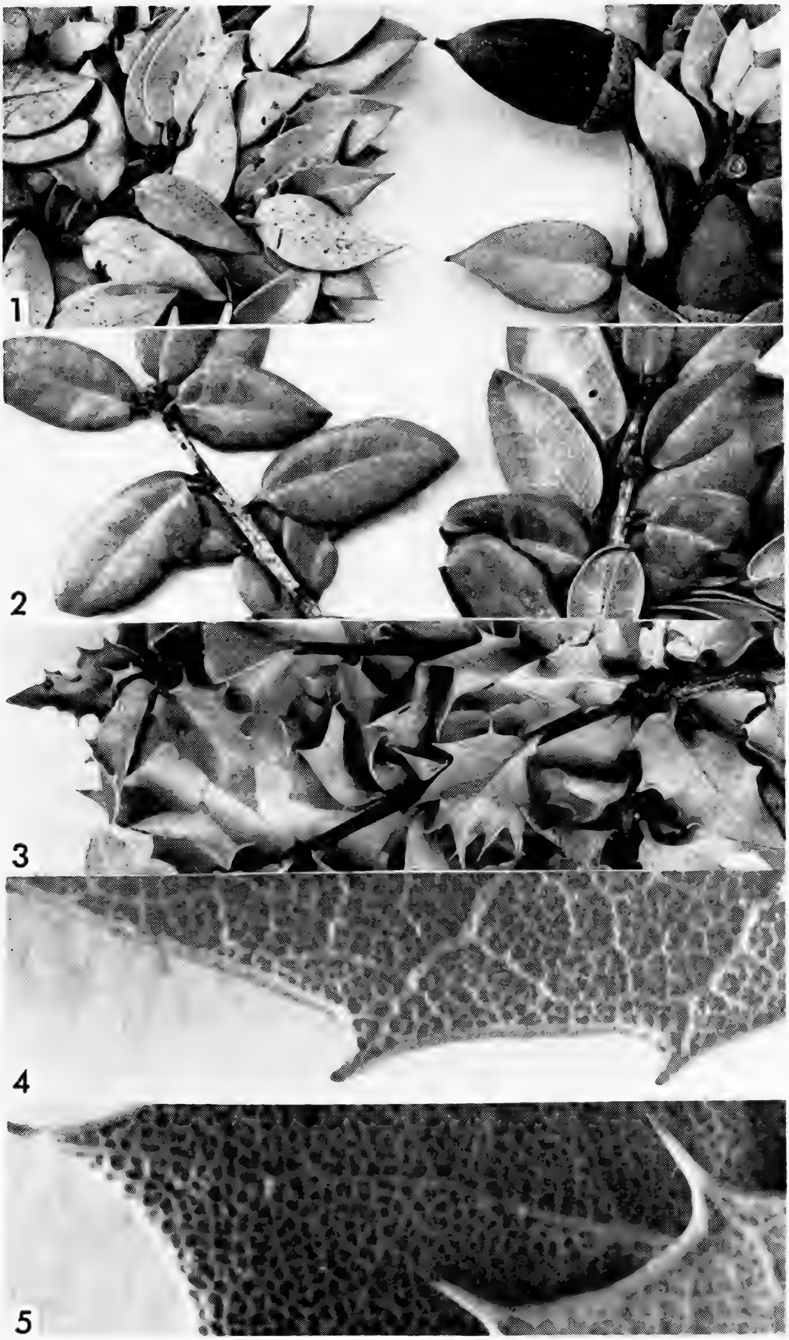
Explanation of Figures 1–5

Figs. 1–3, 5. *Quercus cedrosensis*: 1, The type collection from Cedros Island, *Muller 10775* (× 1.4); 2, a common leaf form from near San Vicente on the mainland, *Muller 10724* (× 1.4); 3, a typical stump sprout in the Cedros Island population, *Muller 10777* (× 1.4); 5, a typically toothed specimen from Cedros Island, *Muller 10772* (× 10)—note the extreme elongation of the spinescent teeth and the breadth of the sclerenchymatous sheaths of the veinlets, particularly on the lower surface, which almost occlude the chlorenchymatous alveolae.

Fig. 4. *Quercus vaccinifolia*: A typically toothed specimen from Siskiyou County, California, *Muller 9667* (× 10)—in this lower surface view note the very short tips of the teeth and the moderately sclerenchymatous veinlets bordering large chlorenchymatous alveolae.



FIGS. 1–3, 5. *Quercus cedrosensis*. FIG. 4. *Q. vaccinifolia*.

2 to 3 mm. long, ligulate-spathulate, the apical end quite thin, persistent the second year; leaves evergreen, thick and chartaceous, persisting 2 or 3 seasons, densely crowded on the short twigs, 6 to 20 (35) mm. long, 4 to 14 (20) mm. broad, flat or sometimes distinctly concave beneath, entire or irregularly few-toothed or 6- to 8-toothed on each side, the teeth elongate and spinescent (consisting of 1 to 1.5 mm. of sclerenchymatous tissue extending beyond the chlorenchyma), the blade ovate or lanceolate, sometimes oblong or elliptic to subrotund, basally rounded or sometimes cordate, apically acute or sometimes broadly rounded, characteristically spinescent-tipped or the spine rarely lacking, upper surface glabrous or very sparsely stellate-pubescent at the base of the midrib, glossy green, lower surface glabrous or the midrib minutely strigose, glaucous and waxy, marked by white dots (juvenile leaves sparsely pubescent with stellate and simple hairs, especially on the upper surface about the midrib, the blade heavily anthocyanous on the upper surface, the lower surface green); veins 4 to 8 on each side, very inconspicuous or slightly raised on the lower surface, both veins and reticulum highly sclerenchymatous and white, almost eclipsing the chlorenchymatous alveolae (the diameter of each green area little greater than the width of the adjacent white veinlet); petioles about 1.5 to 2.5 mm. long, pruinose, glabrous or sparsely pubescent with small stellate hairs; staminate catkins about 10 to 15 mm. long, sparsely flowered, the rachis somewhat stellate-pubescent, the filaments inserted in a tuft of white pubescence on the receptacle and scarcely longer than the 4 to 8 glabrous red anthers, these barely exserted from the ciliate red perianth; pistillate catkins 4 to 8 mm. long, 1- to 3- flowered on a sparsely pubescent rachis; fruit biennial, maturing in July, simultaneously with or following the next flowering, solitary or paired, subsessile or on a peduncle to 10 mm. long; cups 7 to 12 mm. broad, 5 to 6 mm. high, cup-shaped, the scales very broad and thickened basally, appearing as though fused, green and densely silver-puberulent, the thin brown apices elongate, appressed and ciliate; acorns 15 to 22 mm. long, 6 to 10 mm. broad, very narrowly ovoid to fusiform, acute at apex, glabrous and brown except the silvery puberulent apical quarter, less than one-quarter enclosed at the base.

Range. Baja California, Mexico, on Cedros Island and from the vicinity of San Vicente inland and northward on the peninsula.

Specimens examined: MEXICO, BAJA CALIFORNIA: Isla Cedros: north end, August 9, 1922, G. D. Hanna s.n. (CAS, SBC-MU[2]); north slope of Cerros [Cedros] Peak, elev. 1750 ft., March 9, 1939, *A. L. Haines & G. O. Hale 969* (UCLA, SBC-MU); elev. 1700 ft., *Haines & Hale 970* (SBC-MU); in chaparral on north slope of Manzanita Peak [north end of island], elev. 2700 ft., February 6, 1939, *Haines & Hale 935* (SBC-MU); "Cerros Mountains," elev. 3900 ft., February 15, 1939, *Haines & Hale s.n.* (SBC-MU); head of Cañon de Calabasas, southwest slopes of Cerro

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[2] The abbreviations of herbaria are those of Lanjouw and Stafleu (1959); SBC-MU refers to my private collection of *Quercus* on deposit at the University of California, Santa Barbara.

Cedros, ca. 3600 ft. elev., June 16, 1960, *C. H. Muller 10771–10777* (SBC-MU) [of which no. 10775 is the type (SBC herbarium no. 8766, the holotype, and widely distributed)]; June 17, 1960, *Muller 10799–10803* (SBC-MU); heavily wooded north-facing canyon wall near waterway on northwest slope of Cerro Cedros, ca. 2900 ft. elev., June 17, 1960, *Muller 10791–10794* (SBC-MU); northwest slope of summit of Cerro Cedros ca. 3940 ft. elev., June 19, 1960, *Muller 10817–10818* (SBC-MU). Municipio de Ensenada: Cañon San Carlos above Agua Caliente, March 18, 1956, *J. T. Howell 31102* (DAV); south side of San Antonio Canyon about 2 miles inland from San Antonio del Mar (Johnson's Ranch), September 8, 1930, *I. L. Wiggins & D. Demaree 4762* (DS, SBC-MU); Pine canyon 6 miles south of San Vicente, April 11, 1936, *C. Epling & W. Stewart s.n.* (UCLA); northwest-facing slope of Cerro Colorado in Cañon de Río San Ysidro, 6.6 miles southwest of San Vicente, in and above grove of *Pinus muricata,* ca. 300 ft. elev., February 14, 1960, *Muller 10723–10727* (SBC-MU); near arroyos on north-facing slope in Cañon de los Pinitos, 8 miles south of San Vicente (the *Epling* and *Stewart* locality for which this is a mileage correction), ca. 250 ft. elev., February 15, 1960, *Muller 10729–10732* (SBC-MU); southeast side of Cañon San Antonio, 2.7 miles north-northeast of Rancho San Antonio del Mar (Johnson's Ranch) on road to Rancho Cerro Blanco (Rancho Guzman) and San Vicente (the *Wiggins* and *Demaree* locality for which this is a mileage correction), February 15, 1960, *Muller 10733–10736* (SBC-MU); 4 miles below Socorro, 7 miles above San José (Meling Ranch) on western slope of Sierra San Pedro Mártir, elev. 3000 ft., August 16, 1960, *Muller 10888–10890* (SBC-MU); August 22, 12960, *Muller 10937* (SBC-MU).

Quercus cedrosensis is apparently rather remotely related to *Q. vaccinifolia,* a species of high elevations in the Sierra Nevada of California and descending below 5000 feet only in northern California and Oregon. The Mexican species is distinguished from *Q. vaccinifolia* by its tree habit (although it matures as a shrub in windswept situations and elsewhere on the mainland), its generally maritime and frequently low elevation distribution, the heavily sclerenchymatous nature of its leaf reticulum, its spinescent teeth whenever teeth occur, and its elongate, acute acorns. Further, the brevity of its internodes produces a marked crowding of the leaves which is not approached by *Q. vaccinifolia* and the uniform occurrence of anthocyanin in juvenile leaves is totally lacking in that species. Despite this rather lengthy list of significant differences, the two species are superficially quite similar and might, in the instance of a few specimens, prove difficult to distinguish without intimate acquaintance.

The more characteristic populations of *Q. cedrosensis* are found on insular and inland sites of relatively high elevation (about 3000 feet); the less typical occur on the mainland coast at low elevation. In general, the broader leaf forms with more rounded apices and less frequently spinescent teeth are more common in the coastal San Vicente populations of *Q. cedrosensis* than in the insular and inland populations, suggesting that some low degree of introgression of the San Vicente populations is being reflected. It is impossible at this time to demonstrate the source of such an influence. The upper levels of the Sierra San Pedro Mártir have been searched diligently for *Q. vaccinifolia* with the view of explaining some of the polymorphy of *Q. cedrosensis* about San Vicente. In addition to finding *Q. cedrosensis* at 3000 feet, three additional members of the

Chrysolepidae were encountered as follows: *Q. palmeri* Engelm. at 2800 to 4000 feet. *Q. chrysolepis* Liebm. at 5500 to 7500 feet, and an anomalous entity suggesting *Q. chrysolepis* at 7000 to 9650 feet. With the possible exception of *Q. chrysolepis,* these San Pedro Mártir species would not be expected to have contributed the aberrations of the San Vicente populations, and the presence in the San Pedro Mártir of typical *Q. cedrosensis* makes even this extremely unlikely.

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PARASITISM IN PEDICULARIS [1]

ELIZABETH F. SPRAGUE

The parasite-host relationship for many European species of *Pedicularis* has been well-documented by Wettstein (1891), Boeshore (1920), Hayek and Hegi (1918), and others. Such parasitism accounts for the difficulty in culture noted by such workers as Don (1838) and Tsoong (1955), although a few species have been cultivated and a few are sold for ornamental value. Tsoong (*loc. cit.*) states that *P. fletcheriana* Tsoong "may be easily raised from seed" and that at Perthshire, England, it established itself and freely reproduced. This indicates that at least some species under gven conditions may be saprophytic, mycorrhizal, or completely autotrophic. Sperlich (1902) found some species of *Pedicularis* to be both parasitic and saprophytic, with haustoria of the same plant attached to both dead organic matter and living roots. Certainly many of the meadow-dwelling species are quite opportunistic with regard to available host plants. In Europe, *P. sylvatica* L., and, in America, *P. canadensis* L. and *P. lanceolata* Michx. are regularly sold and cultivated without apparent hosts. They probably thrive as saprophytes

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[1] This paper is adapted from a portion of a doctoral dissertation prepared at the Rancho Santa Ana Botanic Garden and the Claremont University College, Claremont, California. I wish to acknowledge the assistance of Doctors Verne Grant, Sherwin Carlquist, and Philip A. Munz. The illustrations were prepared with the assistance of Messrs. William Klein and C. Dodson. The research was partially financed by two grants from the Claremont University College, Claremont, California, and a fellowship from the Southern Fellowships Fund, Chapel Hill, North Carolina. A grant from the University Center, Richmond, Virginia, assisted with typing and photographic expenses.

because a soil rich in humus is required, although even then they may be difficult to maintain. Attempts to grow thirteen plants of *P. canadensis* at Rancho Santa Ana Botanic Garden, Claremont, California, were not successful either in the greenhouse or in deep humus under *Quercus agrifolia* Neé. Only four to six small leaves per plant were produced, and only five plants persisted to the second year.

Attention was focused on the parasitic nature of seven California species when an attempt was made to cultivate them for experimental purposes. Plants of *Pedicularis densiflora, P. semibarbata, P. groenlandica, P. attollens,* and *P. dudleyi* were transplanted to clay pots and grown in the glasshouse at Rancho Santa Ana Botanic Garden, Claremont, California. None bloomed and even those which were accompanied by associated plants produced only a very few small leaves the second season. A single plant of *P. dudleyi* was grown successfully for the two-year period. Its native habitat, the redwood forest, was probably more successfully simulated under greenhouse conditions.

No species of *Pedicularis* is recorded as requiring exact host specificity even as to genus, but some do "show obvious preference for definite species" (Hayek and Hegi, 1918, page 112, the quotation a translation from the German). The majority of European species are meadow-dwelling and hence the hosts listed are various grasses, sedges and willows; however, Hayek and Hegi note that *P. recutita* L. is found usually on *Deschampsia caespitosa* (L.) Beauv. and *Pedicularis verticillata* L. on *Sesleria caerulaea* Scop. For the California species examined in this study, field observation and laboratory verification indicated the host relationships shown in Table 1. The alpine and meadow species of the Sierra Nevada, *Pedicularis attollens, P. groenlandica* and *P. crenulata,* show typical facultative association with various meadow plants. A fourth Sierran species, *P. racemosa*, grows in deep humus associated with *Abies concolor* and *Pinus monticola*; no haustorial connections were identified. *Pedicularis dudleyi* is associated with such redwood-forest understory plants as *Vaccinium ovatum* and *Lithocarpus densiflora*; roots were not observed.

However facultative the parasite-host relationship may appear to be in most species, observations on *Pedicularis densiflora* and *P. semibarbata* show restrictions unlike those reported for other species. These two species parasitize principally roots of trees or woody shrubs. In addition, there is evidence that the local populations of *P. densiflora* are physiologically distinct. In southern California, *P. densiflora* is associated primarily with *Adenostoma fasciculatum;* in the Santa Lucia Mountains, some populations are associated with *Pinus coulteri* and *Arbutus menziesii,* others with *Adenostoma* and *Arctostaphylos;* in the San Francisco area, *Arbutus menziesii* and *Quercus kelloggii* are the conspicuous hosts except on the top of Mount Diablo, where *Pedicularis* grows in a pure stand of *Adenostoma*. In the two areas on Mount Diablo and in the

TABLE 1. HOSTS AT VARIOUS LOCALITIES OF OBSERVATION FOR FIVE SPECIES OF PEDICULARIS[1]

(Probable host—P. Confirmed host—C.)

PEDICULARIS SPECIES	LOCALITY	HOST
P. densiflora subsp. *densiflora* Benth.	Del Mar mesa, San Diego County	(C) *Adenostoma fasciculatum* H. & A. (P) *Arctostaphylos glandulosa* var. *crassifolia* Jepson
	Cobal Canyon, San Gabriel Mountains, Los Angeles County	(C) *Adenostoma fasciculatum*
	Topanga Canyon, Santa Monica Mountains, Los Angeles County	(C) *Adenostoma fasciculatum*
	Refugio Canyon burn, San Marcos Pass, Santa Barbara County	(C) *Adenostoma fasciculatum* (P) *Arctostaphylos glandulosa* Eastw.
	Klau Mine on serpentine, Adelaide, San Luis Obispo County	(P) *Adenostoma fasciculatum*
	Marquart Ranch, Cambria-Adelaide Road, Santa Lucia Range, San Luis Obispo County	(P) *Arbutus menziesii* Pursh. (?) *Pinus coulteri* Don.
	7X Ranch pass, on serpentine, Santa Rita Canyon, Santa Lucia Range, San Luis Obispo County	(C) *Adenostoma fasciculatum* (?) *Quercus dumosa* Nutt. (?) *Arctostaphylos* sp. (?) *Rhus diversiloba* T. & G. (?) *Diplacus puniceus* Nutt.
	La Honda, Santa Cruz Mountains, San Mateo County	(P) *Arbutus menziesii* (P) *Rhus diversiloba* (P) *Diplacus aurantiacus* Jepson
	Phoenix Lake, Marin County	(P) *Arbutus menziesii* (P) *Quercus kelloggii* Newb.
	Mount Diablo, Toyon Road, Rocky Point, Contra Costa County	(C) *Adenostoma fasciculatum* (P) *Arbutus menziesii* (P) *Quercus kelloggii* (P) *Pinus sabiniana* Dougl. (P) *Rhus diversiloba*
	Mount Diablo, below Rocky Point, Contra Costa County	(P) *Ceanothus* sp.
	Jackson County, Oregon[2]	(P) *Arbutus menziesii*
P. densiflora subsp. *aurantiaca* (Benth.) E. F. Sprague	Lake Almanor, Plumas County	(C) *Pinus ponderosa* Dougl.
	Butte Meadows, Butte County	(P) *Pinus jeffreyi* Grev. & Balf. (P) *Abies concolor* Lindl. & Gord.
	Near Viola, Shasta County	(?) *Pinus ponderosa*
	Near Mineral, Tehama County	(?) *Pinus ponderosa*

Table 1, continued.

Pedicularis Species	Locality	Host
P. attollens Gray	Tioga Pass, Mono County	(P) *Phleum alpinum* L.
	Slate Creek, Middle Ridge, Mono County	(C) *Carex heteroneura* W. Boott.
	Slate Creek, Timberline Station, Mono County	(C) *Carex heteroneura*
	Echo Pass (Phillips and one mile north), El Dorado County	(C) *Trifolium monanthum* Gray (P) *Phleum alpinum*
	Fallen Leaf Meadows, El Dorado County	(P) *Carex* sp.
P. groenlandica Retz.	Tioga Pass and Tioga Lake, Mono County	(C) *Carex helleri* Mkze. (C) *Deschampsia caespitosa* (P) *Carex fissuricola* Mkze.
	Slate Ridge, Middle Ridge, Mono County	(P) *Deschampsia caespitosa*
	Slate Creek, Timberline Station, Mono County	(C) *Poa* sp.
	Sonora Pass, Tuolumne County	(P) *Poa* sp.
	Norden, Placer County	(P) *Carex* sp.
P. crenulata Benth.	Convict Creek, Mono County	(C) *Deschampsia* sp. (C) *Trifolium monanthum* (P) *Poa* sp.
P. dudleyi Elmer	Portola State Park, Santa Cruz County	(P) *Vaccinium ovatum* Pursh (P) *Lithocarpus densiflora* (H. & A.) Rehd. (P) *Ceanothus thyrsiflorus* Esch.
P. racemosa Dougl.	Rainbow Tavern, Highway 40, Placer County	(P) *Abies concolor* (?) *Pinus monticola* Don.
P. semibarbata Gray	Above Lake Arrowhead, San Bernardino Mountains San Bernardino County	(C) *Pinus ponderosa*
	Mount San Gorgonio, at foot of trail to peak, San Bernardino County	(C) *Pinus ponderosa*
	Wrightwood, San Gabriel Mountains, San Bernardino County	(C) *Pinus ponderosa* (?) *Poa scabrella* (Thurb.) Benth.
	Mount Pinos, Kern County	(C) *Pinus ponderosa*
	Echo Lake, Eldorado County	(C) *Arctostaphylos patula* Greene
	Norden, Placer County	(?) *Abies concolor*

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[1] All localities are from California except one, as stated, from Oregon.

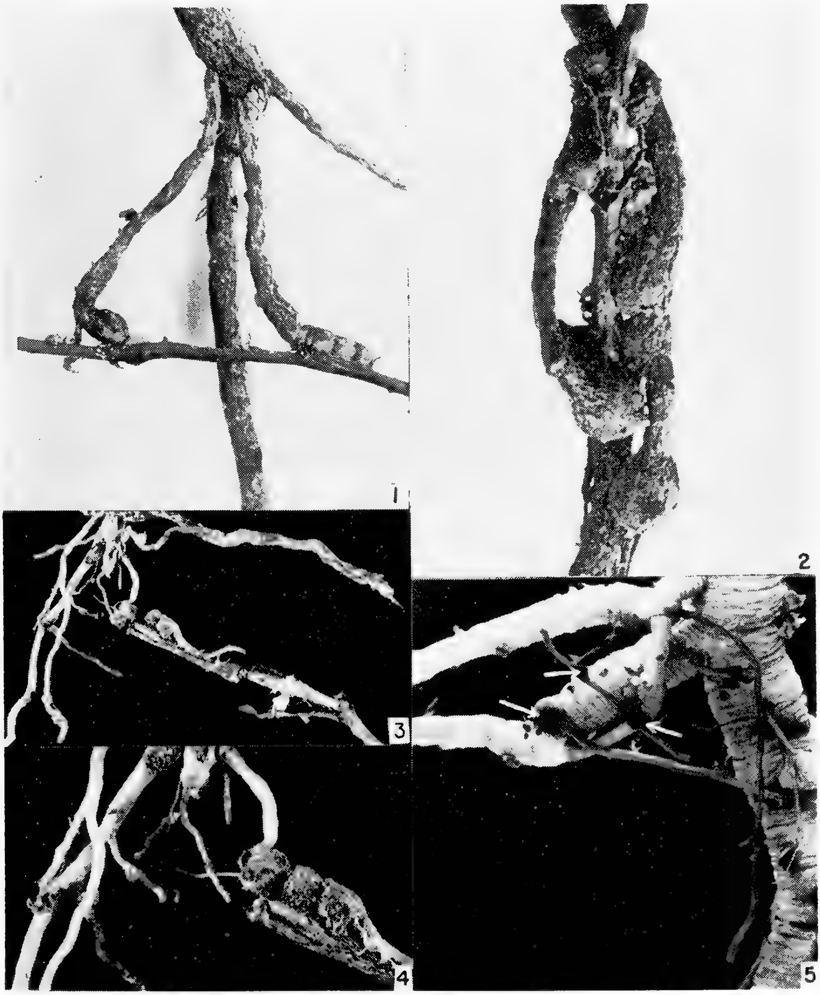
[2] *Hitchcock 64988,* June, 1931 (RSA).

Santa Lucia Mountains, where two distinct populations associated with different hosts were observed within potential breeding range, the plants in each area appeared distinctive, although the difference could not be defined. In addition, *Pedicularis densiflora* subsp. *aurantiaca* seemed to be very nearly host specific; at least, haustoria were never found on roots of species other than *Pinus ponderosa*. *Pedicularis semibarbata,* likewise, was almost exclusively on *Pinus ponderosa;* at Echo Lake, El Dorado County, in an old burn, the nearest yellow pine was 80 feet away, but the *Pedicularis* was attached to its far-reaching roots.

Pedicularis densiflora and *P. semibarbata* have undergone an extreme divergence from a habitat of moist meadows and cool mountains such as that most species occupy to an almost arid habitat. The water requirements of such species must be critical. Under such conditions, woody shrubs and trees would provide both the most adequate supply throughout the growing season and an adjacent perennial root which could be annually tapped.

In addition to these close vascular plant associations, there seems to be some evidence that under more favorable climatic conditions certain species may be largely saprophytic or mycorrhizal rather than parasitic. On plants of *P. densiflora* at Phoenix Lake, Marin County, where humus and climate provide more continuously available moisture than in many areas within their range, very few small haustoria and no actual connections with adjacent plants were observed on six uprooted individuals. In a low drainage area near Viola, Shasta County, no haustoria were observed on *P. densiflora* subsp. *aurantiaca*. In both places, abundant mycelia in the rhizosphere suggested that mycorrhizae many function. Mycorrhizae may be important where species are largely saprophytic, also. The only material examined microscopically was taken from southern populations and showed no evidence of fungal elements.

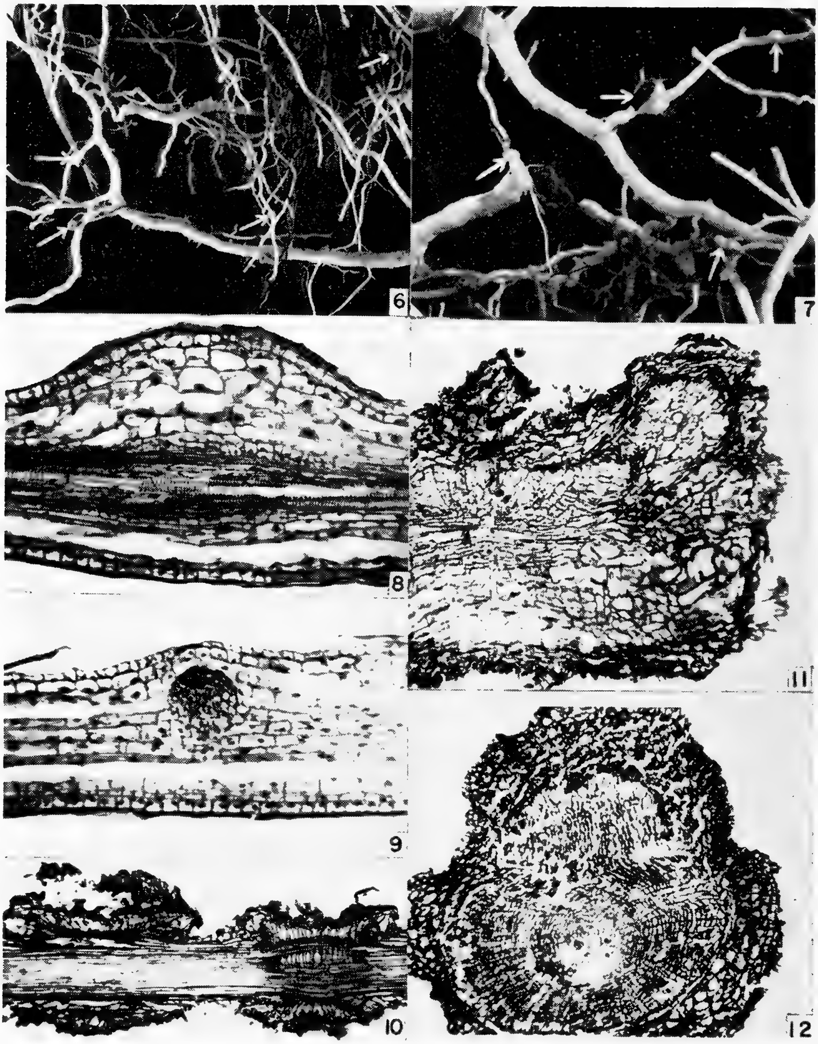
It was generally agreed among earlier investigators that members of the tribe to which *Pedicularis* belongs (Euphrasieae of Pennell, 1935; Rhinantheae of Wettstein, 1891) "take much from the earth" (Pitra, 1861, page 66, the quotation a translation from the German) and little from their hosts. Kerner (1895) observed the close contact of the epidermal cells with the humus. Hayek and Hegi (1918) reported that some species take organic materials to the detriment of the host. The importance of the host to the parasite is evidently due to a "disproportion between the parasite's water requirement and powers of the root to satisfy them" (Skene, 1924). Kostytschew (1922) showed that the cut shoots of *Euphrasia* absorbed water two times as fast, and those of *Melampyrum* ten times as fast, as the uncut shoots absorbed through their own roots. A similar distinction was found in the water absorption capacities of cut versus uncut shoots in *Pedicularis densiflora, P. semibarbata,* and *P. groenlandica*. According to Tubeuf (1923, page 564, referring to unpublished work of Senn and Hagler), *Euphrasia stricta*



FIGS. 1–5. 1, 2, haustoria of *Pedicularis densiflora* on *Adenostoma fasciculatum*, Del Mar, San Diego County; 3–5, haustoria of *Pedicularis semibarbata* on *Pinus ponderosa*: 3, Wrightwood, San Bernardino County; 4, 5, Mount Pinos, Kern County (note wrinkling of the large contractile root). (Fig. 1, × ⅝; 2, × ⅝; 3, × ½; 4, × 2; 5, × ½)

Host. and *Pedicularis sylvatica* exhibit osmotic pressures significantly higher than those of their hosts. Although the loss of water to the parasite must put a considerable strain upon the absorbing system of the host, there are few references in the literature to any deleterious effects upon the host.

The nature of the haustorium was discussed and illustrated by Wettstein (1891), who considered it a reduced lateral root produced in the



FIGS. 6–12. 6, 7, haustoria of *Pedicularis attollens* on *Poa* sp.; 8, median section through haustorium of *Pedicularis semibarbata* on *Pinus ponderosa*; 9, section through haustorial primordium of *Pedicularis attollens*; 10, longitudinal section of old haustorial connections of *Pedicularis attollens* on *Poa* sp.; 11, section of haustorium of *Pedicularis semibarbata* on *Pinus ponderosa*; 12, section of haustorium of *Pedicularis densiflora* on *Adenostoma fasciculatum*. (Fig. 6, × ½; 7, × 1½; 8, × 17; 9, × 25; 10, × 22; 11, × 15; 12, × 15.)

spring. Assimilation from the host continues through the summer, then the haustorial connection weakens. With resorption of the organic union with the host (fig. 10), the haustorium serves as a storage organ. According to Maybrook (1917), Leclerc du Sablon studied the haustoria in

1886 and concluded that they are exogenous in origin in both *Melampyrum* and *Pedicularis,* arising from peripheral parenchyma which is stimulated by contact with the host to multiply and by ordinary elongation penetrate the host, destroying the forepart and perforating the tissues by chemical absorption. Maybrook's work on *P. vulgaris* Tournef. led him to agree with these findings. The position of haustoria on rootlets of *P. groenlandica* and *P. attollens* (figs. 6, 7) would indicate that contact with the host stimulates production of haustoria. The present observations, however, agree with those of Wettstein (*op. cit.*), namely, that the haustoria are modified branch roots, endogenous in origin, and usually annual, as indeed they would have to be considering the contractile nature of the principal fleshy root system. However, observations on the very large haustoria of *P. densiflora* indicated they were the result of two or more years' growth.

Haustoria on all the species have a similar appearance; they are pale, fleshy lumps, usually occurring on the smaller branch roots. They vary in size with the species, with lesser variation between individuals of a given species. Large connections over 1 cm. in diameter of *P. densiflora* on *Adenostoma* (figs. 1, 2) are not frequent; they were found close to the "trunks" of the host and in the drier localities (Topanga Canyon and Del Mar mesa, table 1). The largest haustoria of *Pedicularis densiflora* subsp. *aurantiaca* on *Pinus* were 7 mm. in diameter. The haustoria of *Pedicularis semibarbata* (figs. 3–5, 11) were mostly small in comparison, but three of 4, 5, and 6 mm. were measured. Most haustoria observed on other species were very small, 1 to 3 mm. or less (figs. 6, 7), but even these small ones enclosed a large portion of the rootlets to which they were attached.

In transection the mature haustorium exhibits an outer zone of thick-walled tissue, lacunar collenchyma, then a wide cylinder of thick-walled parenchyma filled with starch and other material. The vascular cylinder consists of a comparatively wide outer phloem band and an inner core of protoxylem and metaxylem tracheids and vessels, together with considerable xylem parenchyma (figs. 8–12). A mass of short vessel elements arranged randomly intermingle with those of the host (figs. 11, 12), so that a most intimate and effective contact is made.

Sperlich (1902), in his examination of *Pedicularis* and related genera, frequently found tracheids wanting when the haustoria were saprophytic. He also identified storage products in addition to starch, such as albuminoid crystals, amylodextrin, phosphoric acid and nitrates, varying with the species and seasons. Examination of the present species under consideration showed starch and also large quantities of other products which had the appearance of albuminous material.

How early the haustorial attachment must be made probably depends on the vigor of the seedling as well as on the amount of soil moisture available. We do not know whether annual species are more or less dependent upon host plants than perennials are. Neither Prain (1891), who listed fourteen annual species in India, nor others have commented on this. The fibrous roots of *P. groenlandica* and *P. attollens* appear to have a greater number of haustoria than other California species observed; this may reflect a specific need for more food and water (although the former often grows in running water) from the host plant, or it may be that the smaller haustoria are less effective than the larger ones (e.g., those of *P. densiflora*). Also, this greater number may be an artifact of preparation; one can wash out the mass of *P. groenlandica* rootlets in a piece of sod more easily than one can dig extensive areas in the sun-baked hardpan of a chaparral-covered slope to obtain the entire root system of *P. densiflora.*

Seeds of *P. densiflora, P. semibarbata, P. groenlandica,* and *P. attollens* were germinated in loam. The seedlings were transplanted to humus, or in the case of *P. densiflora* and *P. groenlandica,* to pots containing appropriate host plants. None of these became established nor did the roots develop macroscopic haustoria. Lack of success in establishing seedlings and in transplanting these species was probably due in part to their parasitic nature and to the lack of adequate haustorial connections or of an appropriate host.

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NOMENCLATURE, LIFE HISTORIES, AND RECORDS OF NORTH AMERICAN UREDINALES[1]

GEORGE B. CUMMINS AND JOHN W. BAXTER[2]

NOMENCLATURAL NOTES

1. PUCCINIA AGRIMONIAE (Arth.) Arth. Manual of Rusts in U.S. and Canada, p. 295. 1934. The type specimen consists of leaves of *Agrimonia pubescens* Wallr. bearing uredia of *Pucciniastrum agrimoniae* (Diet.) Tranz. and unattached teliospores that are identical with those of *Puccinia lateripes* Berk. & Rav., Grev. 3:52. 1874. The contaminant teliospores probably are from infected *Ruellia strepens* L. which Bartholomew collected at the same place and time (Sumner, Missouri, 7 Oct. 1907, *F. Columb. No. 2667*). Therefore, *Puccinia agrimoniae* falls into synonymy under *Puccinia lateripes*.

2. PUCCINIA BOUVARDIAE Griff., Bull. Torrey Club 20:297. 1902. *Puccinia anisacanthi* Diet. & Holw., Bot. Gaz. 31:329. 1901. Reidentification of the host plant of the type of *P. bouvardiae* as *Anisacanthus thurberi* (Torr.) Gray instead of *Bouvardia triphylla* Salisb. made clear the relationship of these two rusts which are recorded from southern Arizona and Mexico. *Puccinia bouvardiae* falls into synonymy under *P. anisacanthi.*

3. **Puccinia eumacrospora** Cumm. nom. nov. *Puccinia macrospora* Arth. Mycologia 1:244. 1909; not *Puccinia macrospora* (Lk.) Spreng. Syst. 4:569. 1827.

4. PUCCINIA XANTHIIFOLIAE Ell. & Ev., Jour. Myc. 6:120. 1891. *P. helianthi* Schw., Schr. Nat. Ges. Leipzig 1:73. 1822. That these two entities are the same was demonstrated by Baxter (1958), who successfully inoculated seedlings of *Helianthus annuus* L., grown in the greenhouse, with urediospores from *Iva xanthifolia* Nutt. collected near Guernsey, Wyoming, in 1957. In 1960, urediospores from *Helianthus annuus* collected by Baxter near Greeley, Colorado, infected *Iva xanthifolia* at Milwaukee, Wisconsin. *Puccinia xanthiifoliae* falls into synonymy under *P. helianthi.*

LIFE HISTORY STUDIES

PUCCINIA ESCLAVENSIS Diet. & Holw. Aeciospores of *Aecidium mirabilis* Diet. & Holw. on *Mirabilis longiflora* L., produced uredia and telia of *Puccinia esclavensis* on *Panicum bulbosum* H. B. K. in a field inoculation by Baxter near Portal, Arizona, August, 1960. In May, 1961, over-

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wintered teliospores were used in greenhouse inoculations of *Mirabilis jalapa* L., producing spermagonia and aecia.

New Records

1. Aecidium bouvardiae Diet. & Holw. On *Bouvardia glaberrima* Engelm. near Southwestern Research Station, Portal, Cochise County, Arizona, 16 August, 1960, *Baxter* (PUR); Garden Canyon, Huachuca Mountains, Cochise County, Arizona, 5 September, 1959, 10 September, 1960, *Goodding 239–59, 266–60* (PUR). These are the first records of the fungus from the United States. The species is heteroecious. In 1961, Cummins noted intimate association with rusted *Leptochloa dubia* (H. B. K.) Nees in the Santa Rita and Chiricahua Mountains, Arizona, and used aeciospores successfully to infect *L. dubia* in a field inoculation conducted at the Southwestern Research Station near Portal. The fungus is a species of *Puccinia,* as yet unidentified.

2. Aecidium chamaecristae Arth. On *Cassia fasciculata* Michx., Ames, Iowa, 5 June, 1960, *Baxter* (PUR). The species was known before only from Kansas and Nebraska.

3. Bubakia mexicana Arth. On *Croton* sp., Garner State Park, Uvalde County, Texas, 26 June, 1961, *Miller* (PUR). This is the first record of this rust from the United States.

4. Melampsora arctica Rostr. On *Salix anglorum* Cham., Breccia Peak, above Togwotee Pass, Wyoming, 29 August, 1960, *Cummins 60–98* (PUR). This species has not been found previously in Wyoming and only rarely in the United States. The site is in alpine tundra.

5. Phakopsora crotalariae (Diet.) Arth. On *Crotalaria vitellina* Ker., Acapulco, Mexico, October 1894–March 1895, *Palmer 217* (PUR). This material, the first North American record, was found on a phanerogamic specimen in the Chicago Natural History Museum.

6. Puccinia acrophila Pk. On *Synthyris pinnatifida* S. Wats. var. *pinnatifida,* near timberline, north side of Teton Pass, near Wilson, Wyoming, 5 September, 1960, *Cummins 60–126* (PUR). This rarely collected species has not been recorded on this plant in Wyoming.

7. Puccinia coronata Cda. On *Agropyron trachycaulum* Malte and *Bromus anomalus* Rupr., Slide Lake, Gros Ventre River near Jackson, Wyoming, 30 August, 1960, *Cummins 60–99, 60–103* (PUR); on *Calamagrostis rubescens* Buckl., Indian Paint Brush Canyon Trail, Grand Teton National Park, Wyoming, 17 August, 1960, *Cummins 60–20* (PUR). Old aecia (spermagonia lacking) occurred on *Elaeagnus canadensis* (L.) A. Nels. in close association at all sites.

8. Puccinia deschampsiae Arth. On *Deschampsia caespitosa* (L.) Beauv., Signal Mountain, Grand Teton National Park, Wyoming, 6 September, 1960, *Cummins 60–127* (PUR); near Wind River Lake, Togwotee Pass, Wyoming, 25 August, 1960, *Cummins 60–84* (PUR). Previous records are from Colorado, Alberta, and Alaska.

9. PUCCINIA DRABAE Rud. On *Draba incerta* Payson, *D. sphaerocarpa* Macbr. & Payson, Breccia Peak, above Togwotee Pass, Wyoming, 29 August, 26 August, 1960, *Cummins 60–97, 60–86* (PUR). The site is in alpine tundra. *D. sphaerocarpa* is a new host for this rarely collected fungus.

10. PUCCINIA MONOICA Arth. On *Poa secunda* Presl., Breccia Peak, above Togwotee Pass, Wyoming, 23 August, 1960, *Cummins 60–80* (PUR). This is the first record of the species on *Poa* and the Festuceae. Old aecia on *Smelowskia calycina* (Stephan) Mey. occurred in the area and probably belong in the life cycle.

11. PUCCINIA MONTANENSIS Ell. On *Agropyron spicatum* (Pursh) Scribn. & Sm., Togwotee Pass road, 16 mi. east of Moran, Wyoming, 22 August, 1960, *Cummins 60–62* (PUR). Old aecia were common at the site on *Berberis repens* Lindl. and probably belong in the life cycle. The only demonstrated aecial host is *B. fendleri* Gray, but the distribution of the fungus on grasses far exceeds the distribution of this barberry. *B. repens* probably serves in northern areas.

12. PUCCINIA MUSENII Ell. & Ev. On *Lomatium montanum* C. & R., Breccia Peak, above Togwotee Pass, Wyoming, 26 August, 1960, *Cummins 60–90* (PUR). This relatively rare fungus has not been reported on species of *Lomatium.*

13. PUCCINIA PAGANA Arth. On *Lloydia serotina* (L.) Reichb., Breccia Peak, above Togwotee Pass, Wyoming, 23 August, 1960, *Roger S. Peterson* (*Cummins 60–80*), (PUR). The location is above timberline. The only previous record is the type, collected on Pike's Peak, Colorado, in 1904 as on *Allium reticulatum* Don (Clements, Cryptog. Form. Colo. No. 141 as *Puccinia mutabilis*). Arthur questioned the identity of the host plant when he described *P. pagana*. Cummins visited the type locality in July, 1961, and found *P. pagana* on *Lloydia serotina* but no rust fungus on the intermingled *Allium*. There is no doubt that the host of the type is also *Lloydia serotina*.

14. PUCCINIA PATTERSONIANA Arth. On *Agropyron spicatum* (Pursh) Scribn. & Sm., Togwotee Pass road, 16 miles east of Moran, Wyoming, 22 August, 1960, *Cummins 60–61* (PUR). This fungus has not previously been recorded for Wyoming.

15. PUCCINIA WULFENIAE Diet. & Holw. On *Veronica wormskjoldii* R. & S., summit of Togwotee Pass, Wyoming, 20 August, 1960, *Cummins 60–55* (PUR). This relatively rare fungus has not previously been recorded on a species of *Veronica*.

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LITERATURE CITED

Baxter, J. W. 1958. Notes on Rocky Mountain rust fungi. Trans. Wis. Acad. Sci. 47:131–135.

REVIEW

Southern California Gardens, An Illustrated History. By Victoria Padilla. University of California Press, Berkeley and Los Angeles. 1961. 379 pages. 170 illustrations, 15 in color. $10.00.

The passing parade of plants, people and events presented to the reader of this history of ornamental horticulture in southern California is an impressive one indeed. The story of "Southern California Gardens" begins with the Franciscan missionaries who came northward from Baja California to form a chain of missions from San Diego to Sonoma from 1769 to 1823. They brought with them a number of plants mostly for agricultural purposes, but some were ornamentals and among these were several trees which are today so much a part of our landscape that we take them for granted. Olive, pepper, fig, and citrus trees are but a few. The story is carried on from this early beginning down to the present time.

Through the early history, but particularly beginning with the last quarter of the 19th century, are told the stories of those horticulturists and gardeners responsible for bringing plants from other parts of the country and from Europe, those who had the vision to realize that new plants could be grown here, and who persisted and were successful in their efforts. It is surprising, in fact, how many plants were brought here before the beginning of our present century. For those who have lived in southern California, reading Miss Padilla's personal sketches of these horticulturists is reading the stories of one's friends. Her characterizations are warmly and personally told.

Miss Padilla is a gardener herself and has a personal knowledge of and acquaintance with the people and the plants that she has written about. She has been a prominent member for many years of the Southern California Horticultural Institute, the organization which sponsored the publication of this history.

The format of the book is excellent, and the photographs, including several in color, are of good quality and well reproduced. A list of the plant introductions of Dr. Franceschi, Hugh Evans, E. O. Orpet, and the former Evans and Reeves nursery firm, and the horticultural features of the several parks of the City of Los Angeles add to the interest of the book. A bibliography gives some of the sources of material consulted by the author. The nomenclature of the plants is accurate. There is, however, one criticism which this reviewer offers regarding the way in which the names of the horticultural or cultivated varieties (cultivars) are written. According to the International Code of Nomenclature for Cultivated Plants, names of cultivated varieties (cultivars) are to be enclosed in single quotes and *not* double quotes. Throughout this book double quotes are used, this in direct contradiction to the International Code. There did not seem to be any explanation on the part of the publisher for not following this very simple international rule.

Interesting and authoritative, and written in a charming style, this book is highly recommended for all those interested in southern California horticulture and gardens, and there is, in fact, enough of general interest to recommend it for all those interested in California horticulture and gardens. Elizabeth McClintock, Department of Botany, California Academy of Sciences, San Francisco, California.

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AN ANATOMICAL STUDY OF THE SECONDARY TISSUES IN ROOTS AND STEMS OF UMBELLULARIA CALIFORNICA NUTT. AND LAURUS NOBILIS L.

Baki Kasapligil

This paper, dealing with the secondary tissues of roots and stems of *Umbellularia* and *Laurus* is a continuation of the author's comparative studies (1951, 1954) of these laureceous genera seeking evidence regarding their phylogenetic relationships.

Normal secondary growth is essentially the same in the roots and stems of both gymnosperms and woody dicotyledons, but because routine collections of woody plants do not usually include roots, details of root structure are less well known than are those of stems. Roots are considered "conservative" organs, but Beakbane (1941) found the anatomy of apple roots to be affected by the environment. Fegel's work (1941) demonstrated the relatively primitive structural features of roots, and Noelle (1910) applied the anatomical characters of roots to the classification of the Coniferae.

Materials and Methods

Native material of *Laurus nobilis* L. was collected at Antalya, Turkey, while native material of *Umbellularia californica* Nutt. was collected in California. Cultivated material of both species was collected in the Botanical Garden of the University of California at Berkeley.

The material was studied partly in freehand sections and partly after maceration. Useful microtechnical methods were found in the publications of Gassner (1931), Ball (1941), and Foster (1949, Appendix).

Histology of Secondary Xylem Elements

Roots

Periderm. There are no essential differences in the periderm of *Umbellularia* and *Laurus*. The outermost cell layer of the pericycle functions as a phellogen and produces 8–10 regular rows of phellem toward the periphery. The primary cortex breaks up and disappears. Phellem cells die as their cell walls gradually acquire suberized thickenings. Meanwhile, the phellogen also forms a phelloderm tissue toward the inside, which is composed of parenchymatous cells containing starch grains and oil globules. Phelloderm cells closely resemble cortical parenchyma cells and they join the phloem parenchyma farther toward the inside. It is almost impossible to make a sharp distinction between phelloderm and phloem. Idioblastic secretory cells are abundant and diffusely distributed in phelloderm, while lenticels appear in the periderm during later stages of secondary growth.

Madroño, Vol. 16, No. 7, pp. 205–236, July 13, 1962.

SECONDARY PHLOEM. The primary phloem is obliterated during the secondary growth of *Umbellularia* roots, but sometimes remains distinguishable as a faint line in transverse section. The secondary phloem is composed of cells which are more or less uniform in cross section. A large portion of this tissue consists of parenchyma cells containing starch grains. Sieve tubes and companion cells form small groups which can be identified by the absence of starch grains. Phloem rays are indistinguishable and no fibers were observed. Parenchyma cells containing tannic substances are abundant; they are distributed at random in the secondary phloem and phelloderm.

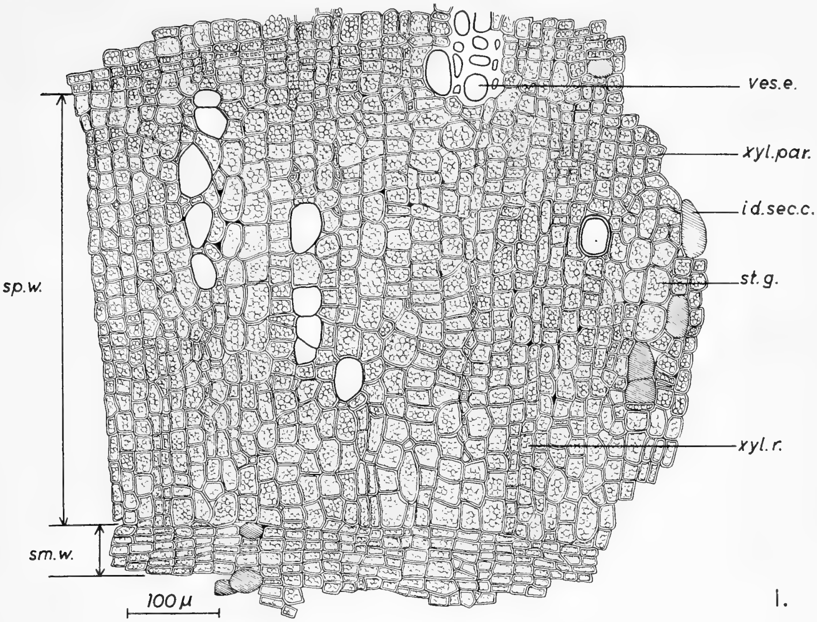
The secondary phloem of *Laurus* exhibits certain differences. It contains fibers, of reduced cross sectional area and angular form, with thick walls and reduced lumina. Phloem rays expand in conical shape and can be distinguished easily. The tannin-containing cells in the secondary phloem and phelloderm are arranged in regular tangential rows.

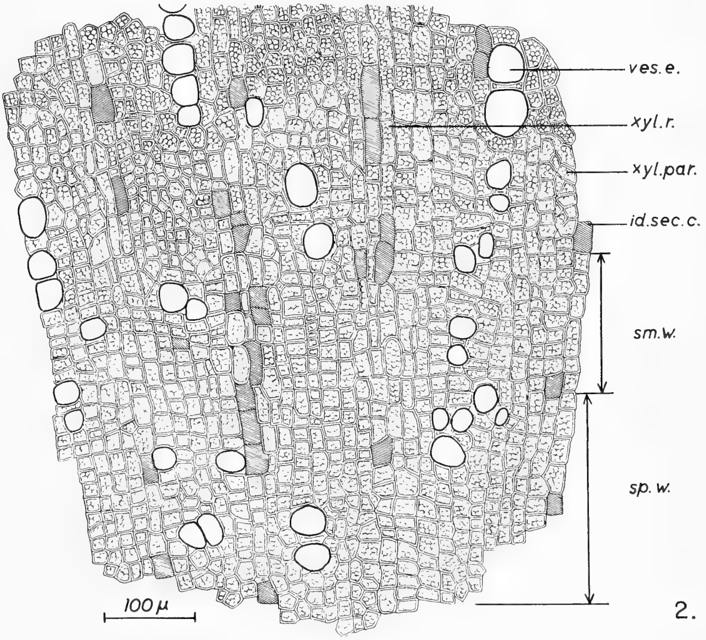
SECONDARY XYLEM. **a. Transverse sections.** The root wood of both genera is diffuse porous (figs. 1 and 2). Huber (1935) and Gilbert (1940) consider diffuse porosity more primitive than ring porosity. Vessel elements in *Umbellularia* have large diameters in spring wood and small diameters in summer wood. Occasionally 10–12 vessel elements of varying diameters are grouped together in summer wood. Vessel elements with large or small diameters are distributed in spring and summer woods of *Laurus* more or less in the same ratio. As an average there are about 64 vessel elements per square millimeter of *Umbellularia* root compared to about 100 for *Laurus*. No tyloses are produced; apparently the vessels in the roots of both genera are entirely functional. Alten (1908) pointed out the abundance of tylosis formation in root woods of many trees. However, the studies of Klein (1923) Liese (1925) and Fegel (1941) show the absence of tyloses in the root woods of forest trees.

The outer and inner boundaries of the growth layers of summer wood are distinct in both genera. The width of growth layers is variable, but the proportion of spring and summer woods within the growth layers seems to be constant. Summer wood occupies approximately one tenth of the growth layer in *Umbellularia* and about one third of the growth layer in *Laurus*.

Xylem rays are heterocellular, uni-, or multiseriate in both genera. Ray parenchyma cells contain an abundance of starch grains and tannic substances. Idioblastic secretory cells occur commonly within the xylem rays. Xylem rays are less abundant in *Umbellularia* than in *Laurus*. In *Umbellularia,* the cells of ray parenchyma are larger in spring wood than in summer wood; in *Laurus* they are of nearly uniform size.

Xylem parenchyma is apotracheal-diffuse in both genera, i.e., the parenchyma cells are distributed throughout the root wood independent of vessel elements. This is a very different situation from the paratracheal and metatracheal distribution patterns of the xylem parenchyma in stem





FIGS. 1–2. Transverse sections of root wood: 1, *Umbellularia californica;* 2, *Laurus nobilis*. Legends: ves. e.=vessel element, sm.w.=summer wood, sp.w.=spring wood, xyl.par.=xylem parenchyma, xyl.r.=xylem ray, id. sec.c.=idioblastic secretory cell, st.g.=starch grains.

woods which will be described later. Apotracheal-diffuse type is considered as an unspecialized feature by Metcalfe and Chalk (1950). The xylem parenchyma cells form radially extending rows mixed with wood fibers.

In *Umbellularia* the pith consists of thin-walled parenchyma cells; in *Laurus* it consists of sclerenchymatous cells. In both cases the cells contain much starch.

b. Radial sections. In both genera, superimposed series of vessel members are very distinct if they fall on the plane of the sections (fig. 4). Xylem rays are composed of rectangular parenchyma cells containing starch grains. Libriform wood fibers are empty and dead, while the wood parenchyma cells are filled with starch grains. Idioblastic secretory cells appear rectangular or isodiametric in form, and they occur frequently in xylem rays as well as outside of the rays.

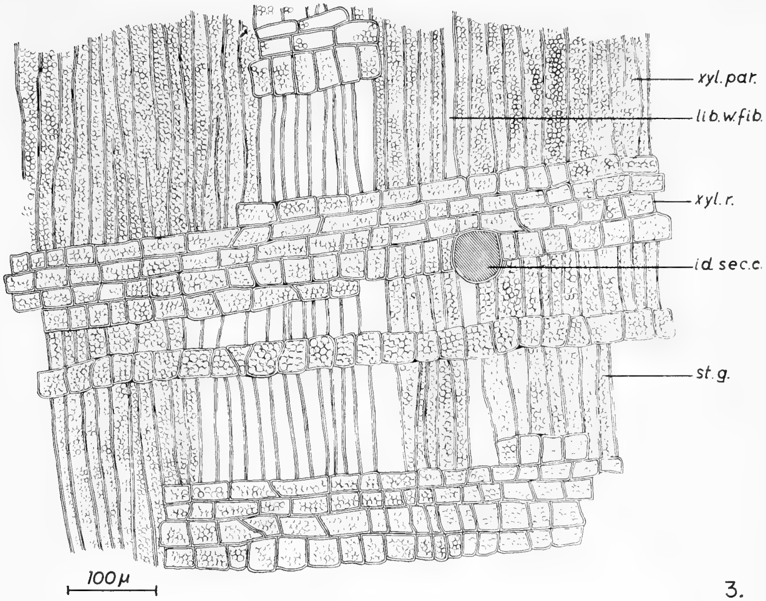
c. Tangential sections. In *Umbellularia* roots the xylem rays are 1–4 cells wide and 5–17 cells high (fig. 5), with a single cell at their pointed upper and lower margins. Xylem parenchyma occupies the spaces between the rays with a few libriform wood fibers. Generally, the xylem parenchyma appears as long, narrow cells with tapering ends, but often the parenchyma cells also form superimposed vertical series. These series overlap one another so that there is no storied condition. Idioblastic secretory cells within the xylem rays are either scattered individually or form small roundish groups of 2–3 cells or even vertical series of 3–5 cells (fig. 5).

The xylem rays of *Laurus* roots are 1–3 cells wide and 1–13 cells high in transectional outlines. Idioblastic secretory cells may be scattered individually or may form small groups within the rays, but they generally occupy upper and lower margins of the rays. The rays taper gradually toward the upper and lower margins, which are generally straight instead of pointed (fig. 6). Usually these margins are in contact with xylem parenchyma. The "vertical xylem parenchyma" forms superimposed series of 3–8 cells, and these series run parallel to xylem rays. Libriform wood fibers occur in spaces between xylem rays and vertical series of wood parenchyma and are more abundant than in *Umbellularia*.

Stems

The secondary xylem of *Umbellularia* and *Laurus* is described and illustrated in various atlases and books for timber identification (Brown and Panshin, 1940, and Record, 1934, for *Umbellularia;* Greguss, 1945, and Huber, 1954, for *Laurus;* Stern, 1954, for these and many other Lauraceae). However, the secondary structure of stems will be described here briefly to provide a basis for the comparison with the root structure of *Umbellularia* and *Laurus*.

UMBELLULARIA CALIFORNICA. A phellogen tissue is formed by the outermost cell layer of cortex parenchyma. The epidermal tissue is broken in



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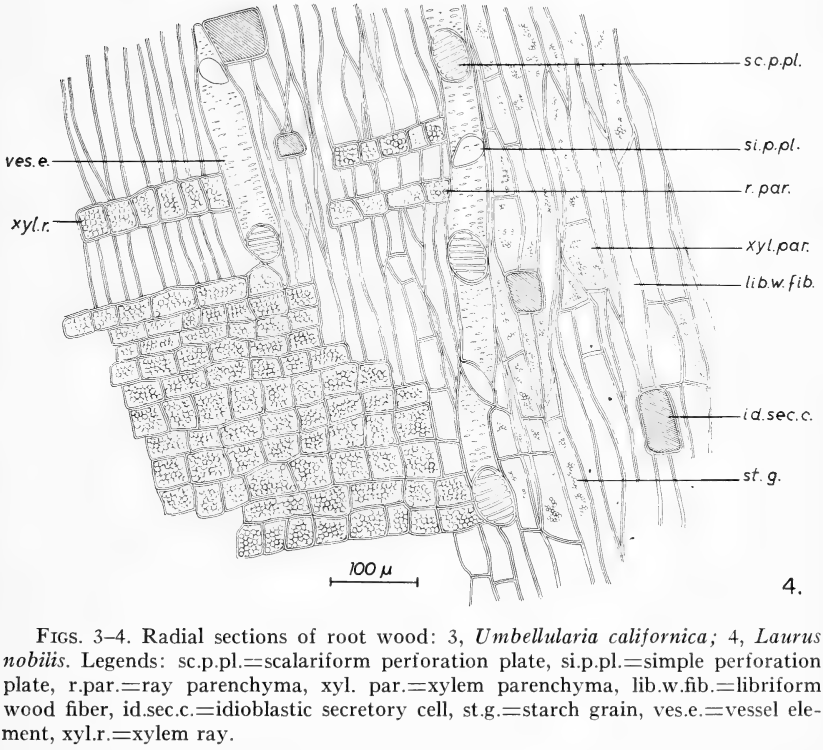

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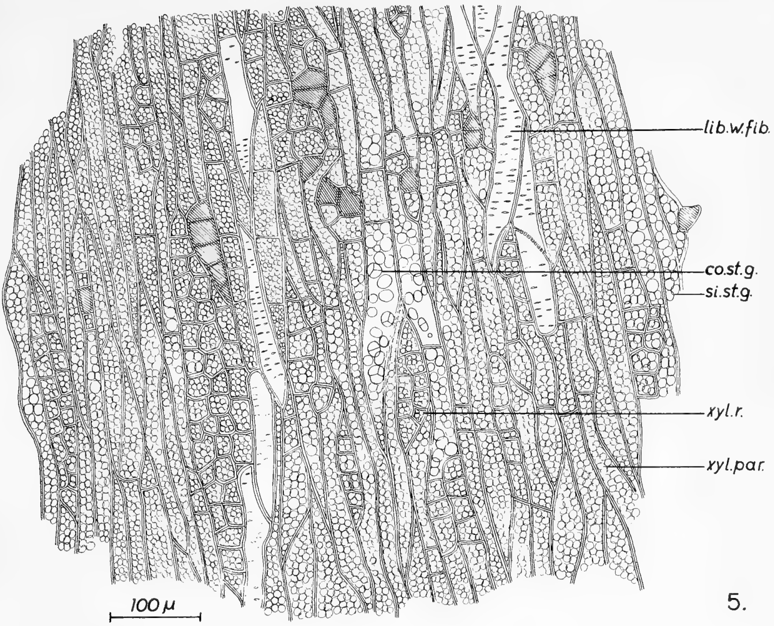
Figs. 3–4. Radial sections of root wood: 3, *Umbellularia californica;* 4, *Laurus nobilis.* Legends: sc.p.pl.=scalariform perforation plate, si.p.pl.=simple perforation plate, r.par.=ray parenchyma, xyl. par.=xylem parenchyma, lib.w.fib.=libriform wood fiber, id.sec.c.=idioblastic secretory cell, st.g.=starch grain, ves.e.=vessel element, xyl.r.=xylem ray.

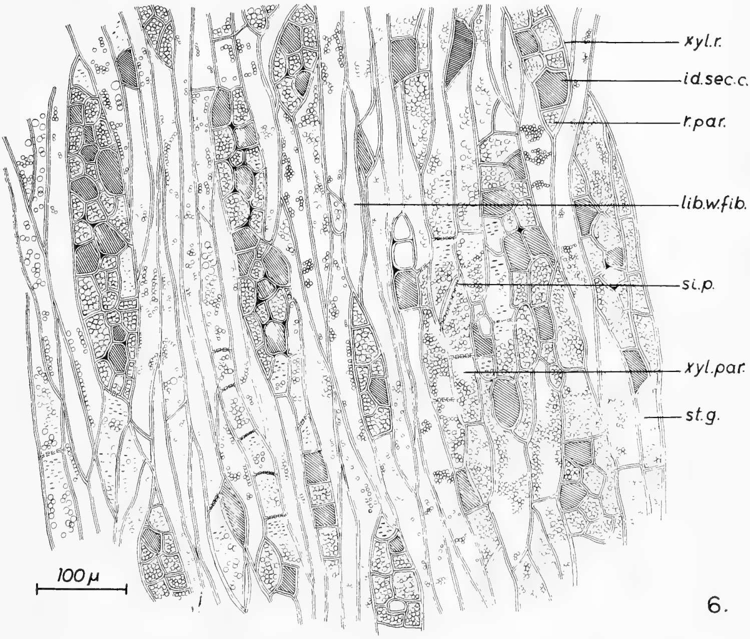
places as the result of secondary thickening of the stem. Phellem and phelloderm layers produced as the result of the activity of this secondary meristematic tissue are shown in fig. 7. The cortex parenchyma below the periderm consists of 8–10 cell layers in which idioblastic secretory cells are distributed without a regular pattern. The innermost cell layers of the cortex—adjacent to the primary phloem—form one to several layers of hippocrepiform sclereids (cf. Bailey and Swamy 1948). The sheath of hippocrepiform sclereids in stems is composed of one or more cell layers which form a regular cylinder interrupted by phloem fibers. The inner tangential walls and the radial walls of these sclereids are thick and lignified heavily, while their outer tangential walls are unthickened. Thus the hippocrepiform sclereids appear U-shaped in transectional view resembling endodermal cells at the tertiary stage of thickening. The thick walls of these sclereids are provided with simple pits. These pits are generally opposite the pits of the adjacent cells, forming simple pit pairs. However, blind pits are also observed along the radial walls. Hippocrepiform sclereids of secondary stems 6–7 years old are living cells with large lumina. The cytoplasm is peripheral, while the central part of the cell is occupied by a vacuole. Some of these sclereids contain granular tannic substances and appear dark.

The derivative cells of the vascular cambium form the secondary phloem externally and in this way the primary phloem is pushed outward. The primary phloem in older portions of the stem is crushed by the internal pressure and in the later stages of development the primary phloem may be entirely obliterated. However, the phloem fibers with thick and resistant cell walls remain in groups along the outer boundary of the primary phloem (fig. 7).

Stem wood is hard and exhibits distinct growth layers. Heart and sap woods are distinguishable in old and thick stem portions. Heart wood is grayish or dark brown while the sapwood is whitish or light brown. Porosity is of the diffuse type as in the root wood. Xylem rays are very fine in transverse section and hardly distinguishable to the naked eye. Typically the rays are heterocellular and the xylem rays together with phloem rays form continuous vascular rays. The rays are not as dense as in the stem wood of *Laurus* and there are about ten rays per millimeter in transverse section.

Wood fibers form regular rows extending radially. The xylem parenchyma exhibits paratracheal-vasicentric arrangement. One to three cell layers of xylem parenchyma encircle the vessel elements as seen in the lower left corner of figure 7. The distribution of xylem parenchyma in the stem wood of *Umbellularia* exhibits a more advanced and specialized condition when compared to the apotracheal-diffuse type of arrangement in the root wood of the same species. The xylem parenchyma cells in the stem have thick lignified walls and contain starch grains. The primary xylem elements are readily identified in small groups adjacent to the pith.





FIGS. 5–6. Tangential sections of the root wood: 5, *Umbellularia californica;* 6, *Laurus nobilis.* Legends: xyl.r.=xylem ray, id.sec.c.=idioblastic secretory cell, r.par.=ray parenchyma, lib.w.fib.=libriform wood fiber, si.p.=simple pits, xyl.par.=xylem parenchyma, co.st.g.=compound starch grain, si.st.g.=simple starch grains.

They possess thicker cell walls and small diameters and lumina as compared to the secondary xylem elements. The pith is composed of large isodiametric parenchyma cells. The outer 4–5 cell layers of the pith cylinder in the old portions of stems remain alive and contain starch grains while the inner cells of the pith die. The simple pits of the pith parenchyma are distinct, but the intercellular spaces are obscure.

LAURUS NOBILIS. Epidermis, periderm and cortex tissues of the *Laurus* stem are essentially similar to those in the *Umbellularia* stem.

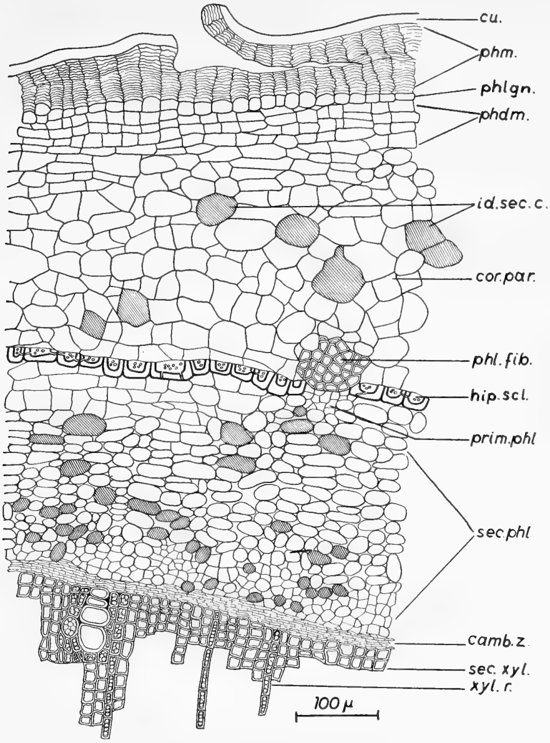
The primary and secondary phloem groups are intersected by phloem rays. Figure 8 represents a transverse section of a young stem in which the primary phloem tissues are not obliterated. It was not possible to draw a clear demarcation line between primary and secondary phloem. However, the fiber groups shown in figure 8 help determine the approximate position of the primary phloem groups. The phloem fibers appear as polyhedral, thick walled cells grouped compactly in transectional view. The position of the secondary phloem is determined approximately in figure 8 according to its position relative to the vascular cambium. The vascular cambium appears as if it contains 30 cell layers since the stem material was collected during cambial activity in July. Theoretically only one cell layer forms the cambial initials while the rest of the cells represent undifferentiated derivatives of the cambium in both inner and outer directions. However, the vascular tissues produced by the earlier activity of the cambium are already differentiated into secondary structure.

The secondary xylem is diffuse porous. The vessel elements are scattered individually or in twos in the spring wood, while three or four of them are arranged in small radial rows in the summer wood. The growth layers are distinct due to the fact that the wood fibers along the border lines of the growth layers are flattened and have very small diameters. Xylem rays are heterocellular, uni-, or biseriate. There are 12 xylem rays per millimeter in transverse section. The xylem parenchyma of the stem exhibits metatracheal arrangement which represents a more specialized condition compared to the apotracheal diffuse arrangement of the xylem parenchyma of the secondary roots of the same species.

MORPHOLOGY OF THE SECONDARY XYLEM ELEMENTS

Anatomical features exhibited by various sections of root and stem woods of *Umbellularia* and *Laurus* have been described above. In addition, macerated material of root and stem woods was studied in the hope of finding other characters that might be considered of phylogenetic importance.

The phylogenetic value of wood anatomy in systematic studies was shown clearly by Record (1934), Chalk (1937), Heimsch and Wetmore (1939), Tippo (1946) and others. Metcalf and Chalk (1950) emphasize the fact that wood structures exhibit more conservative characters than do external features of plants.



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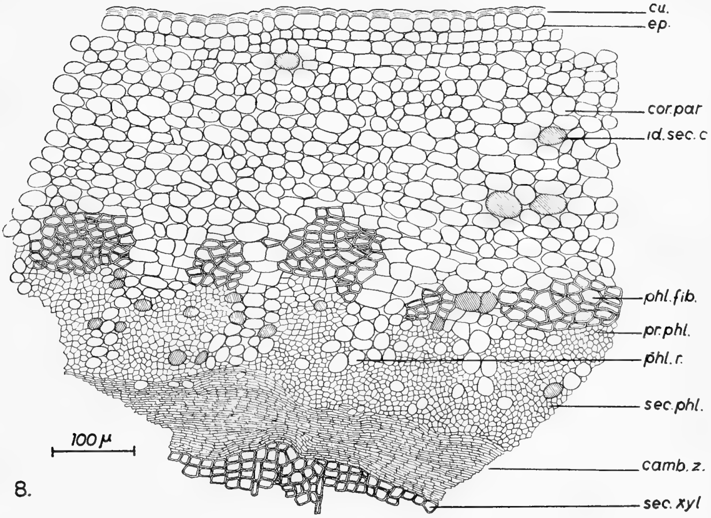

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FIGS. 7–8. Portions of transverse stem sections showing secondary growth: 7, *Umbellularia californica;* 8, *Laurus nobilis.* Legends: cu.=cuticle, phm.=phellem, phlgn.=phellogen, phdm.=phelloderm, id.sec.c.=idioblastic secretory cell, cor.par.= cortical parenchyma, phl. fib.=phoem fibers, hip.scl.=hippocrepiform sclereids, prim.phl.=primary phloem, sec.phl.=secondary phloem, camb.z.=cambial zone, sec.xyl.=secondary xylem, xyl.r.=xylem ray, ep.=epidermis.

The dimensions of wood elements are significant for both diagnostic and phylogenetic interpretations. In general, long and narrow wood elements are considered more primitive than short and wide ones. However, the dimensions of wood elements exhibit considerable variation in various organs of the same plant or even in different regions of the same organ, and Sanio (1872) demonstrated the length increase of the wood elements from central toward the peripheral regions of *Pinus sylvestris* roots. Gerry (1915) showed that the root tracheids are longer than stem tracheids in *P. palustris* and *P. strobus*. Anderson (1951) found that the length of the tracheids in conifers tends to increase with the increase of distance from the pith and that the tracheids of spring wood are shorter than those of summer wood within the same "annual ring." Dimensional variations of the xylem elements in the root and stem woods of *Umbellularia* are obvious in tables given below. An interesting subject for further investigation would be the relationship of these variations to different stages of growth.

The morphological features of wood elements may also be used to interpret the degree of specialization. The conclusions regarding the primitive and advanced characters of the secondary xylem elements reached by wood anatomists (Bailey and Tupper, 1918; Bailey and Howard, 1941; Fegel, 1941; Frost, 1930a, b, 1931; Gilbert, 1940; Metcalfe and Chalk, 1950; Tippo, 1946) are summarized below.

Primitive Characters	Advanced Characters
1. Diffuse porous.	1. Ring porous.
2. Scattered vessel elements.	2. Grouped vessel elements.
3. Small perforation plates with many bars.	3. Wide perforation plates with a few bars.
4. Scalariform perforation plates.	4. Simple perforation plates.
5. Polyhedral vessel elements.	5. Round vessel elements.
6. Inclined end-walls.	6. Transverse end-walls.
7. Fiber tracheids with bordered pits.	7. Libriform wood fibers with small simple pits.
8. Scalariform and bordered pits.	8. Simple pits.

The anatomical features set forth above have been used as a basis to judge and compare the primitive and advanced characteristics of the xylem elements in the secondary structures of roots and stems in *Umbellularia* and *Laurus* in the present paper. According to the suggestion of Chalk and Chattaway (1934), the vessel elements were measured from tip to tip to obtain the length dimension. To calculate average dimensions, at least fifty measurements have been made for each element. The terminology proposed by the Committee on Nomenclature of the International Association of Wood Anatomists (1957) has been followed in describing the wood elements.

Secondary Xylem Elements of Umbellularia Roots. Wood parenchyma, fiber tracheids, and septate fiber tracheids are abundant.

The average length of vessel elements is 250 microns and their average width is 40 microns. Therefore the vessel elements in question fall into the group "small and short" in Metcalfe and Chalk's (1950) classification. In general they are shorter and narrower than the vessel elements found in the stem wood of the same species.

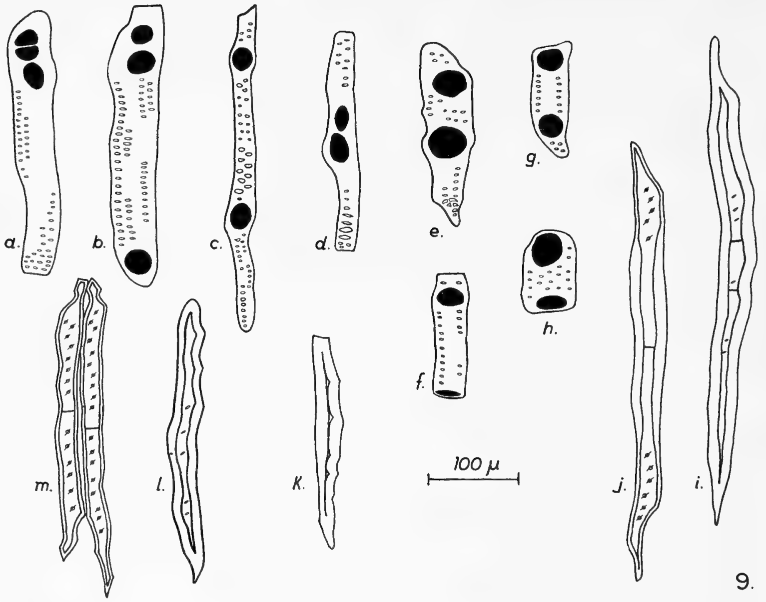
The ligulate tips of the vessel elements are generally long and broad (fig. 9, c). Vessel elements approaching a cylindrical shape are rare (fig. 9, f-h). In transectional view they are polyhedral in form (fig. 1).

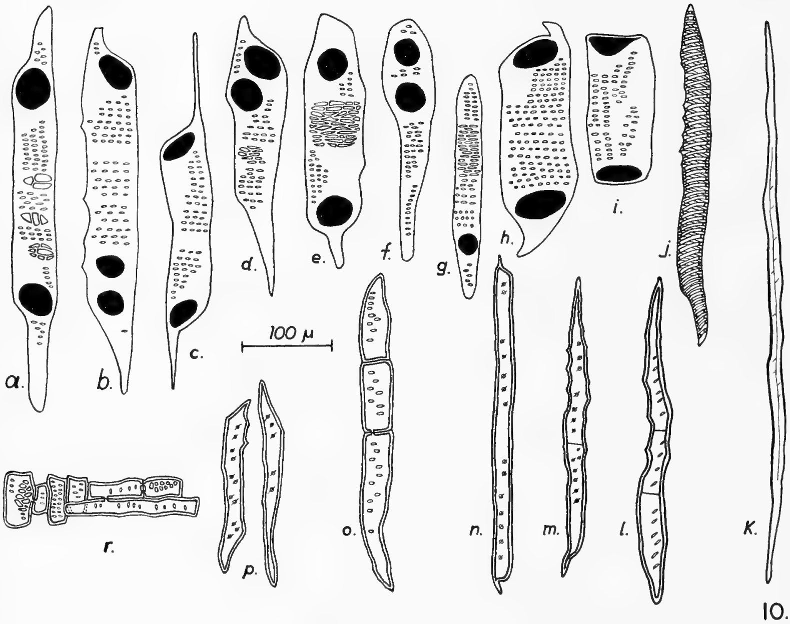
The perforation plates of the vessel elements are generally simple, oblique, and distant from the ligulate tips. Scalariform perforation plates are very rare. A scalariform perforation plate with a single bar is shown in fig. 9, a. Although the vessel elements are usually provided with two simple perforation plates (fig. 9, c, e-h), vessel elements with three simple perforation plates have also been observed (fig. 9, b). In the latter instance, there are two simple perforation plates in one end of the vessel element and one perforation plate in the other end of the element. Some vessel elements have two perforation plates side by side in the middle of a vessel element without perforations at the cell ends (fig. 9, d). These latter two cases are characterized by profuse pitting at the ligulate tips of the vessel elements (fig. 9, a, d).

The simple pits on the lateral walls of the vessel elements are small and generally at equal dimensions. Opposite and alternate pitting may be found on the walls of the same vessel element. The ligulate tips of the vessel elements are usually pitted, but no pitting is found in cases where the tips are short.

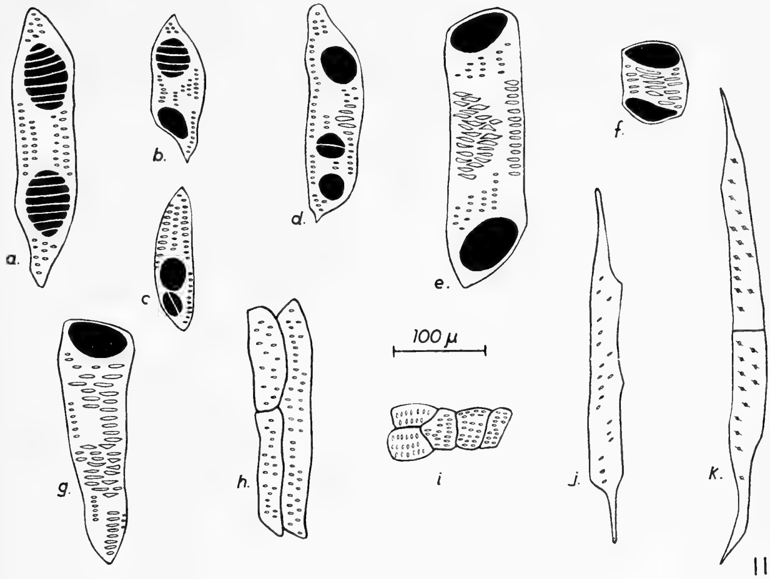
The fiber tracheids and the septate fiber tracheids possess pits. The septations of these elements are primary walls and do not exhibit secondary thickenings (fig. 9, m). An interesting type of septate fiber tracheid is shown in figure 9, j, in which the lateral walls are about three times thicker than the terminal portions of the lateral walls. These tracheids recall "gelatinous fibers" (cf. Esau, 1953, p. 205), but their thick walls did not shrink during the process of dehydration.

The wood fibers have very thick secondary walls with vestigial simple pits. Some of the wood fibers have wide lumina (fig. 9, l), but some of them have an extremely reduced lumen (fig. 9, k) appearing like a line along the longitudinal axis of the cell. Septate wood fibers (fig. 9, i) are very similar to septate tracheids, but are distinguished from the latter by the presence of vestigial simple pits. Septate wood fibers may possess one or two partition walls of a primary nature. According to Metcalf and Chalk (1950), septate tracheids and septate fibers commonly occur in tropical woods and serve as a useful feature for determining phylogenetic relationships. As a matter of fact, most Lauraceae are distributed in tropical regions and contain either one of the septate elements or both types in their woods. The wood fibers of *Umbellularia* roots are shorter but wider than the fibers of the stem wood.

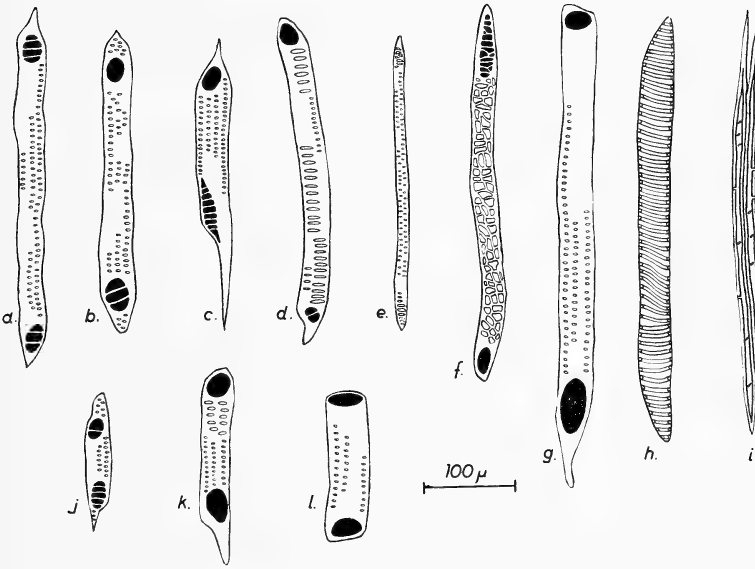




FIGS. 9–10. Tracheary elements of *Umbellularia californica*: 9, root wood; 10, stem wood. (Explanation in text).



11.



12.

FIGS. 11–12. Tracheary elements of *Laurus nobilis*: 11, root wood; 12, stem wood. (Explanation in text).

The parenchyma cells of the root wood possess lignified cell walls, but their cell walls are thinner than the cell walls of other xylem elements. Xylem parenchyma cells are elongated cells, while the ray parenchyma cells are smaller and tabular in shape.

SECONDARY XYLEM ELEMENTS OF UMBELLULARIA STEMS. Vessel elements of stem wood average 336 microns in length and 53 microns in width. This dimensional variation is not as pronounced as the size variation of the vessel elements in the root wood. The transverse outlines of the vessel elements do not exhibit sharp corners. Generally, they approach drum shape in spite of much variation in their form (fig. 10, i). They are provided with simple perforation plates, and scalariform perforations have never been observed. The ligulate tips of the vessel elements are generally small, those with transverse perforation plates having no ligulate tip (fig. 10, i). These characters indicate that the vessel elements of the stem wood exhibit a higher degree of specialization than the vessel elements in the root wood of *Umbellularia*.

The ligulate tips of the vessel elements may be long and wide at both ends of the cells, tapering gradually (fig. 10, a, b), or they may extend in slender needle-like form at both ends (fig. 10, c). These two are primitive types resembling tracheids. Some vessel elements have a single ligulate tip in one end of the cell that is mucronate, i.e., the end wall of the vessel element abruptly becomes a short tail (fig. 10, e). Some ligulate tips are curved inwardly. This is generally observed in short and wide vessel elements (fig. 10, h).

Although the vessel elements usually have two simple perforation plates, some of them are provided with three perforation plates (fig. 10, b) and still others have only one (fig. 10, g). Two perforation plates may be located side by side in one end of a vessel element and the other end of the cell in such vessel elements tapers gradually (fig. 10, d, f).

Intervascular pits on the lateral walls of the vessel elements are small and simple. Reticulate and broad simple pits are restricted to the surfaces of the lateral walls in contact with the xylem parenchyma cells (figs. 10, a, d, e, g). Scalariform pitting has not been observed.

Fiber tracheids have approximately the same diameter as those in root wood. The fiber tracheids are either uniform in width, and terminating in small ligulate tips at both ends (fig. 10, n), or they may be constricted, terminating in sloping end walls (fig. 10, p).

Septate fiber tracheids (fig. 10, m) are fusiform cells with gradually tapering ends. Their lateral walls are thickened equally in all directions. Fiber tracheids with unequal secondary wall thickening have not been found in the stem wood.

Libriform wood fibers have very thick secondary walls and highly reduced lumina which can be distinguished sometimes as a fine line extending lengthwise (fig. 10, k). Vestigial simple pits of the wood fibers are also extremely reduced, and they appear as small oblique lines along both sides of the lumen trace. Wood fibers with wider lumina are not rare, and their diameters are smaller than the wood fibers of the root wood.

Septate wood fibers are very similar to septate fiber tracheids in regard to their shapes and sizes, but they can be distinguished from the latter by the presence of simple pitting (fig. 10, l). They possess one or two partition walls; their lateral walls with secondary thickenings are thinner than the lateral walls of the septate fibers found in the root wood of *Umbellularia*.

Xylem parenchyma cells have thick secondary walls with simple pitting, forming superimposed vertical series (fig. 10, o). They resemble closely septate wood fibers even in macerated state, but are distinguished from the latter by the presence of secondary thickenings in their transverse walls (cf. fig. 10, a, l).

Ray parenchyma cells are rectangular cells with straight or slightly pointed end walls. Generally they possess simple pitting, but they also exhibit reticulate pitting on the areas in contact with vessel elements (fig. 10, r).

Table 1. Comparison of the Dimensions of Secondary Xylem Elements in the Roots and Stems of Umbellularia californica and Laurus nobilis.

Wood Elements	Average length (microns)				Average width (microns)			
	Root Wood		Stem Wood		Root Wood		Stem Wood	
	*U.c.**	*L.n.**	*U.c.*	*L.n.*	*U.c.*	*L.n.*	*U.c.*	*L.n.*
Vessel elements	250	263	336	353	40	84	53	29
Fiber tracheids	412	451	417	348	27	34	24	25
Septate fiber tracheids	512	555	504	459	26	30	27	23
Libriform wood fibers	443	521	511	456	19	18	13	12
Septate wood fibers	542	......	487	......	19	....	16	....
Xylem parenchyma	167	160	170	93	31	31	23	19
Ray parenchyma	63	60	74	44	36	29	21	28

* *U.C.* = *Umbellularia californica* Nutt.
* *L.n.* = *Laurus nobilis* L.

SECONDARY XYLEM ELEMENTS OF LAURUS ROOTS. The average length of the vessel elements in the root wood is 263 microns and the average width is 84 microns (table 1). Obviously they are shorter and wider compared to the vessel elements of the stem wood. They fall into the group of "small and short vessel elements" in the classification of Metcalfe and Chalk (1950) since their average width is smaller than 100 microns and their average length shorter than 350 microns. The ligulate tips of vessel elements are short and pointed (fig. 11, a, b, d). The transectional outline of the vessel elements is polyhedral.

The perforation plates of the vessel elements are either scalariform or simple and exhibit three types of combinations in individual vessel elements: a) both perforation plates may be scalariform (fig. 11, a); b) one of the perforation plates may be scalariform and the other one simple (fig. 11, b); c) both perforation plates may be simple (fig. 11, e, f). The number of bars in the perforation plates is generally 7–8, but rarely there may be only a single bar. Although in general there is one perforation plate at each end of the vessel elements, there are exceptions to this rule. Some vessel elements may have three perforation plates. For example, figure 11, d, illustrates a vessel element with two simple and one scalariform perforation plates. Still some vessel elements may have but one simple perforation plate (fig. 11, g). A solitary scalariform perforation plate has never been observed. The vessel elements with a single perforation plate exhibit abundant pitting on their lateral walls, and the imperforate end of the vessel element tapers gradually so that such vessel elements acquire a funnel shape. Both of the perforation plates may be located side by side in one end of some vessel elements, (fig. 11, c); the imperforate end of such a vessel element tapers gradually and possesses many simple pits. In general the simple perforation plates are either straight or slightly sloping (fig. 11, e-g). These three illustrations also show that the vessel elements terminating with simple perforation plates have either very short ligulate tips or none. The cylindrical vessel elements with simple perforation plates shown in figures 11, e and f, undoubtedly represent the most advanced types, but they occur together with the primitive types possessing scalariform perforation plates.

The vessel elements exhibit three types of pitting: a) scalariform pitting (fig. 11, d-g); b) reticulate pitting (fig. 11, e, g); c) simple pitting (fig. 11, a-c). According to Bailey (1954) scalariform pits represent a primitive type, but interestingly enough the scalariform pits are associated quite often with simple perforation plates in the same vessel elements, forming vertically arranged regular rows on the lateral cell walls. The scalariform pitting does not occur in the vessel elements of *Umbellularia,* hence they are more specialized than the vessel elements of *Laurus.* Reticulate simple pits are restricted to the wall areas of the vessel elements in contact with the ray parenchyma cells in the root wood of *Laurus.* Simple pits, however, are located on the lateral walls as well as in the ligulate tips of the vessel elements. Although some vessel elements possess exclusively simple pits, still others exhibit all three types of pitting at the same time (fig. 11, e).

The fiber tracheids are abundant in the root wood, and they are longer and wider than those in the stem wood (cf. table 1). The size variation of the fiber tracheids in the root wood is not as pronounced as the wide range of variation shown by the fiber tracheids of the stem wood.

The septate fiber tracheids are also longer and wider than those of the stem wood. They may be provided with one or several septa. Lumina are wide and they taper gradually toward the ends (fig. 11, k).

Libriform wood fibers possess secondary walls with varying degree of thickening. Consequently they exhibit wide as well as narrow lumina. Those with wide lumina resemble fiber tracheids, but they are distinguished by the presence of vestigial simple pits (fig. 11, j). The proportion of libriform wood fibers in the secondary xylem of *Laurus* roots is relatively smaller than the proportion of wood fibers in the secondary xylem of stems. Septate wood fibers have not been observed, and the septate elements resembling fibers are actually tracheids.

Xylem parenchyma cells exhibit a greater size variation than those in the stem wood. They are provided with oval simple pits. Cell shape is elongated and terminates in straight or abruptly tapering end walls (fig. 11, h).

Ray parenchyma cells are isodiametric and show slight variation in size (fig. 11, i). They are provided with simple as well as with reticulate pitting.

SECONDARY XYLEM ELEMENTS OF LAURUS STEMS. The vessel elements exhibit considerable size variation (cf. fig. 12, g, j). As an average they are longer and narrower than the vessel elements of the roots (cf. table 1). The ligulate tips of the vessel elements are more conspicuous, more slender and longer than those of the root wood (fig. 12, c, d, g, j, k). This situation is similar to that described for *Umbellularia*. The vessel elements which approach the cylindrical form are rare (fig. 12, l). The transectional view of the vessel elements is angular in form.

Tertiary thickenings in the form of spiral bands on the secondary walls have not been observed although they were reported by Greguss (1945). The vessel elements are generally plugged by tyloses which do not occur in the vessel elements of the root wood of *Laurus*. The formation of tyloses in the vessel elements of *Laurus* stem distinguishes these elements from the vessel elements of the root and stem of *Umbellularia*. The presence of tyloses in other members of Lauraceae is reported in the literature. For example, Carpenter and Leney (1952) demonstrated the formation of tyloses in vessel elements of *Sassafras albidum* (Nutt.) Nees.

The vessel elements are provided with scalariform or simple perforation plates like those in the secondary xylem of the roots. However, a notable difference is the occurrence of reticulate perforation plates (fig. 12, e, f). The number of bars in scalariform perforation plates is reduced, and perforations with one or two bars are fairly common. The vessel elements always possess two perforations which are terminal in position. The occurrence of one or three perforations has not been observed although this situation is common in the vessel elements of the secondary xylem of the root. Either both of the perforation plates may be scalariform (fig. 12, a, j) or one of them scalariform and the other one simple (fig. 12, b-d) or both of them may be simple (fig. 12, g, k, l). The vessel elements with reticulate perforation plates also exhibit similar variation (fig. 12, e, f). In general, the perforation plates are inclined; occasionally they become horizontal in cylindrical vessel elements.

Scalariform, reticulate, and oval simple pits occur in varying combinations. Scalariform and simple pits may occur together on the longitudinal walls of vessel elements (fig. 12, d, k). Reticulate pits are commonly associated with reticulate perforation plates (fig. 12, f). Simple pits are arranged oppositely as well as alternately in vertical rows.

The fiber tracheids and septate fiber tracheids are rare in the secondary xylem but common in the primary xylem. The latter may be provided with one or two septa. The fiber tracheids in the stem are smaller than those in the roots.

Libriform wood fibers are the dominant wood elements of the stem structure. They are characterized by their gradually tapering forms, thick secondary walls, narrow lumina, and very small diameters (fig. 12, i).

Septate libriform wood fibers do not occur in stem wood.

Xylem and ray parenchyma cells of the stem wood are similar to those in the root wood. However, there are fewer parenchyma cells in the stem wood than in the root wood.

Conclusion and Summary

1. The secondary root and stem structures of *Umbellularia californica* and *Laurus nobilis* are compared anatomically. The pith of *Umbellularia* roots is composed of parenchyma cells, while the pith of *Laurus* roots consists of sclerenchyma cells. Idioblastic secretory cells and cells containing tannic substances are abundant throughout the secondary root and stem tissues of both genera.

2. Diffuse porosity is a common feature of the secondary xylem in the roots and stems of both species.

3. The wood parenchyma of *Umbellularia* roots exhibits an "apotracheal-diffuse" arrangement, while the wood parenchyma of *Umbellularia* stems exhibits a more advanced "paratracheal-vasicentric" arrangement. Wood parenchyma of *Laurus* roots is "apotracheal-diffuse," while the stem wood is "metatracheal," a more specialized condition.

4. The vessel elements in the secondary xylem of *Umbellularia* roots are provided with elongated ligulate tips, inclined perforation plates, and in transectional view, they are angular in form. These are considered primitive as compared to the vessel elements in the stem wood of the same species, the latter having short ligulate tips, transverse simple perforations, and a circular form in transectional view.

5. The arrangement of wood parenchyma and the comparative morphology of the tracheary elements reveal the fact that primitive characters are retained in roots, thus providing a useful anatomical tool for phylogenetic studies.

6. The vessel elements of the root and stem woods of *Umbellularia* are devoid of tyloses. Likewise, the tracheary elements in the root wood of *Laurus* lack tyloses, but the vessel elements of the stem woods of *Laurus* are often plugged by the development of tyloses.

7. The vessel elements in the root and stem woods of *Laurus* possess scalariform, reticulate, and simple perforation plates, and their longitudinal walls are provided with scalariform and simple pitting. In these

respects they resemble the tracheids. The vessel elements of *Umbellularia* are more specialized than those of *Laurus*.

8. Fiber tracheids, septate fiber tracheids, and libriform wood fibers occur throughout the secondary tissues of both species in varying sizes and proportions. On the other hand the septate libriform wood fibers and "gelatinous tracheids" are restricted to the secondary xylem of *Umbellularia*, but are entirely absent in the secondary xylem of *Laurus*.

9. These differences suggest that the phylogenetic affinity between these two genera is somewhat distant within the family, although both genera perfectly fit the natural group of Lauraceae in many respects.

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RUFUS DAVIS ALDERSON
(1858–1932)

Reid Moran

The name of R. D. Alderson has been known to botanists both from his large collections in San Diego County, California, and from the writings of E. L. Greene, who based several species on these collections and named for Alderson a phacelia, a helianthemum, and a rose. Yet to present-day botanists, Alderson is no more than a name.

Rufus Davis Alderson was born in Alderson, [now West] Virginia, November 2, 1858, the younger son of Rufus Davis Alderson and Hester Ann Ammen Alderson. After teaching for three years in West Virginia, he attended the National Normal School, in Lebanon, Ohio, receiving a bachelor of science degree in August 1882. His subjects included botany, zoology, natural philosophy, physiology, herbarium, and astronomy. After two more years of teaching, he was from 1884 to 1887 the proprietor and editor of the Alderson *Statesman*. The word "PRINTERY" on his door struck the fancy of a fellow editor, who, about 1885, wrote in the Pomeroy, Ohio, *Democrat:*

FIG. 1. Rufus D. Alderson. "In California about 1895."

"It has taken us full thirty-five years along printer's lane to reach a *printery*. . . . We have seen binderys, bakerys, hennerys, piggeries, hoggeries, doggeries and groggeries, but never till auspicious fate led us into the Greenbrier Valley and up to the throne of the STATESMAN did we see a printery. In the Sancterry—we mean sanctum—was the editor. A pleasant, courteous young gentleman, who has served the State and a pleased constituency as a member of the Legislature, and who is greatly interested in all that pertains to Alderson and surrounding country. . . . The sanctum of the statesman who runs the STATESMAN serves the quadruple purpose of consultation room, library, editorial office and sleeping room. . . . Here into the bachelor boudoir come the exchanges and their editors, and here come the politicians, deacons, doctors, leaders, drivers and proprietors of enterprise to consult and move ahead."

In November 1887, apparently after a break with his childhood sweet-heart, Emma B. Perry, Alderson came to San Diego. For a time he was foreman in a print shop, and it is thought that he did some newspaper work. On September 6, 1888, he married Minnie E. Matchin; they were divorced two years later. Between 1889 and 1897, he taught school in San Diego County, his posts including Potrero, Warners, Descanso, El Nido, Glencoe, Santa Ysabel, Spring Hill, and Bloomdale. His salary was $60 to $70 per month, and his contracts varied from half a month to eight months, one reading "length of term subject to amount of money available." From 1891 to 1895, most of his teaching was at Santa Ysabel, about 35 miles northeast of San Diego. During this time, he rented a small ranch at nearby Witch Creek, whose name appears on so many of his herbarium labels. In 1892 he returned to West Virginia to marry Emma Perry on August 8, leaving with her immediately for California again. In 1897 he was listed as living in Del Mar. That year, in rather frail health, he returned to West Virginia to live. Advised by his doctor to work outdoors, he took up cattle breeding and dairy farming and during the next 28 years built up a high-producing herd of Jersey cattle. He died at Lewisburg, West Virginia, May 11, 1932.

Alderson's daughter, Mrs. Ira D. Humphreys, remembers him as self-disciplined and a perfectionist, with an inquisitive mind, broad interests, and an exceptional memory, a man who worked long hours, never took a vacation, and while indoors always had a book in his hand. He read aloud to his family from history and literature.

At the age of fifteen, Alderson was already identifying native plants, as shown by notes and dates in his worn copy of Wood's "American Botanist and Florist," edition of 1874. It is not known how much he collected before leaving West Virginia, but after his return apparently his botany was mostly of a more practical sort; and seemingly few specimens of his from West Virginia have found their way into public herbaria. Millspaugh (1913:11) listed "R. W. Alderson" among those collectors a few of whose specimens were in the herbarium of Professor Sheldon, now in the herbarium of West Virginia University. Apparently the "D" of Alderson's signature was misread for "W": according to a letter from Weldon Boone, this "D" was sometimes open and could be so misread.

In San Diego County, Alderson collected plants at least from 1891 to 1896 but apparently most actively in 1893 and 1894. He also collected some insects and mollusks. Some details of his botany come from eight letters, now in the archives of the University of Notre Dame, written between April 16, 1893, and March 27, 1895, mostly at Witch Creek, from Alderson to Professor E. L. Greene at the University of California. Greene's letters have not been found. Alderson first wrote to Greene at the suggestion of H. W. Henshaw of the U.S. Biological Survey, who was visiting naturalist Frank Stephens, Alderson's neighbor at Witch Creek.[1]

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[1] Concerning the life of Frank Stephens, see Stephens 1918 and Huey 1938.

Alderson introduced himself to Greene as a student and teacher of botany and inquired about Greene's monograph on oaks, very highly recommended by Henshaw, and about other publications to help him identify plants. He later thanked Greene for a copy of Greene's "Manual of the Botany of the Region of San Francisco Bay," saying that for use in the schools it was much better than Rattan's "A Popular California Flora," then in use.

In October 1893, Alderson sent a large shipment of specimens to Greene for identification, saying that he had collected between 500 and 600 species that season. Many of these were from about Witch Creek; but he had also made two collecting trips over the Cuyamaca Mountains to Campo and thence to San Diego, one early in May, the other in late fall. In April 1894, he wrote that he was collecting again and wanted to make a clean sweep, taking everything. This year, with Greene in Europe, he had some plants determined by Samuel B. Parish of San Bernardino, a keen student of the flora of southern California.[2] Though it was a dry year and collecting relatively poor, the next February he shipped Greene 328 specimens with labels and eight more for which he did not know the names.

In April 1894, Alderson inquired of Greene as to possible purchasers of plant specimens to help defray cash expenditures in collecting. And in January 1895, he wrote that he preferred to sell to Greene rather than to exchange, for he had been getting many plants from other parts of the state by exchange and had not the room to store them.

There is no record that Alderson was associated with the San Diego Society of Natural History, but it appears that he was acquainted at least with T. S. Brandegee[3] and therefore probably with the other botanists of San Diego. In February 1895, Alderson wrote Greene that he hoped to visit the Colorado Desert with a party of naturalists and a florist. Labels for that year show that he was at Palmetto Springs on the Colorado Desert on the last day of March, that Brandegee was there on the first of April, and that Frank Stephens was at Vallecitos, about 10 miles to the northwest, on the first and third of April. We may probably assume that they all got together.

When Alderson went East, at least a good part of his herbarium went with him. Though much of it has since been lost, a remnant of some 275 specimens has recently been given by his daughter to the San Diego Museum of Natural History, where there were already about 100 of his specimens received with the herbarium of Mary Snyder. Many of the specimens sent to Greene apparently are still in the herbarium of the University of California at Berkeley, though the types, at least, went with Greene to the University of Notre Dame. There is a large representa-

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[2] Concerning the life of S. B. Parish, see Jepson 1932.

[3] Concerning the life of T. S. Brandegee, see Setchell 1926.

tion in the Dudley Herbarium, at Stanford University, from the Parish herbarium; but to judge from the specimens cited by Wiggins (1929), the set is far from complete. Other specimens are at Harvard University, the Missouri Botanical Garden, the University of Michigan, the United States National Herbarium, and probably various other institutions.

Alderson sent his specimens to Greene under numbers, though Greene did not cite these numbers and apparently they were not always kept on the labels. Many of Alderson's specimens in the Dudley Herbarium are numbered, not chronologically, perhaps in the same series; others are unnumbered. When he added printed labels to his own herbarium sometime after the collecting season of 1894—the last season represented in what I have seen of this herbarium—Alderson renumbered his specimens to beyond 12,400. The new numbers are written on the labels where they might be taken for field numbers, not only on his own specimens but also on many collected by S. B. Parish and by Frank Stephens. Besides the new numbers, specimens in his own herbarium sometimes also bear numbers corresponding to those on his specimens in the Dudley Herbarium, mostly penciled on the sheets, probably before the labels were added. Specimens from the herbarium of Mary Snyder and probably others sent out in exchange, bear his new herbarium numbers. Specimens he collected in 1895 and 1896 have numbers in the 900's to 1200's, apparently in continuation of the original series; but again, others are unnumbered.

My thanks are due to Dr. Robert McIntosh of the Greene-Nieuwland Herbarium, University of Notre Dame, for copies of the Alderson-Greene correspondence; to the Serra Museum of San Diego for several old records; to Miss Annetta Carter and Mrs. R. S. Ferris for checking herbarium labels; to Professor Joseph Ewan for various suggestions; and especially to Mrs. Ira D. Humphreys of Ronceverte, West Virginia, for many details of Alderson's life and for the fine portrait.

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THE OCCURRENCE OF NEW ARCTIC-ALPINE SPECIES IN THE BEARTOOTH MOUNTAINS, WYOMING-MONTANA

Philip L. Johnson [1]

During three summers of field work, 1958–1960, in the Beartooth Mountains, Wyoming-Montana, an extensive study was made of the alpine plant communities in relation to cryopedogenic (soil frost) processes and patterns (Johnson and Billings, 1962). Extensive alpine tundra is found in these mountains between elevations of 10,000 and 12,000 feet. The range is traversed by United States Highway 312 northeast of Yellowstone National Park. This study was concentrated on the southern end of the mountain range because of the better developed vegetation, the diversity of patterned ground features, and accessibility. From field observation the Beartooth tundra in Wyoming appears to have received much less glaciation than farther north in Montana which may account for the floristic diversity. Of particular interest are the numerous alpine bog habitats which are decidedly less frequent in the Rocky Mountain alpine zone than in Arctic regions. Many of these bog habitats are underlain with permafrost within three feet of the surface.

As a group the thirteen species discussed herein are of particular ecological interest because they are known primarily from the North American Arctic flora. It seems apparent that bog habitats and solifluction slopes have served as a refugia for Arctic plants since the last glacial period. The present hypothesis is that a bog environment is capable of dissipating the present excessive summer heat load by the high latent heat of vaporization associated with evaporation from a wet site. This hypothesis is analogous with the investigations of Dahl (1951) in Scandinavia where the lower altitudinal limit of many alpine species is correlated with maximum summer temperatures. It is probable that this correlation affects the plant through a critical maximum temperature as suggested by field studies of photosynthetic and respiration processes (W. D. Billings, personal communication).

Seven species, *Phippsia algida*, *Carex misandra*, *Kobresia macrocarpa*, *Eriophorum callitrix*, *Koenigia islandica*, *Rumex acetosa*, and *Draba glabella*, are new records in the Beartooth Mountains and in Wyoming. The remaining six species, *Festuca baffinensis*, *Kobresia bellardii*, *Carex capitata*, *C. nelsonii*, *Juncus albescens*, and *J. castaneus*, are new records in the Beartooth Mountains and rare species in Wyoming. Only *Carex capitata* and *Rumex acetosa* have been reported from Montana.

Phippsia algida (Phipps) R. Br. is a densely caespitose plant having boat-shaped leaf tips and resembling a small *Poa*, but it is a member of

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[1] Present address: Rocky Mountain Forest and Range Experiment Station, Laramie, Wyoming.

the tribe *Agrostideae*. The plants are relatively common only in wet sand or gravel at the base of late melting snowbanks. These sites, drenched with snowmelt water most of the growing season, are subjected to considerable needle-ice activity throughout the summer and fall. *Phippsia* forms an open community between alpine bog vegetation and late snowbeds devoid of plants. *Koenigia islandica* L. and *Epilobium alpinum* L. are frequent associates. The species, according to Porsild (1952), is strongly nitrophilous. It has a circumpolar, widespread, high Arctic distribution, and has also been collected at several sites in Clear Creek County, Colorado (Harrington, 1954). Collections were made on both sides of Beartooth Pass; one in the head of Wyoming Creek (18 July 1960, *Johnson 168*), and another east of Frozen Lake (10 August 1960, *Johnson 219*).

CAREX MISANDRA R. Br. is common to infrequent on slightly raised mineral soil within wet sedge bogs. It was found associated with *Kobresia macrocarpa* Clokey and *Poa longipila* Nash. The plants are densely caespitose with 3–5 spikes on long slender, often drooping peduncles. The species is known to have a circumpolar, high Arctic distribution, however, Harrington (1954) reports collections from north central Colorado and from northern Utah (Lewis, 1958). Collections were made on a solifluction terrace in the head of Wyoming Creek (5 August 1960, *Johnson 204*, and 10 August 1960, *Johnson 233*).

KOBRESIA MACROCARPA Clokey [*K. bellardii* var. *macrocarpa* (Clokey) Harrington] is an alpine sedge relative previously reported only from central Colorado (Harrington, 1954). It differs markedly from *K. bellardii* in having a larger inflorescence, stouter culms and wider leaves. No intergradation was observed. Both species are apparently rare in Wyoming, although they are close associates in the Beartooth tundra on well developed soils in alpine turf. The collections are: 30 August 1960, *Johnson 184* on a gentle slope east of Twin Lakes; 5 August 1960, *Johnson 205A*, and 10 August 1960, *Johnson 233A* from a sedge meadow on a solifluction terrace in the head of Wyoming Creek; and 20 August 1960, *Johnson 257* from a steep northwest slope north of Gardner Lake.

ERIOPHORUM CALLITRIX Cham., a cotton grass, is confined to three bog sites east of Beartooth Pass. Two of these sites are known to be underlain with permafrost. The species is codominant with *Carex scopulorum* Holm on water-saturated peats formed behind solifluction terraces. The plants form individual tufts with solitary spikelets subtended by black to lead-colored spathes and scales. The species is widely distributed in the North American Arctic and subarctic regions, but no previous reports are known from the Rocky Mountains according to Porsild (1952). The collections are: 21 June 1958, *Johnson 58B* and 27 July 1958, *Johnson 58* from near the head of Twin Lake cirque; 24–30 July 1959, *W. M. Johnson*, near the head of the North Fork of

Popo Agie Creek in the Wind River Mountains, Fremont County, Wyoming (identified by A. E. Porsild).

KOENIGIA ISLANDICA L. is one of the few annuals in the Arctic-alpine flora. The plants, which seldom exceed 3 cm. in height, are locally very numerous in saturated sands, moss mats and organic soil which receive snowmelt water throughout the summer. *Koenigia* may extend into wet sedge meadows around the base of sedge hummocks, but it is mostly confined to the margins of alpine bogs, lake shores, and stream drainages adjacent to late snowbeds. The one or two pairs of sessile cauline leaves and the terminal, apetalous flower of plants exposed to direct sunlight develop more anthocyanin pigment than plants growing in partial shade. The distribution of this plant is considered circumpolar, low Arctic. It has recently been collected at several alpine stations in Colorado including Mount Evans and Rocky Mountain National Park. The species was observed at several sites on both sides of Beartooth Pass (4 August 1959, *Johnson 116*).

RUMEX ACETOSA L., green sorrel or sour dock, is naturalized from Europe throughout much of temperate, eastern North America. It appears, however, to be native in the American Arctic. A single record is known from Glacier National Park, Montana (6 July 1922, *J. W. Severy 36*) along Gunsight Pass Trail. The only plants of the species encountered recently were growing in moist alpine turf on a steep northwest slope north of Gardner Lake (26 July 1958, *Johnson 63B*). It is assumed that this collection represents a southern range extension of native Arctic populations rather than an introduced weed, since the plant is not otherwise known to occur in Wyoming.

DRABA GLABELLA Pursh is the probable identification of a collection which has been tentatively confirmed by Dr. Reed C. Rollins of the Gray Herbarium (Rollins, 1961). If true, this site represents a long southern extension of its known Arctic distribution. Porsild (1952) reports the species as, "strongly nitrophilous, favouring animal dung." The widely scattered plants were growing in sheep trails on a very steep, exposed northwest slope north of the highway at Gardner Lake (8 July 1959, *Johnson 112*).

It should be pointed out that this species is in addition to eleven alpine *Draba* species reported by Rollins (1953) from Clay Butte, a glacial monadnock of sedimentary rocks seven miles west of Beartooth Pass. Five of these species and *D. glabella* were collected from granitic parent material in the course of this study (Johnson and Billings, 1961).

Several additional collections from the Beartooth Mountains are from similar habitats. Thanks to the annotations of Dr. A. E. Porsild, *Festuca baffinensis* Polunin, is now distinguished from *F. brachyphylla* Schult. by a culm which is puberulent on the upper half and a usually shorter, dark purple panicle. A previous collection from Park County, (*Porter*

& Rollins 5875) has been so annotated. The present collection (5 August 1960, *Johnson 203*) is from a frost boil in the head of Wyoming Creek.

KOBRESIA BELLARDII (All.) Degland [by some, *K. myosuroides* (Vill.) Fiori and Paol.] was first collected in Wyoming near the head of the North Fork of Popo Agie Creek, Fremont County in the Wind River Mountains (24–30 July 1959, *W. M. Johnson*). It is now recorded from Park County (30 July 1960, *Johnson 185*) from a gentle alpine slope east of Twin Lakes. It was associated with, but distinct from, *K. macrocarpa*. In the Colorado alpine tundra, *K. bellardii* is dominant, forming nearly pure stands on undisturbed snow-free ridges; the genus is evidently rare in Wyoming.

CAREX CAPITATA L. is known from one previous collection in Wyoming (1893, *Frank Tweedy 3*, Big Horn Range, Sheridan County). It was again encountered at 11,000 feet elevation on a ridge top one mile northwest of Beartooth Pass (20 August 1958, *Johnson 55*). The species is known from Eurasia, southern South America, and Arctic North America, extending southward as far as Colorado, Utah, and Nevada (Lewis, 1958).

CAREX NELSONII Mack. is restricted to Colorado, Utah, and Wyoming. Within Wyoming three previous collections represent the species in Carbon and Albany Counties, all within 30 miles of the Colorado state line. A very substantial northern range extension is represented by plants found in a wet sedge meadow in the head of Wyoming Creek (10 August 1960, *Johnson 232*).

JUNCUS ALBESCENS (Lange) Fern. (*J. triglumis* L.) and J. CASTANEUS J. E. Smith are known in Wyoming by one previous collection, both from the Medicine Bow Mountains, Albany County. Both species are low Arctic-Alpine species known in Colorado. It is not surprising, then, to find them in wet stream gravel with *Juncus biglumis* L. in northern Wyoming. The collections are: *J. albescens, Johnson 221A*, 31 August 1959; *187B,* 29 July 1960; *205B,* August 1960; *235,* 10 August 1960; *J. castaneus, 121B,* 31 August 1959; and *186*, 29 July 1960. All specimens were collected from wet gravel on solifluction terraces in the head of Wyoming Creek; the two species are usually found together.

Specimens of these species are deposited in the Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyoming. All Johnson collections cited without initials are those of the author. Help with the identifications was received from C. L. Porter, A. E. Porsild, and Reed C. Rollins and is gratefully acknowledged. Appreciation is also expressed to the National Science Foundation for financial support under a N.S.F. grant (G-5574, W. D. Billings, Environmental Biology).

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THE UNIQUE MORPHOLOGY OF THE SPINES OF AN ARMED RAGWEED, AMBROSIA BRYANTII (COMPOSITAE)[1]

WILLARD W. PAYNE

The true ragweeds, wind-pollinated composites of the genus *Ambrosia*, include our most serious hay fever plants. They are generally herbs or subshrubs. Their indument commonly consists of delicate hairs and glands, although some species become more or less hispid. Spines are not characteristically borne on the vegetative body of ragweeds, in spite of the fact that most ragweed species are found in open or disturbed habitats where spiny plants are common. The species to be discussed, *A. bryantii*, is interesting not only for possessing spines, but for the nature of the spines themselves, which, to my knowledge, are unique among similar structures in vascular plants.

Armature of plants is accomplished in a number of ways, and the fact that many unrelated species possess spines is frequently used in teaching to illustrate convergent evolution. With the exception of the case of *A. bryantii*, presented below, spines which serve to protect the plant (thorns, prickles and other spine-like structures being included here under the term "spines") are formed from organs and tissues which are not directly associated with the flowers or fruits. They may be modified leaves (*Berberis thunbergii* DC.), leaf margins (*Cirsium* spp.), stipules (*Robinia pseudoacacia* L.), lateral branches (*Gleditsia triacanthos* L.), terminal shoots (*Rhamnus cathartica* L.), or epidermal emergences (*Rosa* spp.). Only one near relative of *Ambrosia* is spiny, i.e., *Xanthium spinosum* L. In this species the spines appear to be modifications of the two prophylls

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[1] Publication Number 22 on atmospheric pollution by aeroallergens, under research grant Number E–1379 from the National Institute of Allergy and Infectious Diseases, Public Health Service. Thanks are due Mr. D. M. Porter who supplied the specimens for the drawings, and Dr. W. H. Wagner, Jr. who helped in preparing the manuscript.

of the lateral branches, each prophyll being entirely changed to a three-branched spine.

In addition to such vegetative spines, which are more or less permanently associated with the plant, many species produce spiny fruits. Fruit spines may be of value to the organism as a means of dissemination of the seeds, or as protective structures which tend to prevent animals from eating the developing embryos, or often they serve both functions. Ordinarily, however, such spiny fruits are not retained by the parent plant as protective organs for the plant *per se*, but are shed when the seeds have developed.

In all respects the species under discussion here conforms to the genus *Ambrosia*, although I fail to find that the proper name combination has been made. Curran (1888) placed it in the genus *Franseria* before the true nature of the group was known. It was placed in the monotypic genus *Acanthambrosia* by Rydberg (1922) on the basis of having more than one achene per fruit. As Shinners (1949) pointed out, however, characters of this nature are not sufficient to distinguish genera in the Ambrosieae. Accordingly, the new combination is made below:

Ambrosia bryantii (Curran) Payne, comb. nov. *Franseria bryantii* Curran. Proc. Calif. Acad. ser. 2, 1:232. 1888. *Acanthambrosia bryantii* (Curran) Rydb., N. Am. Fl. 33:22. 1922.

In the genus *Ambrosia,* considerable modification of the floral structures has occurred. Pollen and fruit production are carried out by different heads on different parts of the plant. Staminate heads are borne in spikes at the tips of the branches. Each head consists of a cluster of centripetally developing, sterile flowers partially enclosed by a cup-shaped involucre, the phyllaries of which are fused laterally. Pistillate heads are found in the axils of leaves and bracts located below the staminate spikes. The pistillate flowers are borne singly or in clusters of from two to five. The involucre of the pistillate head has become concrescent, the phyllaries being united to form a hard, resistant, flask-shaped structure within which the achenes are borne. The tips of the phyllaries which form the involucral case are usually represented by more or less prominent spines. The spines may be blunt or sharp, straight or hooked at the tips, but in all species except *A. bryantii* they are short, usually shorter than the body of the fruit (fig. 1,C). The pappus is entirely lacking on both the male and the female flowers. Thus the fruit consists of one or more achenes enclosed by the spiny, indehiscent covering formed by the involucre of the pistillate head. In most species all of the fruits are shed at the end of the growing season, or as rapidly as they mature.

Ambrosia bryantii is found on the desert plains of central Baja California, Mexico, where it is common and often quite abundant. It forms a small, perennial shrub which bears clusters of long, chalky spines along its stems. These spines are usually more abundant toward the stem apices

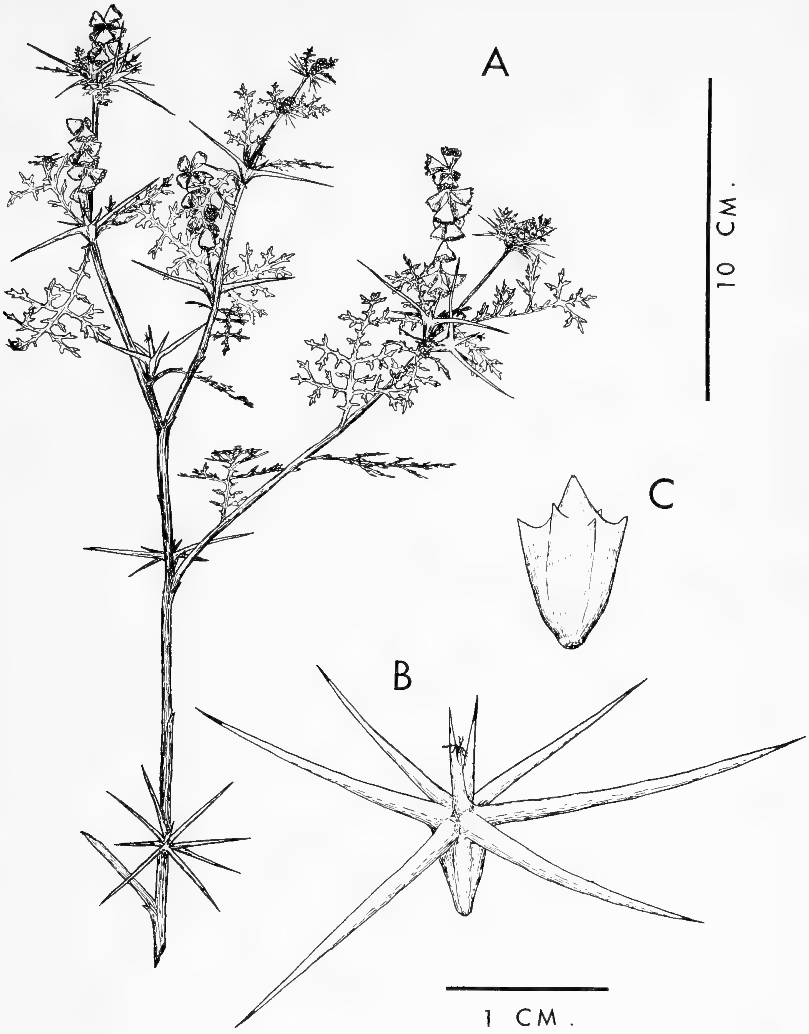

FIG. 1. A, habit sketch of *Ambrosia bryantii* showing spiny aspect of a branch; B, single fruit of *A. bryantii* showing the long spines at the apex of the fruit; C, fruit of giant ragweed, *A. trifida* L., a common, annual species of the eastern United States. A and B drawn mainly from *D. M. Porter 451*, from 29 miles south of El Crucero, Baja California, Mexico.

where one commonly finds inflorescences in all stages of development (fig. 1,A). When examined closely, these spines are seen to be borne on the fruits (fig. 1,B). The spines appear in every way to be homologous with the processes of the pistillate involucres of other species of *Ambrosia*. In *A. bryantii*, however, they are greatly exaggerated, forming very sharp spines 1.5 to 3.5 cm. long, with a basal diameter of 2 to 3 mm.

The unusual and significant fact is that some of the fruits remain permanently attached to the plant through several growing seasons. Examination of many specimens has shown that a certain number of the fruits which develop during the perennial growth of the plant are thus retained and serve the function of armature.

In summary, the spines of *A. bryantii* represent what appears to be a unique morphological type of protective device, at least in the North American flora. They are actually borne on the fruits of the plant. The whole plant tends to become spiny because some of the fruits remain permanently attached to the stems. This unusual armature of *A. bryantii* adds another striking illustration to the many examples of convergence in the evolution of vascular plants.

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NOTES AND NEWS

The following publications are of interest.

Drawings of British Plants, by Stella Ross-Craig. Since mention was last made in MADROÑO of this beautifully executed series, the following numbers have appeared: Part XIII. Umbelliferae (2), Araliaceae, Cornaceae, 30 plates, 1959 [this completes Volume IV which comprises Parts X–XIII, 40 shillings. Cloth bound]. Part XIV. Adoxacaeae—Dipsacaceae, 39 plates, 1960. Part XV. Compositae (1), 28 plates, 1960. Part XVI. Compositae (2), 33 plates, 1961. Part XVII. Compositae (3), 36 plates, 1962. G. Bell and Sons, Ltd., London. Parts XIV and XVII are quoted at 10/6; the others at 9/6. The publishers state that photographs or blocks may be obtained for reproduction purposes.

Arizona Flora, by Thomas H. Kearney, Robert H. Peebles, and collaborators. Second edition, 1085 pp. University of California Press, Berkeley and Los Angeles. 1960. A fifty-page supplement by John Thomas Howell and Elizabeth McClintock of the California Academy of Sciences, and collaborators, provides material accumulated since the publication of the first edition in 1951. Three species (*Typha angustifolia, Potamogeton richardsonii, and Elatine californica*), reported in the January, 1961, issue of MADROÑO as new to the flora of Arizona, could have been included in the Supplement had the editors of MADROÑO realized the imminent appearance of the second edition.

Ecosystems of the East Slope of the Front Range in Colorado, by John W. Marr. University of Colorado Studies, Series in Biology, No. 8, pp. 1–134. University of Colorado Press, Boulder, November, 1961.

The Systematics of Oenothera, Subgenus Chylismia, by Peter H. Raven. University of California Publications in Botany 34 (1): 1–122. University of California Press, Berkeley and Los Angeles, 1962.

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FACTORS INFLUENCING SURVIVAL AND GROWTH OF A SEEDLING POPULATION OF ARBUTUS MENZIESII IN CALIFORNIA

John Pelton

Differential survival in the seedling stage of potentially competing species is widely recognized to be of major significance in determining vegetational patterns and succession. Furthermore, an understanding of seedling ecology is essential to evaluate relative adaptation of different life cycle stages of a species, and to understand the mechanics of natural selection in plants. A brief review of these problems has been previously published by the writer (Pelton, 1953).

Arbutus menziesii Pursh, Pacific Madrone, is an ericaceous tree ranging from southern California to southern British Columbia. Tarrant (1958) has summarized much of what is known of the autecology of this species. The present study of a naturally-occurring seedling population of *Arbutus* was done from February to August of 1958 in the Santa Cruz mountains of central coastal California.

Grateful acknowledgment is extended to Dr. Victor C. Twitty, Head of the Department of Biological Sciences, and to Dr. Ira L. Wiggins, former Director of the Natural History Museum, both of Stanford University, for kindly providing facilities; to Mrs. Roxana S. Ferris, Dr. John H. Thomas, and Dr. Wallace Ernst for aid in plant identifications; to Dr. H. N. Hansen and Dr. J. R. Parmeter of the Department of Plant Pathology of the University of California, and to Dr. W. W. Wagener of the Division of Forest Disease Research of the Southwestern Forest and Range Experiment Station for examinations of pathological material; and to my wife, Jeanette S. Pelton, for help throughout the study.

General Methods

The individual fates of several hundred emerging *Arbutus* seedlings were followed over a six month period, and mortality was correlated with observed or measured microenvironmental factors. Smaller numbers of seedlings of a few other species, especially *Sequoia sempervirens* (Lamb.) Endl. and *Heteromeles arbutifolia* (Ait.) M. Roem., also occurred in the plots and were included in the study.

The study area consisted of several hectares of second-growth *Arbutus-Quercus-Sequoia* forest on the northeast-facing slope of the Santa Cruz mountains, at about the 184 meter contour on Martin Creek. The plots were situated on both sides of the Old La Honda Road which bisects the area, 0.8 km. beyond the intersection with Portola Road, in San Mateo County.

Fifteen plots 30 cm. on an edge were established arbitrarily where seedlings were emerging in large numbers and representing the range of micro-

Madroño, Vol. 16, No. 8, pp. 237–276. October 25, 1962.

habitats in the study area. All seedlings were individually staked and charted to insure re-identification. Twice a week for most of the study period each seedling was examined and probable causes of mortality evaluated. Measurements of selected seedlings were made once a week, and the root systems of representative individuals adjacent to the plots excavated monthly.

Environmental measurements were made within the seedling stratum of air and soil temperatures, precipitation, vapor pressure deficit, evaporation, light intensity, soil moisture, pH, wilting percentage, and other conditions. In addition, rodent and bird exclosures were utilized for certain plots, and the vegetational structure and composition analyzed. Details of all these procedures are described below.

RESULTS

VEGETATIONAL ANALYSIS. The results of the vegetational analysis are summarized in Tables 1 and 2. The study area was not homogeneous, but ranged from a closed dense *Arbutus-Sequoia* forest above the road ("shade plots," fig. 1) to a semi-open and lower *Arbutus-Quercus* forest below the road ("sun plots"). Plots which were intermediate in environment were grouped in a third category ("all other plots"). Both evergreen (*Q. agrifolia* Nee) and deciduous (*Q. kelloggii* Newb.) *Quercus* species were of significance in the latter two forest types. These forests were on a northeast-facing slope of a narrow ravine, and graded into chaparral on adjacent ridges and south-facing slopes.

The entire area had been both lumbered and burned, the latter having been indicated by fire scars and multiple trunks. The closed forest in which the shade plots were located had almost no saplings of any species. The semi-open sun plot forest showed considerable numbers of *Arbutus* and *Quercus* seedlings and saplings. Less common trees not listed in Table 1 included *Aesculus californica* (Spach) Nutt., *Umbellularia californica* (Hook. and Arn.) Nutt., and *Pseudotsuga menziesii* Franco. The rarity of the latter tree and the almost complete absence of *Sequoia* seedlings suggest that a conifer overstory will not dominate the study area in the foreseeable future.

Tall shrubs (averaging over 1.5 m. at maturity) were locally abundant on the sun and miscellaneous plots, but rare on the shade plots. *Heteromeles arbutifolia* and *Corylus californica* (A. DC.) Rose were most frequent, with occasional individuals or clumps of *Ceanothus sorediatus* Hook. and Arn., *Rhamnus californica* Esch., *Holodiscus discolor* v. *franciscana* (Rydb.) Jepson, and *Sambucus mexicana* Presl ex DC. Low shrubs included mostly *Symphoricarpos mollis* Nutt., *Lonicera hispidula* v. *vacillans* A. Gray, and *Rhus diversiloba* T. & G., with occasional *Rosa gymnocarpa* Nutt. and *Rubus vitifolius* subsp. *ursinus* (Cham. & Sch.) Abrams, all least abundant again in the shade plots. Herbaceous species included *Trientalis latifolia* Hook., responsible for most of the density figures for "herbs" in Table 2, *Dryopteris arguta* (Kaulf.) Watt., which

FIG. 1. View of forest in an area where *Arbutus* dominates over one of the shade plots (not visible).

TABLE 1. SUMMARY OF THE TREE STRATUM WITHIN THE STUDY AREA

PLOT LOCATION	TREE SPECIES	Density per hectare				Basal area of trees over 10 cm. DBH (sq. m. per ha.)	Frequency[3] of trees over 10 cm. DBH	Average % cover
		Saplings less than 2.5 cm. DBH[1]		Trees[2] over 2.5 cm. DBH				
		Over 1 year & under 30 cm. tall	Over 30 cm. tall	2.5-10 cm. DBH	Over 10 c.m. DBH			
SHADE	A. menziesii	0	0	0	561	49.0	60	49
	Q. agrifolia	0	239	0	0	0	0	0
	S. sempervirens	0	0	79[4]	478	90.7	60	42
	Totals	0	239	79	1039	139.7		94[5]
SUN	A. menziesii	1580	400	99	200	34.2	25	38
	Q. kelloggii	99	498	197	200	6.9	50	15
	Q. agrifolia	988	597	99	200	6.2	50	21
	Totals	2667	1495	395	600	47.3		75[5]
ALL OTHER PLOTS	A. menziesii	0	67	0	1065	53.9	83	59
	Q. kelloggii	67	200	0	133	3.0	17	2
	Q. agrifolia	534	400	0	67	1.1	17	12
	Totals	601	667	0	1265	58.0		85[5]

[1] Diameter at breast height.
[2] Or multiple trunks.
[3] Percentage of 5 × 5 meter plots occupied.
[4] Of sprout, not seedling, origin.
[5] Includes minor species not listed.

was absent from the sun plots, and *Bromus laevipes* Shear., *Satureja douglasii* (Benth.) Briq., and *Pityrogramma triangularis* (Kaulf.) Maxon, all three absent from the shade plots. The moss stratum, composed of several mosses and an *Anthoceros* sp., was present only on the sun plots where litter was scant. Mineral soil exposure averaged 8% on the sun plots and 0% on the shade plots. Nearly 30 additional vascular plants not listed above also occurred in the study area. Voucher specimens for most of these, including several seedling stages of *Arbutus* and certain other species, are in the herbaria of the writer or Butler University.

The average maximum height of the *Arbutus* canopy was 15 m. in the dense *Arbutus-Sequoia* phase, with occasional *Sequoia* emerging to a maximum of 32 m. The maximum height of the *Arbutus-Quercus* canopy averaged only 10 m. The 75% cover provided by the latter forest was at its maximum during the major part of this study; the deciduous *Q. kelloggii* had fully leafed out by the end of March, and the forest canopy did not begin to open significantly until *Arbutus* began abscising part of its foliage in August.

In general terms, that portion of the study area referred to as *Arbutus-Quercus* is comparable to the "Broad Sclerophyll Forest" of Cooper (1922), the "Black Oak-Madrone Forest" of Mason (1947), the "Mixed Evergreen Forest" of Munz and Keck (1959), Whittaker (1960), and Thomas (1961a), and the "Woodland" of Jensen (1939). The "shade" plots, on the other hand, are transitional with the "Redwood" (*Sequoia*)

TABLE 2. SUMMARY OF SHRUB AND HERB STRATA WITHIN THE STUDY AREA

PLOT LOCATION	SHRUB AND HERB STRATA	AVERAGE DENSITY PER SQ. METER	AVERAGE PER CENT COVER
SHADE	Tall shrubs	.02	27
	Low shrubs	14	
	Herbs	6	
	Moss	....	0
SUN	Tall shrubs	.1	36
	Low shrubs	45	
	Herbs	6	
	Moss	....	16
ALL OTHER PLOTS	Tall shrubs	.1	64
	Low shrubs	27	
	Herbs	34	
	Moss	....	0

forest of most of these authors. The entire study area is mapped as potential conifer cropland by the Forest Service (1950).

A number of vegetational and environmental studies have been made in the Santa Cruz mountains near the study area, including the classic researches of Cooper (1917, 1922) as well as the more recent ones of Springer (1935), Moeur (1948), and Oberlander (1953). Floristic work in the area has been recently reviewed by Thomas (1961b).

PHYSICAL FACTORS. Measurements of certain environmental conditions near the sun and shade plots are in figures 2 and 3. Where practicable, measurements were made within the air or soil strata in which the seedlings actually grew. Air and soil temperatures were recorded with Six's type maximum-minimum thermometers, the former at 2 cm. above the soil or litter surface and the latter at 3 cm. below this surface. A small ventilated reflective metal shelter was employed for the air thermometers. Maximum air temperatures on sun plots (Station 1, lower graph of fig. 2) reached 42°C. on July 15, but although actual surface soil temperatures were much higher, no stem girdle of seedlings resulted owing to hypocotyls having long since passed the "succulent stage" (Baker 1950:255).

Minimum air temperatures were likewise reached in the semi-open Station 1, but at no time did they fall below 2°C. Frost was therefore not a factor in mortality even though seedlings were emerging during the normally coldest part of the year. The nearest official weather station having long term temperature records (Redwood City) suggests that January and February of 1958 were appreciably warmer than normal although there was only slight deviation during the remainder of the study (United States Department of Commerce 1959). Under dense *Sequoia* canopy (Station 2) the maximum temperatures were greatly depressed but the minimum temperatures were only slightly raised, resulting in a much smaller diurnal variation. Soil temperatures at 3 cm. (upper graph

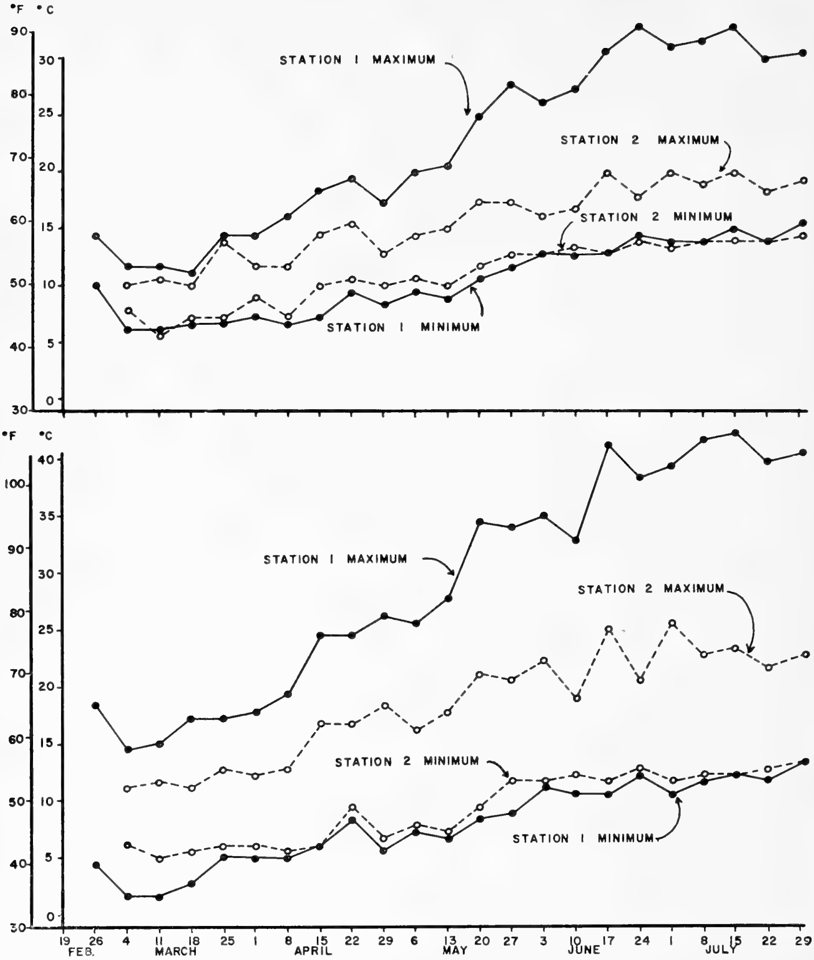

FIG. 2. Soil temperatures (above) at 3 cm., and air temperatures (below) at 2 cm. Station 1 semi-open, Station 2 in deep shade.

fig. 2) showed a pattern similar to that of air temperatures except for a tempering of the extremes. It is significant, however, that temperatures of 33°C. were reached at this level twice at Station 1. Such high temperatures at this depth help explain the soil drought which rapidly obtains in the upper soil level of semi-open areas following rains (fig. 3).

Vapor pressure deficit measurements were taken on each visit to the area among the sun plots between 12 noon and 1 p.m., as close to the ground as a small sling psychrometer could be used (about 30 cm.). There was a detectable upward trend as the season progressed (fig. 3), but the summer advection fogs from the ocean characteristic of the *Sequoia* belt (Cooper 1917) raised the humidity significantly above that which would

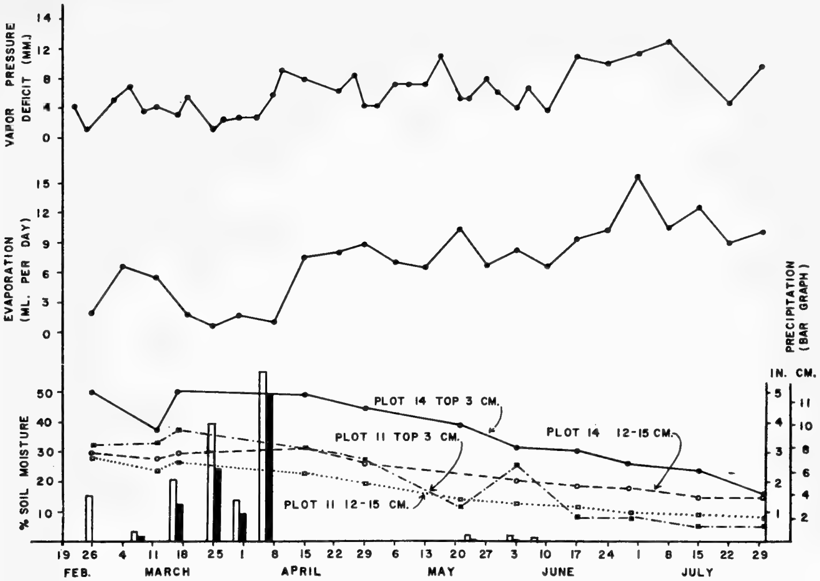

FIG. 3. Vapor pressure deficit, evaporation, precipitation, and soil moisture. Plot 11 in semi-open, plot 14 in shade. Shaded bars represent precipitation under dense canopy, unshaded bars under an opening, only the latter record being available on February 26.

otherwise prevail. Although the study area was near the inland edge of the fog belt, this factor is doubtless significant in prolonging survival in the face of intensifying summer drought. In addition, several light showers in May and June had a detectable effect on depressing the vapor pressure deficit.

Evaporation data as shown in figure 3 represent the average of corrected readings of two standardized and periodically checked spherical porcelain atmometers placed with the base of the spheres 10 cm. above the soil surface among the sun plots. The figures represent the maximum evaporation stress to which the seedlings were subjected. Again, an upward trend is apparent in spite of depression during rainy and foggy periods.

Precipitation data were obtained from two 7.5 cm. diameter rain gauges, one under an opening in the canopy among the sun plots, and the second under complete cover adjacent to the shade plots. Precipitation was concentrated in winter and early spring, as is normal for Mediterranean-type climates. Excluding the February rain, at which time only one gauge was operating, an average of 30% more precipitation was received under the light than under the dense canopy. Since the gauges were but 50 m. apart and in similar positions with regard to topography, rainfall interception by the vegetational canopy was probably responsible for this difference. Official precipitation records from nearby weather stations indicate that the rainfall during the study period was 2.7 times normal, reflecting the unusually wet year for the region.

Light intensity was measured photoelectrically by reflection for each seedling plot. This was done five times between 9 a.m. and 3 p.m. on a clear day in early May. The resulting foot candle figures were arbitrarily corrected for estimates of the cover of low vegetation below the level at which readings could be made. The final results facilitated the distinction of "sun" from "shade" plots, although not permitting expression in absolute terms. In the former plots, sun reached the seedlings a small to moderate part of each day, but only an occasional sun fleck penetrated to the shade plots.

Soil moisture determinations were made adjacent to six sun and shade plots at two-week intervals. Two depths were sampled in duplicate with a soil tube, the top 3 cm. of mineral soil, and the depth range of 12 to 15 cm. Data for one representative shade plot (Plot 14) and one sun plot (Plot 11) are given in figure 3. Greenhouse determinations of permanent wilting percentages (method of Daubenmire, 1959) for these soils gave the following results:

PLOT	DEPTH (CM.)	WILTING (PER CENT)	DATE WILTING FIRST REACHED IN FIELD (PER CENT)
14	1–3	19.8	July 29
14	12–15	13.9	....
11	1–3	18.5	May 21
11	12–15	11.8	June 17

In marked contrast to Plot 11, Plot 14 reached the wilting percentage only by July 29 at the surface and at no time deeper than this. Soil drought arrived much earlier and reached a greater intensity on sun than shade plots.

The contrast of mineral soil drought does not take into account the litter through which seedling roots often did not penetrate. The sun plots were all similar in having usually less than 1 cm. of litter, often exposing mineral soil or moss on small hummocks. Litter on shade plots averaged 5 cm., but reached 8 cm. on Plot 14. Although the but slightly decomposed (mor-type) litter was thicker under *Sequoia,* the large coriaceous leaves of *Arbutus* often forced roots to grow horizontally for long periods. Litter of sun plots was dry to the touch within a day following rains, but the lower layers of shade plot litter were moist in July on some plots. It is clear that the "sun" and "shade" plots differed in other important conditions than light alone. The shade plots can best be viewed as densely shaded sites with heavy litter and moist mineral soil, while sun plots are those of moderately open sites with thin litter, if any, and dry soil. Past and present soil disturbance by rodents was also much more important in the semi-open than in the shade, and the incidence of injurious invertebrates and fungi also differed.

The soils in the study area are classifiable as the "rough broken phase" of the Altamont clay loam, a residual group largely derived from interbedded sandstones and shales, and retentive of moisture but well drained. Rocks are uncommon, and a B horizon is not distinguishable. Electro-

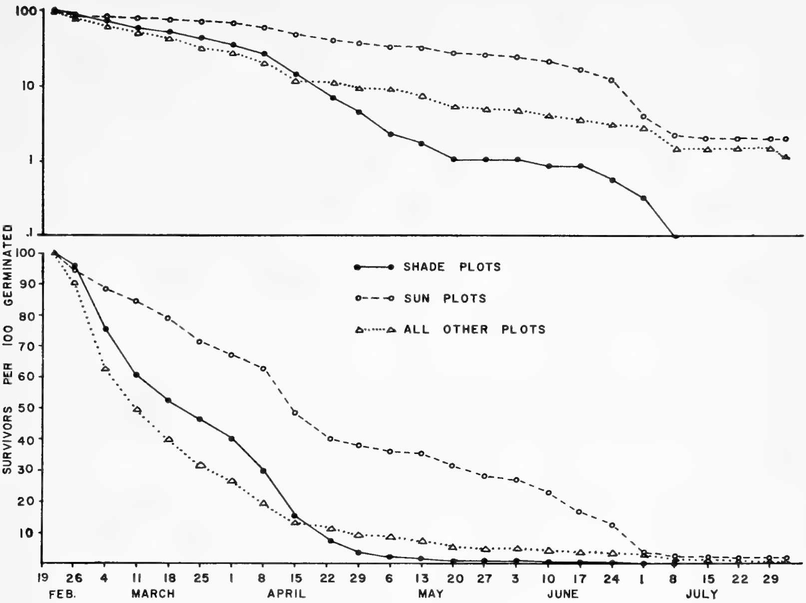

FIG. 4. Survivorship curves of *Arbutus* on log scale (top) and arithmetic scale (below).

metric pH determinations of the top 3 cm. of mineral soil ranged from 5.7 to 6.6, averaging 5.96. At 15 cm. the range was 4.7 to 6.5 with a mean of 5.65. The surface soil pH of the thin-littered sun plots averaged slightly lower (5.9) than that of the thickly covered shade plots (6.2); this anomaly probably resulted from rodents mixing acid subsoil with topsoil on only the sun plots.

MORTALITY. *Arbutus* seedling mortality results are presented graphically in figures 4, 5, and 6. The survivorship curves in figure 4 compare the seasonal advance in mortality on shade, sun, and all other plots. Since a straight line on a log scale indicates a constant mortality rate, the top curves show that such a condition prevailed only during certain periods in each habitat. The greater mortality in the shade at almost all times is evident in comparison with the sun plots.

Most *Arbutus* seedlings had already germinated by the time the study was initiated on February 19, but all were in the early cotyledon stage. Of the ultimate total number, 92% had germinated on the sun plots, 77% on the shade plots, and 86% on all others. The remaining seedlings appeared sporadically up to April 8 on the sun plots and April 15 in the shade. Consequently, the curves of figure 4 are expressed as survivors per 100 germinated rather than as survivors of an initial maximum population. A total of 829 *Arbutus* seedlings approximately equally divided between the sun, shade, and other plots varied from 20 to 108 per plot 30 cm. on a side, or 222 to 1200 per square meter.

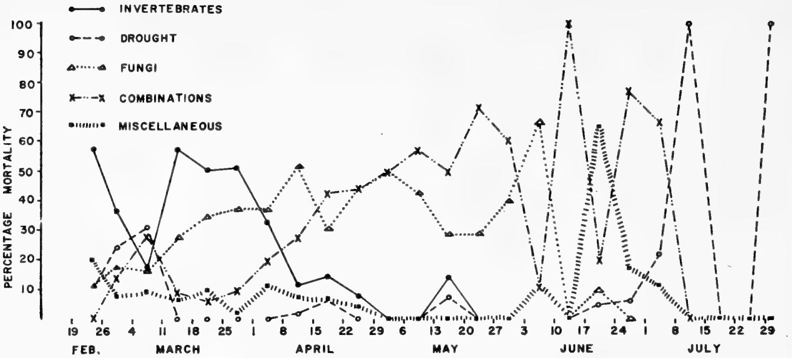

FIG. 5. Seasonal variations in causes of mortality of *Arbutus* seedlings on all plots combined, expressed as a percentage of total mortality for a given week.

At the termination of the study on August 2 no *Arbutus* seedlings were present on the shade plots, 2% had survived in the sun, and 1% on all other plots. Seedlings of other species which happened to occur on the plots, totalling 75, were also included in the study. Of these, *Sequoia* was represented by 32 individuals, all on the shade plots, of which none survived beyond April 23. Twenty-one seedlings of *Heteromeles* were present on sun and other plots (none in the shade), one of which was living at the end of the study. There were no survivors from three seedlings of *Sanicula crassicaulis* Poepp. ex DC., three of *Satureja douglasii,* or of eight unidentified plants of several other species. Four seedlings of *Pyracantha* sp. and one of an *Acacia* sp., probably carried in by birds from nearby gardens, also failed to survive. On the other hand all three seedlings present of *Lonicera hispidula* survived the entire period. Other species having occasional seedlings in the locality but not on the plots included what were probably *Rhus diversiloba, Osmorrhiza chilensis* H. & A., *Rosa gymnocarpa, Rhamnus californica, Dentaria californica* Nutt., *Bromus laevipes, Symphoricarpos mollis,* and *Hedera helix* L. (probably bird-disseminated from nearby gardens).

Figure 6 is a summary of *Arbutus* mortality under different conditions. The damage by invertebrates was probably mostly by slugs (Order Pulmonata). A small species of this group was found feeding upon seedlings on several occasions in early morning, although most damage was nocturnal. Frequently the cotyledons were completely eaten, leaving the decapitated hypocotyl, and sometimes the entire shoot disappeared. Two plots were temporarily covered on sides and top with 3 mm. mesh hardware cloth exclosures to test for bird or rodent feeding, but without effect on injury by this cause. By comparing the data in figure 5 with that in figure 3, it can be seen that mortality of this type correlated positively with precipitation. It was also of greater relative importance on the shade plots than the sun plots (fig. 6). In addition, covering of seedlings by falling leaves increased their chances of being eaten. All these observations would tend to implicate slugs or other soil-dwelling invertebrates. A mite (Order

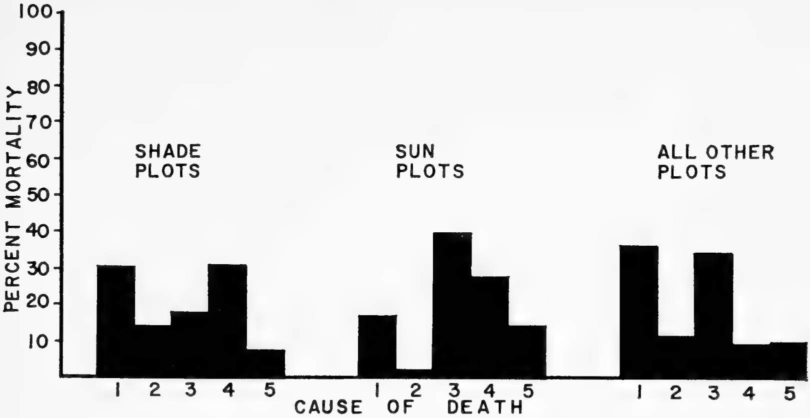

FIG. 6. Causes of mortality of *Arbutus* seedlings in different habitats. Numerals on horizontal line refer to: 1 = invertebrates, 2 = drought, 3 = fungi, 4 = combinations, 5 = miscellaneous.

Acarina) was found in abundance on hypocotyls of several seedlings early in the season, but damage seemed slight. Mites have been reported to be vectors of damping-off fungi, however, and may have contributed to mortality from this cause (Wilde, 1958). Insects were only rarely found feeding on seedlings. A total of 29.2% of the total mortality on all plots was classified under the heading of invertebrates, slugs probably accounting for nearly the whole amount.

Drought, when acting alone, is operative very soon after germination, and again, towards the end of the study, in July, when only a handful of seedlings remained (fig. 5). The early mortality, which included the great majority of the drought-killed plants, was due to recently emerged seedlings being rooted only in rapidly drying surface litter, even though this mortality occurred at the height of the wet season. The presence of a thick litter on the shade plots and its absence on the sun plots explains the anomalously larger mortality from drought in the shade (fig. 6). Actually, there was no mineral soil drought even in the surface soil on the shade plots until July (fig. 3). The more extreme sun plots, on the other hand, lacked growth water (moisture above the wilting percentage) at the surface by late May and at 15 cm. by late June. So few seedlings had survived by this time, however, that the toll from drought alone was very small (6%) on the sun plots in terms of the initial number of seedlings. Total mortality on all plots from drought acting alone was only 10.4%.

Death of *Arbutus* seedlings from fungus attack was more important quantitatively, comprising 28.1% of total mortality on all plots. This factor was positively correlated with precipitation, by June becoming of little importance as a factor in seedling mortality (figs. 3 and 5). Surprisingly, fungi were of much greater relative importance on sun than on shade plots. In part, this is a natural consequence of the lesser mortality from invertebrates on the sun plots, thereby leaving a larger proportion to be killed by other agents. Also, several etiological agents were involved in the fungus attacks, one of which occurred only in the sun. Fungus damage was classified in the field into three categories: (1) Typical post-emergence damping-off, with collapse of the hypocotyl (and usually root decay also); (2) Root decay alone; (3) Leaf spot, usually with root decay as well. On the sun plots these conditions were in the proportion of 39%, 25%, and 36%, respectively. Leaf spot was absent from shade plots, giving a ratio of 59%, 26%, and 0%. The other plots were intermediate.

From external appearances it is probable that most of the damping-off and root decay of the *Arbutus* seedlings was produced by water molds (*Pythium, Phytophthora,* etc.). The unusually heavy rains in March and April (fig. 3) correlated well with maximum seedling damage, as is normal for these fungi. In addition, *Rhizoctonia* seemed also to be present on a number of seedlings, and semi-parasitic mycorrhizal fungi may have played a role as well. The leaf spot of *Arbutus,* which was present only on the seedlings growing on the sun plots, developed at the height of the March rainy period, but owing to its crippling effect, mortality was mostly delayed until April. The spots generally started as small necrotic areas which gradually enlarged until coalescence of several spots killed most of the cotyledon, although epicotyledonary leaves, the epicotyl, or the hypocotyl were often also affected. The disease was mainly concentrated on plants of a single sun plot with much exposed mineral soil. If the etiological agent were a bacterium which required splashing from mineral soil to the cotyledons by raindrops, the absence of the disease from the thick-littered shade plots might be understood.

A total of 22.7% of all mortality was attributed to "combinations" of factors. Of this amount 67% was a consequence of rather mild drought preceded by crippling from root decay fungi. If fungi had not limited the depth and volume of root penetration, the seedlings presumably could have survived at least until the summer drought intensified. This category predominated after the rainy season when the weakened root systems resulted in drought-death (fig. 5). The effect of the light showers in May and June in temporarily reducing mortality from this cause is clearly shown.

On the shade plots 25% of the "combination" category was considered to have been a consequence largely of deep shade, which predisposed the seedlings to death from another cause such as drying litter. Again, root fungi were usually involved here also, and occasionally mechanical injury from rains, falling leaves, leaf chewing, and other factors. Even on the most densely shaded plots, low light intensity was probably never by itself a cause of death during the period of study, the proximal or immediate cause of mortality always being some other factor. One completely albino seedling even survived for 25 days.

An average of 9.6% mortality was attributed to "miscellaneous" causes. Much of this category resulted from causes which were too uncertain to classify. On the sun plots, however, 67% was the result of mechanical disturbance by rodent undermining. Also included were seedlings covered by fallen leaves or exfoliating bark of *Arbutus* for extended periods. The average angle of slope of the plots (18.4°), however, resulted in a gradual shifting of the litter downslope such that a seedling would usually be released within a few days and in such cases covering was considered a predisposing or contributing ("crippling") rather than a proximal (or immediate) environmental factor contributing to mortality. Temporary covering not only predisposes seedlings to injury from drought and fungi but during the moist season to attacks by slugs as well. Conversely, drought predisposes seedlings to covering by litter, since wilted seedlings are easily bent by falling leaves or even by heavy rains, and once bent horizontally are readily covered by downslope shifting of litter.

On October 7, 1961, the study area was again revisited. The winter and spring of this year received less than half normal precipitation, and yet the number and size of visible *Arbutus* seedlings of the 1961 season was comparable to that observed in 1958 on and near certain sun plots. All but two seedlings, adjacent to one sun plot, were dead but had probably survived to about mid-summer. The two living seedlings had 4 to 6 live but wilted and reddish leaves (the cotyledons had dried) and probably could have been expected to survive if the normal fall rains materialized. Neither living nor dead seedlings were visible on the shade plots nor on any sun plot where mineral soil was not exposed, emphasizing again the inhibiting influence of litter as well as of shade.

With regard to seedlings of other species than *Arbutus,* a similar complex pattern of mortality causes occurred. Of the *Sequoia* seedlings, 32% were eaten by invertebrates and 6% succumbed to drought in the rainy season as a result of rooting in thick litter which soon dried out in the upper layers. Damping-off and root decay fungi accounted for 13%, but at least 23% died from drying of the litter combined with attacks by root fungi. Other combinations (16%) or miscellaneous (10%) accounted for the remainder of the *Sequoia* seedlings by the early date of April 23.

Over half of the *Heteromeles* seedlings dried primarily by direct fungus attack, either typical damping-off, or much more commonly (38% of total mortality from any cause) from a leaf spot apparently caused by *Fusicladium dendriticum* (Wallr.) Fckl. v. *eriobotryae* Scalia. Combinations of factors killed 14%, the remaining seedlings dying from miscellaneous causes excepting one survivor which was nearly dead from leaf spot and probably did not survive the year.

GROWTH. Weekly measurements of shoot length, cotyledon and leaf size, and hypocotyl diameter of several marked seedlings on each plot were made until death of the plants. Plants adjacent to and of size comparable to those being measured were excavated monthly (fig. 7). Several points are noteworthy. First, the very small amount of growth of all *Arbutus* seedlings over the span of half a year is evident. Even by August the cotyledons had not died, although by then they were wilted, and only three to five nodes were visible by this time. The greater root system was present on plants in the sun, except where fungus attacks reversed this relation. Rotting of the root tip often stimulated branching. A slight bend in the hypocotyl usually resulted when a seedling was bent by rain or leaf litter for a few days, although one of the "E" seedlings probably grew between two impenetrable leaves before becoming vertical. Leaf injury by slugs (or insects) was evident on several plants. In the sun the hypocotyls changed from pale green or yellowish-white to pink or even red in about a month, but remained pale in the shade for much longer. By early May in the sun hypocotyls began shrinking with the collapse of the cortex following periderm production, as is normal in woody species, becoming brown or dark red and hard and wiry. On the other hand in the shade the hypocotyls were still quite succulent even by June, and none survived there long enough to appreciably harden.

Within a few months a number of the roots developed what appeared to be short, stubby mycorrhizal nodules (fig. 7), similar to the "root tubercles" in *Arbutus unedo* L. (Rivett, 1924). They occurred at the tips of certain main roots or on short branches, and developed into small and frequently branched pear-shaped tubercles enveloped in a dense mantle of hyphae from which minute root hair-like setae projected. Root hairs appeared to be absent from all naturally-occurring *Arbutus menziesii* seedlings, which agrees with observations by Rivett (1924) on other species of the genus.

Arbutus menziesii provides an interesting juvenile morphology which may not have been previously recorded. The epicotyledonary leaves of seedlings for several nodes are opposite, doubly serrate, glandular hairy, and thin (fig. 7), while mature foliage is alternate, essentially entire, glabrous, and coriaceous. Leaves of sprouts and saplings intergrade between these extremes.

Discussion

In spite of good seed crops being produced regularly (Tarrant, 1958), *Arbutus* seedlings are reported to be uncommon in comparison with stump sprouts (Jepson, 1910). On nearby Jasper Ridge, Cooper (1922) recorded no *Arbutus* seedlings in a *Quercus-Arbutus-Aesculus* forest. *Arbutus* seedlings and saplings of a number of age classes were present on the study area (Table 1), however, but only in the semi-open forest, along road cuts, or at the bases of large fallen trees. Healthy two- to several-year old seedlings and saplings were also present under moderate *Arbutus-Quercus* canopy. Nevertheless, the classification of this species by a majority of silviculturists as "tolerant" of shade (Baker, 1949) is probably based entirely on the behavior of mature trees and stump sprouts rather than seedlings, and the writer agrees with the considerable segment of dissenting opinion reported by Baker to class the tree as "intermediate," based upon its local behavior. Even in the absence of general fire or other disturbance, *Arbutus* probably maintains its position in dense forests not only by stump sprouting but perhaps also by a process similar to "gap phase" reproduction described elsewhere by Bray (1956).

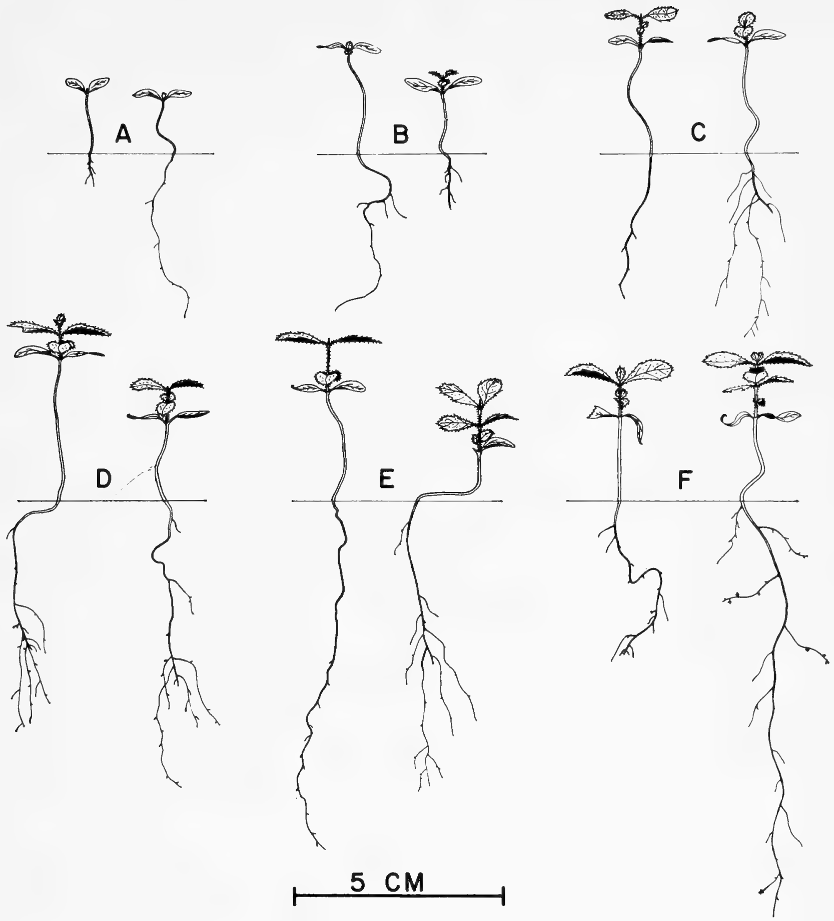

FIG. 7. Representative seedlings of *Arbutus* showing the usual range of behavior found in the field. A to F represent monthly intervals from March to August. The seedling on the left of the letter is in each case from near one of the shade plots while that on the right is from near a sun plot.

Shade can best be considered a predisposing factor increasing susceptibility of *Arbutus* seedlings to other more immediate causes of mortality, as has been found to be the case with other species (Baker, 1950: 266–267). In the present study, shade was always associated at least with a thick drying litter. Much earlier mortality occurred on the shade plots, in spite of the fact the mineral soil never reached the wilting percentage even at the surface at these sites (fig. 4). This is, however, partly due to the greater incidence of slugs on the shade than on the sun plots (fig. 6). The direct effects of shade were seen in the prolonging of the succulent hypocotyl stage and the usually smaller root-shoot ratio. Since one albino seedling survived for 25 days, we may assume that enough food reserves were present in green seedlings so that shade alone could not eliminate them before this time.

Seedbed requirements of *Arbutus menziesii* elsewhere are not known. Sudworth (1908) states that germination is best in moist soil when seed is well covered, while lack of seed covering and drier soils inhibit seedlings. There is apparently nothing in the nature of *Sequoia* or *Arbutus* litter which prevents germination. Instead, the ease of drying of upper litter layers (associated with extremely high wilting percentages of litter), in conjunction with the dense shade usually provided in such habitats, renders them highly unfavorable. Normal germination varies from February to April, depending on climate (Tarrant, 1958). The early (mostly February) germination in the present study probably reflects the unusually warm January and February of 1958, and also the southerly location of the area in relation to the main range of the species.

Germination of *Arbutus* is epigeous, and the cotyledons remain photosynthetic for several months. The mesomorphic traits of the strikingly different juvenile foliage, although perhaps in part of a vestigial nature, probably are adaptive in certain respects. The dense glandular hairs may inhibit the occasional foliage-eating insects, but apparently have no inhibiting effect on slugs. The thin, non-coriaceous, serrate leaf of the juvenile plants may also be photosynthetically more efficient at low light intensities than xeromorphic mature foliage which is usually more exposed to desiccation.

The occurrence of drought-death as classified in figures 5 and 6 is misleading, since this mostly occurred at the height of the rainy season and on the shade plots, when a few sunny days would dry out the upper litter layers. Somewhat later, drought eliminated most of the seedlings which had been crippled by root fungi, often before even the upper layers of the mineral soil had dropped below the wilting percentage. But by June 17 the sun plot soils had dropped below the wilting percentage at the 12–15 cm. level. Although a healthy root system could probably penetrate below this depth within four months, the usually continued drought for four or five more months usually presents an insurmountable obstacle to seedlings of most perennials. That a few *Arbutus* seedlings actually do survive nearly every year is shown by the several seedlings and sapling age classes present on the area, usually in the same microsites in which the healthier current-year seedlings occurred (Table 1). Two or three exceptionally vigorous seedlings of the present season which occurred off the plots in favored sites appeared as if they might survive the summer, but all the *Arbutus* on the plots doubtless would not have survived many more weeks even had they not been excavated for root studies. The fact that two live 1961 seedlings were found near one plot near the end of the dry season in October, in spite of the unusual drought of this year, suggests that the abnormally heavy precipitation of 1958 did not significantly reduce death from drought over that of more normal years, perhaps because precipitation was concentrated in early spring.

Damping-off and root decay fungi have not been frequently incriminated in studies of tree establishment under natural conditions, although they are often destructive in coniferous tree nurseries. The prevalence of these agents in this study, both as predisposing and as proximal causes of mortality, was probably in part associated with the unusually wet spring of 1958. A problem arises, however, in interpreting the relation of root decay and mycorrhizal fungi. It is possible that some of the root decay of seedlings was caused by the same fungus producing the tubercles. The tubercles resemble those of *Arbutus unedo,* where they are considered to be ecto-endotrophic mycorrhiza in which the relationship is one of balanced parasitism rather than symbiosis (Rivett, 1924). If this is true also in *A. menziesii,* it would be understandable that the fungus might gain the upper hand during an unusually wet season and become a crippling parasite. It is probable, however, that the typical damping-off symptoms, and perhaps much of the root decay itself, were produced by other agents even if mycorrhizal fungi were also involved.

Shade and summer drought are doubtless normally more significant in seedling establishment of *Arbutus* than is suggested by the histogram (fig. 6). Shade does not there appear among the causes of mortality because it was classified as a predisposing condition under the heading of "combinations" of factors. Furthermore, on the shade plots, the early and complete mortality resulting from other conditions than shade prevented shade alone from exerting its full potential influence. In a similar fashion, summer drought was a minor factor in this study, most of the drought-killed seedlings of figure 6 having perished at the height of the wet season owing to a thick drying litter. Summer drought would be expected to act as a final "coup-de-grace" for most of the few seedlings which have survived prior dangers and which are often crippled by fungi or shade-induced exhaustion of food reserves. The results of this study emphasize the importance of predisposing or contributing ("crippling") factors even though these may not be the proximal or immediate cause of death.

With regard to *Sequoia sempervirens,* the present limited results confirm the conclusion of Fritz (1950) that litter and shade do not prevent germination of this tree, but rather strongly inhibit survival. The present unusual results, however, which implicate fungi and invertebrates as being of greater importance than drought in causing mortality, may be due to the shady site and unusually wet spring. The *Fusicladium* leaf fungus of *Heteromeles* was also probably favored by this wet weather.

In evaluating survival in seedling populations the following important questions are asked. To what extent are adaptive genetic differences involved in differential survival within seedling populations ("natural selection" in the present sense)? Or, is seedling survival dependent primarily upon the chance vagaries of seed dispersal to physically favorable microsites (the "safe sites" of Harper *et al.,* 1961) combined with the subsequent chance absence of injurious biotic agents?

The difficulty of demonstrating a correlation between genotypes and survival in nature explains the paucity of field data supporting natural selection in plants (Stebbins, 1950: 106). No genetic races of *Arbutus menziesii* have been yet recognized within its range (Tarrant, 1958). Nevertheless, genetic differences were probably present among the *Arbutus* seedlings in the present study which were significant to survival. This was obvious in the case of the few albino seedlings. Date of germination ranged over almost a four month period in *Arbutus,* and probably involved both genetic and environmental factors. Late germination was conducive to drought injury and in fact no late germinating seedlings survived long. *Arbutus* cotyledons varied greatly in size and shape, probably again partly owing to genetic differences; cotyledon structure certainly is involved in shade tolerance.

Presumably, distasteful biochemical products such as may be present in the glandular hairs of *Arbutus* seedlings could influence destruction by slugs. Possibly this feature helps explain why some seedlings of *Arbutus* remained untouched adjacent to others which were thoroughly chewed. Also, adjacent seedlings of this species were not always affected similarly by fungus parasites. In view of the problem of root penetration of layers of rapidly drying litter as well as of their maintenance of contact with moist subsoil during the prolonged summer drought, any genetic variation promoting the development of a diffuse rather than a tap root system by *Arbutus* seedlings would be expected to be selected against. Injury of the tap root by fungi was one of the most frequent causes of mortality.

The fact remains that at least all the "shade" plots were located in "unsafe sites" where the lack of seedlings or saplings of any but the current year showed that survival depended on thinning of the canopy and litter by fire, lumbering, or the falling of one or more trees. Under such conditions, the genotypes within the population could influence only the duration of survival by a few weeks, and natural selection, in the sense of either differential survival to reproductive age or differential reproduction by the resulting survivors, has not occurred. Chance "catastrophic" events, such as covering of seedlings by falling leaves or exfoliating bark and perhaps much of the biotic injury, also were important "non-selective" factors, little influenced by seedling genotypes. On the sun plots, selective pressures would be expected to operate severely on the 2% survivors, although if all seedlings eventually succumbed before maturity the effects of natural selection would there also be nullified. Selection pressure, however, would be somewhat relaxed on these few survivors if the effects of the intensifying summer drought were more than compensated for by the reduced competition for light and moisture occasioned by the lower seedling density resulting from early high mortality. But in the present case this was probably not the situation, even if all survived, since seedling size was small and densities were only locally high enough to result in much mutual shading or root competition during the first year. Consequently, in spite of much or most mortality resulting from "non-selective" factors, *all* survivors must be fit, even though the genetically "fittest" may have been eliminated by chance events. The rigors of the environment are such that although the "fittest" may not survive, the unfit never do.

SUMMARY

Emerging seedlings were marked and their fates followed in comparison with microenvironmental records from February to August in an *Arbutus-Quercus-Sequoia* forest in the Santa Cruz Mountains of central California. By August 2, 2% of the *Arbutus* seedlings had survived in a semi-open forest and 0% in deep shade. Invertebrates, primarily slugs, accounted for 29.2% of the mortality, and were of greatest importance in the shade and during the rainy season. Death from drought acting alone was minor (10.4%), and occurred mainly soon after germination during the wet season in deep shade where thick litter prevented seedling roots from reaching moist mineral soil. Attacks by fungi, especially post-emergence damping-off and root decay types, accounted for 28.1% of the mortality, and were more important for several reasons in the semi-open than in shade. Combinations of factors killed 22.7% of the seedlings, mostly from mild drought preceded by crippling root decay fungi, or weakening by shade. Unknown or miscellaneous causes, especially undermining by rodents or covering by leaves or bark, took the remainder (9.6%) of the *Arbutus* seedlings. A number of seedlings of several other species, especially *Sequoia sempervirens* and *Heteromeles arbutifolia,* were also included in the study and showed a similar high mortality resulting from complex causes. Although chance or non-selective factors were probably responsible for most mortality, natural selection still operates severely on the few survivors.

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A NEW SPECIES OF DOWNINGIA

John H. Weiler

A systematic study of the genus *Downingia* now in progress has revealed a new entity heretofore included by all workers in *D. elegans* (Dougl. ex Lindl.) Torr. Investigation of plants in the field and in cultivation suggests that this new entity should be accorded specific recognition. The new species I have chosen to name for Dr. Rimo Bacigalupi, Curator of the Jepson Herbarium, who has stimulated my interest in *Downingia* and given me a great deal of time and valuable advice.

Downingia Bacigalupii sp. nov. Planta annua caulibus simplicibus vel e basibus ramosis, 0.5–3.0 dm. altis; foliis bracteisque linearibus vel lanceolatis; lobis calycis adscendentibus vel rotatis, quam sinibus lateralibus tubi corollae longioribus; corollis caesiis lineis conspicuis azureis reticulato-venosis, labio inferiore concavo, labium superiore longitudine aequante vel quam id paulo longiore, centraliter albo haud venoso maculis

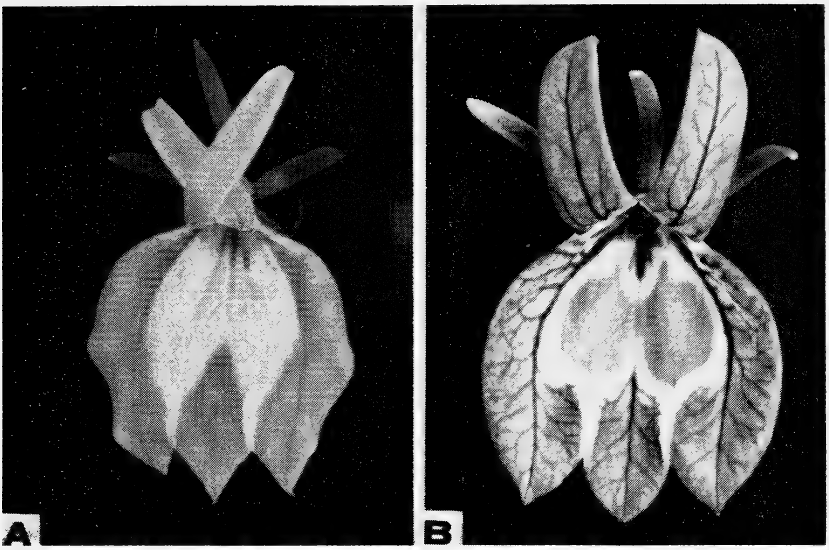

FIG. 1. Perianths of *D. elegans* (A) and *D. Bacigalupii* (B) showing differences in color patterns and conformation of the corollas, ×3.

duabus flavis plerumque ovalibus in medio areae albae obsito; corollae tubo brevissimo latissimoque; lobis labii superioris cuneato-lanceolatis, divergentibus, erectis vel recurvatis; tubo staminali quam corollae tubo valde longiore, prorse curvato, antheris inferioribus duabus apice setigeris; ovario uniloculari, placentis parietalibus duabus; seminis ellipticis angustis striis plus minusve parallelibus obsitis.

There are similarities between *D. elegans* and *D. Bacigalupii* which make it difficult to differentiate the two on herbarium sheets. Both have widely opened corolla-tubes with the sides of the tube forming approximately a 90-degree angle, and both have a long exserted staminal column with a sharply curved anther-tube. It is the combination of these two characters easily seen on mounted specimens which causes people to confuse the two.

When living plants are compared, the most striking differences between plants of the two species are in the colors of the corolla. Corollas of *D. elegans* are a smooth, bright blue, with the lower lip having a central bilobed white spot. This white area is sometimes veined with blue reticulations or may even be completely suffused with blue. In contrast, the corolla of the new species is a lavender-blue, usually with prominent, more deeply colored veins, especially noticeable on the lower corolla-lobes. The lower lip of the corolla has a central white area which is devoid of blue veins and contains two bright orange-yellow spots. Other differences neither as consistent nor as easy to recognize, are size and shape of corolla-lobes. Lobes of the upper corolla-lip of *D. elegans* are narrow, usually parallel or crossed over each other but occasionally divergent, and sharply reflexed. The lobes of the lower corolla lip are cuneate and tapered to a point. In *D. Bacigalupii,* the upper lobes are broader, widely divergent, and erect or arched backward, but not so prominently as in *D. elegans.* The lobes of the lower lip are broader, rounded, and abruptly pointed. Besides morphological differences, the gametic chromosome number of *D. Bacigalupii,* including plants of the type collection, is n=12, whereas that of *D. elegans* is n=10.

Downingia Bacigalupii occurs from southwestern Idaho westward across southern Oregon, as far north as southern Wasco County east of the Cascade Mountains, and in northeastern California as far south as Lake Tahoe. This range overlaps that of *D. elegans* only in southern Wasco County, Oregon. *D. Bacigalupii* grows in vernal pools, roadside ditches, open areas of mountain meadows and in muddy margins of lakes at sites exposed to bright sunlight.

Type. In heavy soil of a large bowl-shaped depression littered with rocks, 2.7 miles southwest of the California-Oregon border along Ager-Beswick road, Siskiyou County, California, June 24, 1960, *J. H. Weiler* and *A. P. Nelson 60205* (UC-1,199,666).

Other collections. CALIFORNIA. Sierra County: 1 mile south of junction to Calpine, *Bacigalupi 4276.* Plumas County: 11.7 miles north of Sattley, Sierra Valley, *Weiler 59190.* Lassen County: 11.1 miles south of Eagle Lake, *Weiler 59203.* Shasta County: Dickson Flat 3.2 miles south of Shasta-Siskiyou County line, *Weiler 60194.* Modoc County: Pitt River Valley south of Alturas, *Mason & Grant 13414.* OREGON. Josephine County: 3.7 miles north of O'Brien, *Weiler 61319.* Jackson County: 1.5 miles east of Klamath Falls Junction, *Weiler 60177.* Klamath County: Modoc Point, Klamath Lake, *Constance 9682.* Wasco County: 0.9 miles north of Schoolie Ranger Station road on the road to Mount Wilson, *Weiler 61397.* Harney County: 1.2 miles west of Riley, *Weiler 61345.* IDAHO. Owyhee County: 10 miles south of Riddle, *Holmgren 7976.*

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THREE NEW SPECIES RELATED TO MALACOTHRIX CLEVELANDII[1]

William S. Davis and Peter H. Raven

Malacothrix clevelandii A. Gray, a cichoriaceous composite of the southwestern United States and northwestern Mexico, has been regarded as a homogeneous species by all previous authors, including the most recent monographer of the genus, E. W. Williams (Am. Midl. Nat. 58:494-512. 1957). Stebbins *et al.* (Univ. Calif. Publ. Bot. 26:401–430. 1953) reported the gametic chromosome number n=7 for a population of this species from coastal California, whereas the plants they examined from

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[1] The authors are indebted to Professors Carl C. Epling, Harlan Lewis, and Henry J. Thompson for their constructive criticism of the manuscript.

Arizona were tetraploid (n=14) and differed morphologically from most California material. Subsequent chromosomal and morphological studies of *M. clevelandii* have shown that, far from being a non-variable species as its lack of synonyms or infraspecific entities might suggest, it is a complex of several closely related entities, for which we propose the taxonomic treatment below.

Malacothrix clevelandii and the related taxa that will be described here are recognized collectively by their erect, inconspicuous heads with the ligules barely exserted; by the presence of one or more persistent pappus setae; and especially by a ring of acute teeth at the summit of the achene. The last-mentioned has proved to be the most useful trait separating them from members of the closely related group of species of which *M. foliosa* A. Gray is a member (fig. 2).

The taxa of the *M. clevelandii* group can be distinguished by means of the following key:

Achenes less than 1.7 mm. in length, fusiform, with 5 of the 15 ribs more prominent than the rest; involucre less than 8 mm. high; persistent pappus seta 1

  Achenes brown or straw-colored; cauline leaves often toothed; plants usually unbranched below; mean pollen diameter 25μ; gametic chromosome number, n=7 . . . . *M. clevelandii*

  Achenes dark purplish-brown, rarely paler; margins of cauline leaves entire; plants often well-branched from the base; mean pollen diameter 30μ; gametic chromosome number, n=14 . . . . *M. similis*

Achenes more than 1.7 mm. in length, subcylindrical, grey-brown to straw-colored; with 15 equally prominent ribs; involucre more than 8 mm. high; persistent pappus setae 1 or 2

  Persistent pappus setae usually 2, the upper portion of the achene smooth; margins of the basal leaves irregularly and doubly dentate; mean pollen diameter 25μ . . . . *M. sonorae*

  Persistent pappus seta usually 1, the upper portion of the achene with ribs; margins of the basal leaves dentate; mean pollen diameter 30μ . *M. stebbinsii*

Pollen diameter was found to be useful for distinguishing taxa of the *M. clevelandii* complex, and, in addition, provided a clue to the level of polyploidy in two of them. Pollen samples were taken from herbarium sheets of *M. clevelandii, M. similis, M. sonorae,* and *M. stebbinsii,* and the size of mature grains was measured with an ocular micrometer. The mean standard deviation and range of the sample from each species are shown in Table 1. The mean of the pollen sample from *M. similis* (n=14) was compared with the mean of the pollen sample from *M. clevelandii* (n=7) by use of Student's *t*-test, and the results show a highly significant difference between the mean pollen sizes. On the other hand, the pollen of *M. clevelandii* and *M. sonorae* was closely similar in size, as was that of *M. similis* and *M. stebbinsii* (Table 1). Since in addition the pollen from *M. similis* and *M. stebbinsii* was mostly tetra-aperturate while that from *M. sonorae* and *M. clevelandii* was predominantly tri-aperturate, we believe that *M. sonorae* is probably diploid, and that *M. stebbinsii* is probably tetraploid.

TABLE 1. DIAMETERS OF POLLEN GRAINS OF SPECIES OF MALACOTHRIX.

SPECIES	NUMBER OF PLANTS	SAMPLE SIZE[1]	RANGE (μ)	MEAN (μ)	STANDARD DEVIATION (μ)
M. clevelandii	29	394	21–31	25	1.8
M. similis	13	347	23–38	30	2.3
M. sonorae	10	260	20–29	25	1.3
M. stebbinsii	49	794	24–36	30	2.1

[1] Pollen from one plant from each locality, 20–50 grains per plant. A plant from the type collection was included in each case. Data obtained from herbarium specimens.

DESCRIPTIONS OF THE SPECIES

MALACOTHRIX CLEVELANDII A. Gray, Bot. Calif. 1:433, 1876 (fig. 1, 2a). Annual herb 5–60 cm. tall, with a single stem or, more rarely, numerous stems from the base; basal leaves linear to narrowly lanceolate, dentate, pinnatifid or lobed, the rachis oblong or wider near the base; cauline leaves often toothed; heads cylindrical to narrowly campanulate, 10–160 (median, 36), 4–8 mm. high, 2–5 mm. broad, 19–67–flowered; ligules yellow; pollen grains 21–31μ (mean=25μ) in diameter; achenes truncate-fusiform, 1.4–1.8 mm. long, 0.22–0.38 mm. wide, slightly curved, brown to straw-colored, finely 15–ribbed, with 5 ribs more prominent than the rest, the achene pentagonal in transverse section, its apex flared, bordered by a ring of 14–17 white-scarious teeth, of which the basal portions extend above the achene lip, the teeth often irregularly cleft, outwardly curved, lance-deltoid, the persistent seta 1. Gametic chromosome number, n=7.

Type. San Diego, California, *Cleveland* (GH; isotype, K).

Representative specimens.[2] CALIFORNIA. Tehama County: 5 miles west of Paskenta, *Baker 12581*. Glenn County: 9 miles east of Alder Springs, *Heller 11452*. Colusa County: upper Sand Creek, *Hoover 3212*. Lake County: Scotts Valley, *Tracy 1646*. Contra Costa County: Mitchell Canyon, Mount Diablo, *Bowerman 1415*. Santa Clara County: Seeboy Ridge, Mount Hamilton Range, *Sharsmith 3270*. San Benito County: Pinnacles, *Howell 12933*. Monterey County: King City, *K. Brandegee* in 1893. San Luis Obispo County: 8 miles east of Santa Margarita, *Ferris & Rossbach 9440*. Santa Barbara County: Painted Cave Ranch, *Eastwood 120*. Kern County: Kern River, *Peirson 8835*. Ventura County: Kinchers, Ojai Valley, *Pettibone & Hubby* in 1896. Los Angeles County: east fork of Santa Anita Canyon, *Howell 3778*. San Bernardino County: Cajon Pass, *S. B. Parish 4868*. Riverside County: Santa Rosa Mountains, *Munz 15087*. San Diego County: Buckman Springs, *Fosberg 8486*. Tuolumne County: above Indian Creek, *Williamson 80*. Mariposa County, Sherlocks, *Congdon* in 1897. Calaveras County: Mokelumne Hill, *Blaisdell*. Amador County:

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[2] The following herbaria have been consulted, and for this privilege the writers are grateful to the curators of the institutions concerned: University of Arizona, British Museum (Natural History), California Academy of Sciences, University of California (Berkeley), University of California (Los Angeles), Pomona College, Rancho Santa Ana Botanic Garden (where vouchers for our chromosome counts are deposited), Royal Botanic Gardens, Kew, and Stanford University.

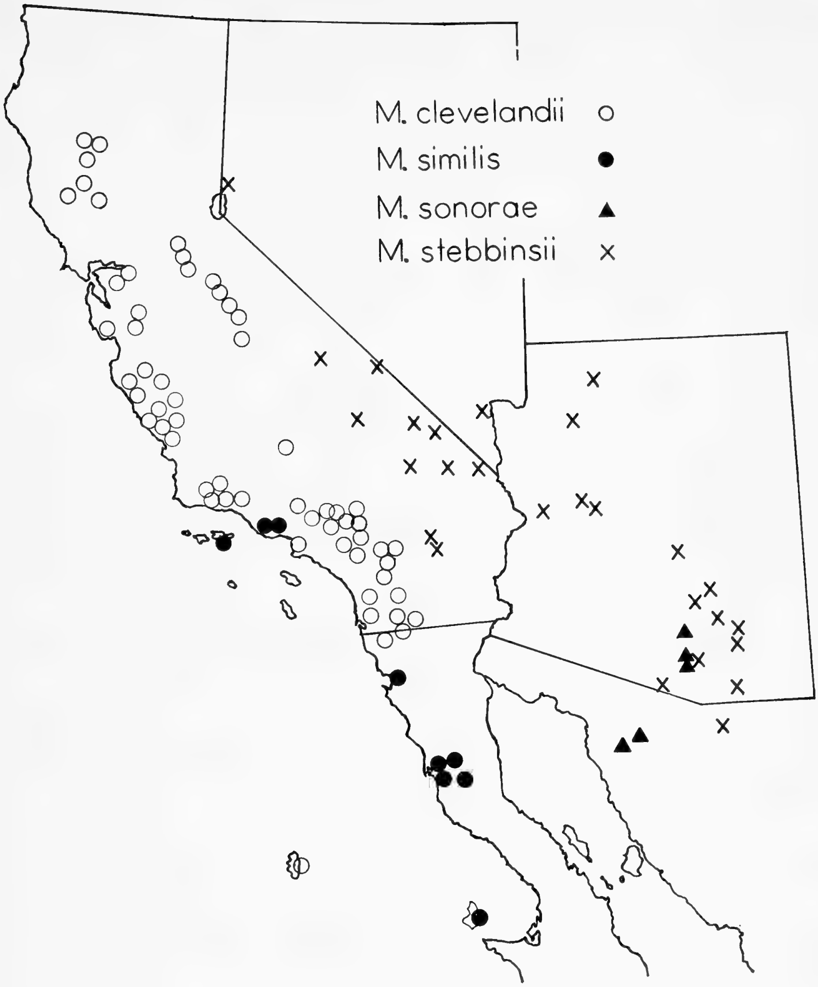

FIG. 1. Distribution of *Malacothrix clevelandii* and allied species in the southwestern United States and northwestern Mexico.

Drytown, *Hansen 401*. BAJA CALIFORNIA, MEXICO. Guadalupe Island, *Palmer 51;* 13 miles southeast of Tecate, *Munz 9520.*

As shown by the specimens cited above and by figure 1, this species occurs on the coastward slopes of the mountains of California and northernmost Baja California. Its occurrence on Guadalupe Island should be confirmed by additional material and by determination of chromosome number. In addition to the report of Stebbins *et al.* of a chromosome number of 2n=14 from the Sharsmith collection cited above from Santa Clara County, we have obtained this number in a collection from the Santa Monica Mountains, Los Angeles County, California (*Raven &*

Thompson 15034) and the gametic number of n=7 in a collection from the San Jacinto Mountains, Riverside County, California (*Davis 99*).

Malacothrix similis sp. nov. (fig. 1, 2c). Herba annua; foliis ad radices linearo-lanceolatis, integris, dentatis, lobatis, vel pinnatifidis; capitulis anguste campanulatis, 6–10 mm. longis, 3–6 mm. latis, floribus 32–73; corollis flavis; achaeniis truncato-fusiformis, 1.4–1.7 mm. longis, subflexuosis, maximam partem purpureo-brunneis interdum stramineis, subtiliter 15-costatis, 5 costis prominulis, 5-angulatis in sectione transversa, parte superiore late dilata, ab annulo setarum circa 18 scabriosarum circumdata; seta perstata 1.

Annual herb 5–32 cm. tall, usually branched from the base, the stems 1–11; basal leaves linear-lanceolate, entire, dentate, lobed, or pinnatifid, the rachis oblong; cauline leaves subentire; heads narrowly campanulate, 5–50 (median, 14), 6–10 mm. high, 3–6 mm. broad, 32–73 flowered; ligules yellow; pollen grains 23–38μ in diameter (mean=30μ); achenes truncate-fusiform, 1.4–1.7 mm. long, 0.26–0.31 mm. wide, slightly curved, dark purplish-brown, sometimes straw-colored, finely 15-ribbed, with 5 ribs more prominent, the achenes pentagonal in transverse section, the apex flared, bordered by a ring of about 18 white-scarious irregular teeth, of which the basal portions extend above the achene lip, the teeth curved outward, lance-deltoid, the persistent seta 1. Gametic chromosome number, n=14.

Type. With *Idria, Yucca, Salvia,* and *Solanum hindsianum,* 16.0 kilometers southeast of El Rosario, Baja California, Mexico, altitude 210 meters, 18 April 1958, *Raven, Mathias* & *Turner 12475* (RSA).

Specimens examined. CALIFORNIA. Santa Barbara County: Santa Cruz Island, *T. S. Brandegee* in 1888. Ventura County: Hueneme, *Peirson 5772*; Hueneme Beach, *Munz 9390*. BAJA CALIFORNIA, MEXICO. South Todos Santos Island, *Moran 2804;* San Quintín, *Bacigalupi 3020, Epling* & *Stewart* in 1936, *Raven et al. 12355;* Rosario wash, *Wiggins 5427;* 3.5 miles east of Rancho San José, *Wiggins 9783;* Arroyo el Agua Marga, *Wiggins 9935, 9935B;* El Rancho Viejo, *T. S. Brandegee* in 1889; Cedros Island, *Anthony 434, Palmer 762.*

The chromosome number of *M. similis* has been determined as n=14 at meiosis in microsporocytes of the type collection. This species is variable and puzzling, separable only with difficulty from *M. clevelandii,* but measurements of the pollen from the collections cited consistently have fallen within the tetraploid-size range. Furthermore, with the exception of two outlying stations in California, this species occupies a coherent area in Baja California south of the range of the diploid *M. clevelandii.* Much of the difficulty with respect to the delimiting of *M. similis* is due to the three collections from California. The dune habitat at Hueneme Beach (Ventura County), however, would be highly anomalous for *M. clevelandii,* and the collections cited are morphologically distinguishable from that species. Plants of *M. similis* from similar beach and coastal plain habitats in Baja California have smaller and darker achenes than the Hueneme collections. Additional collections and chromosome number determinations from Hueneme Beach and from Santa Cruz Island, the

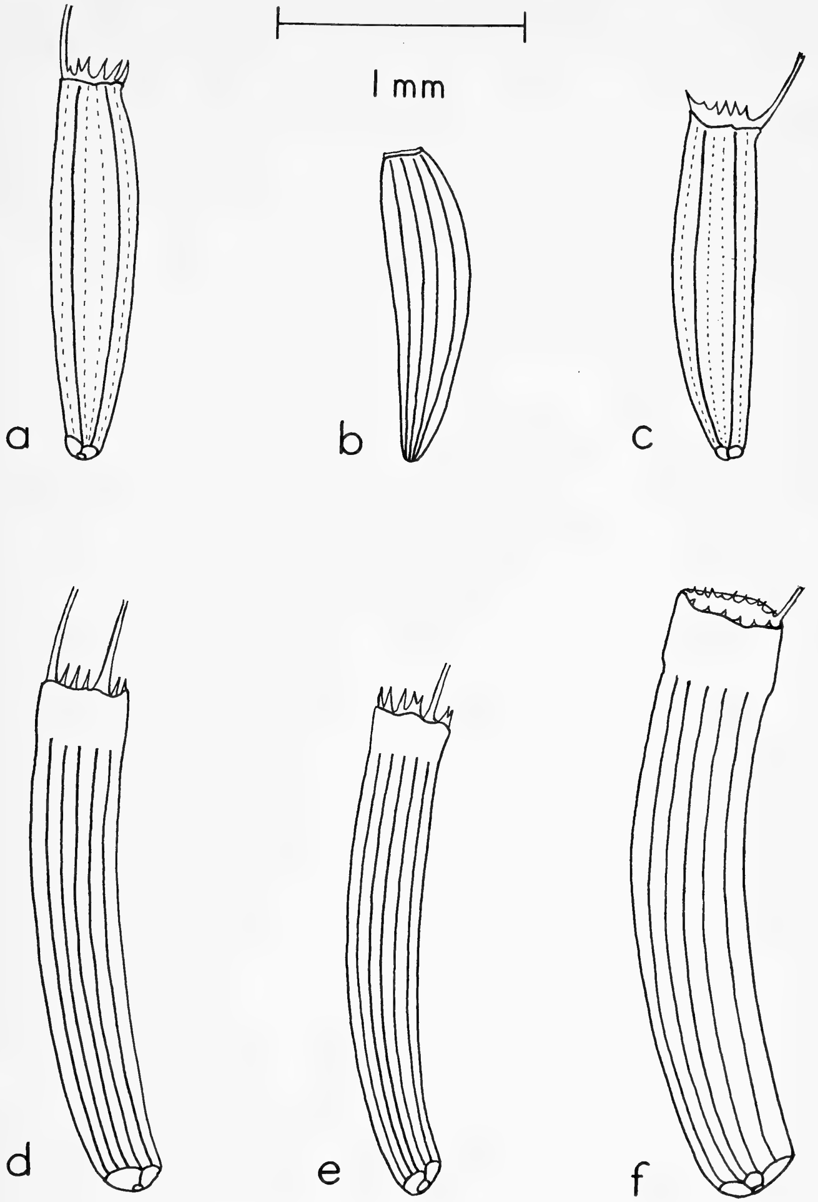

FIG. 2. Mature achenes of species of *Malacothrix*: a. *M. clevelandii;* b. *M. foliosa;* c. *M. similis;* d. *M. sonorae;* e. *M. stebbinsii;* f. *M. fendleri.*

other California station, are much to be desired. In both cases the pollen measurements are consistent with the range of size expected for the tetraploid. We suggest that an understanding of relationships in the complex depends on a more thorough knowledge of *M. foliosa* and related species which inhabit the islands off the coast of California and Baja California, and which may have participated in the alloploid origin of the populations we have named *M. similis*. Measurements of the pollen of different collections of the *M. foliosa* complex suggest that it contains both diploids and tetraploids.

Malacothrix sonorae sp. nov. (fig. 1, 2d). Herba annua; foliis ad radices lanceolatis vel oblanceolatis, inaequaliter pinnatifidis; capitulis campanulatis, 6–9 mm. longis, 4–6.6 mm. latis, floribus 30–61; corollis flavis; achaeniis columnaris 1.7–2.00 mm. longis ad basim attenuatis, subflexuosis, praesertim fuscis nunc stramineis, subtiliter aequaliterque 15-costatis, in sectione transversa rotundis, parte superiore dilata, achaenii parte superiore ad 0.2–0.3 mm. nullomodo costata, ab annula setarum 16–18 scabriosarum circumdata; setis perstatis 2, per occasionem 1, raro 3 vel 4.

Annual herb 10–35 cm. tall, usually unbranched at the base but occasionally with up to 9 stems; basal leaves lanceolate to oblanceolate, irregularly and doubly dentate, the rachis broadest near the apex, narrowed below; heads campanulate, 5–109 (median, 10), 6–9 mm. high, 4–6.6 mm. broad, 30–61-flowered; ligules yellow; pollen grains 20–29 μ in diameter (mean=25 μ); achenes cylindrical (1.6–) 1.7–2.0 mm. long, attenuate toward the base, slightly curved, grey-brown to straw-colored, finely 15-ribbed, all the ribs equal, the achene round in transverse section, the apex slightly expanded, the upper 0.2–0.3 mm. of the achene not ribbed, bordered by a ring of 16–18 white-scarious teeth, of which the basal portions do not extend above the achene lip, the teeth pectinate, straight, acicular, the persistent setae 2, occasionally 1, rarely 3 or 4.

Type. Tucson Mountains, altitude 2600 feet, Pima County, Arizona, 24 April 1903, *Thornber 362* (ARIZ 59,491; istoypes, DS, POM, UC).

Specimens examined. ARIZONA. Pima County: north base of Silver Bell Mountains, *Benson 10716;* Rosemont, *Thornber* in 1907; Sabino Canyon, Santa Catalina Mountains, *Thornber* in 1903; Tucson Mountains, *Thornber 428,* in 1903. Pinal County: between Oracle and Mammoth, *Gentry 6081*. SONORA, MEXICO. Distrito de Altar: Passo San Emeterio, *Keck 4135A;* 4 miles west of Caborca, *Keck 4040*.

The size and number of apertures of its pollen suggest that this distinctive and rather local species may be diploid (n=7), but we have not yet been able to obtain living material from which to make chromosome counts. In achene shape (fig. 1d, a, f) it is intermediate between *M. clevelandii* and *M. fendleri* A. Gray (fig. 2), the latter a diploid[3] species with long-exserted ligules that occurs east of the range of the *Malacothrix clevelandii* complex. The range of *M. sonorae* likewise lies between that of the other two diploids.

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[3] We have made two new gametic chromosome counts of *M. fendleri,* n=7, from the following collections: 1.9 miles north of Chambers, Apache County, Arizona, *Raven 13026;* 5 miles northeast of Bates Well, Pima County, Arizona, *Raven 11699*. Stebbins *et al.* (*op. cit.*) reported the same number for a collection from New Mexico.

We have derived the specific epithet, "sonorae," from the Sonoran Desert in which the range of this taxon lies.

Malacothrix stebbinsii sp. nov. (fig. 1, 2e). Herba annua; foliis ad radices lanceolatis vel oblanceolatis, dentatis, raro pinnatifidis; capitulis campanulatis, 7–10 mm. longis, 3.5–8 mm. latis, floribus 19–70; corollis flavis, raro albis; achaeniis fusiformo-columnaris, 1.7–2.3 mm. longis, ad basim subattenuatis, raro flexuosis, nunc cinearo-fuscis nunc stramineis, subtiliter aequaliterque 15-costatis, in sectione transversa rotundis, parte superiore subdilata, achaenii parte superiore ad 0.14–0.20 mm. non costata, ab annulo setarum 14–17 scabriosarum circumdata; setis perstatis 1, per occasionem 2.

Annual herb 6–60 cm. tall, usually unbranched at the base but occasionally with up to 9 stems; basal leaves lanceolate to oblanceolate, dentate, more rarely pinnatifid, the rachis often narrowed near the base; heads campanulate, 5–66 (median, 20), 7–10 mm. high, 3.5–8 mm. broad, 19–70-flowered; ligules yellow, rarely white; pollen grains 24–36 μ in diameter (mean=30 μ); achenes narrowly fusiform-columnar, tapering slightly to the base, 1.7–2.3 mm. long, 0.3–0.45 mm. wide, rarely curved, grey-brown to straw-colored, finely 15-ribbed, all the ribs equal, the achene round in transverse section, the apex slightly flared, the upper 0.14–0.20 mm. of the achene not ribbed, bordered by a ring of 14–17 white-scarious teeth, of which the basal portions rarely extend above the achene lip, the teeth rarely and irregularly cleft, straight, lance-linear; the persistent setae 1, rarely 2.

Type. Abundant in shade of a large rock, moist soil, Mendoza Canyon, Coyote Mountains, Pima County, Arizona, altitude 3,800 feet, 22 April 1945, *K. F. Parker 5815* (ARIZ 32,709; isotype, UC).

Representative specimens. NEVADA. Washoe County: hills west of Reno, *Hillman* in 1893. Clark County: Nelson, *Jones* in 1907. CALIFORNIA. Inyo County: Titus Canyon, *Eastwood* & *Howell 7786;* 4 miles east of Aberdeen, *Kerr 630*; 2 miles east of Bradbury Wells, *Howell* in 1928; Slate Range, *Alexander* & *Kellogg 1135.* San Bernardino County: Turtle Mountains, *Munz* & *Harwood 3505;* Quail Springs, Little San Bernardino Mountains, *Munz* & *Johnson 5227*; south base of Old Dad-Granite Mountain Range, *Wolf 10092*; Kingston Mountains, *Wolf 10456.* Riverside County: Murray Canyon, *Peirson 2715*; 12 miles southwest of Twentynine Palms, *Alexander* & *Kellogg 2129.* San Diego County, Palm Canyon, Borrego Valley, *Wolf 8451*; San Felipe Hill, *Jones* in 1906. ARIZONA. Mohave County: Yucca, *Jones* in 1884; Chemehuevis, *Jones* in 1903; Diamond Creek Canyon, *Wilson* in 1893. Yavapai County: Burro Creek, *Crooks* & *Darrow* in 1938; Skull Valley, *Jones* in 1903. Gila County: Pine Creek, near Roosevelt, *Peebles et al. 5227;* Mazatzal Mountains, *Eastwood* in 1929, *17163.* Pinal County: near Oracle, *Peebles 6844;* between Superior and Miami, *A.* & *R. A. Nelson 1900;* Galuro Mountains, 12 miles above Mammoth, *Gentry 6051.* Pima County: Baboquivari Peak, *Goodding 4649;* Florita Canyon, *Knipe* in 1938; Oracle Camp, Santa Catalina Mountains, *Simon 224;* Sabino Canyon, Santa Catalina Mountains, *Thornber* in 1905, in 1913. Santa Cruz County: Stone Cabin Canyon, Santa Rita Mountains, *Thornber 5543.* SONORA, MEXICO. 4 miles south of Imuris, *Abrams 13202.*

Pollen of this species is consistently larger than in *M. clevelandii* and *M. sonorae,* both of which are diploids, and, like that of the tetraploid

M. similis, is mostly tetra-aperturate. We believe that the count reported by Stebbins *et al* (*op. cit.*) of 2n=28 for "*Malacothrix clevelandii*" from Tucson, Arizona (for which we can find no voucher) probably refers to *M. stebbinsii.* From a consideration of morphology we believe that *M. stebbinsii* may be an allotetraploid between *M. clevelandii* and *M. sonorae.* Stebbins and his associates postulated that it might be an allotetraploid between *M. clevelandii* and *M. fendleri,* but they were not aware of the probably diploid *M. sonorae.* As we have mentioned above, *M. sonorae* is nearly intermediate between *M. clevelandii* and *M. fendleri,* both morphologically and geographically.

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DOCUMENTED CHROMOSOME NUMBERS OF PLANTS

(See Madroño 9:257–258. 1948)

Species	Number	Counted by	Collection	Locality
PORTULACACEAE				
Montia **perfoliata* (Willd.) Howell	n = 6	P. Raven LA[1]	*H. & M. Lewis* in 1956, LA	Mather, Tuolumne County, California
	n = 12	H. Lewis LA	*H. Lewis* in 1955 LA	Mather, Tuolumne County, California
	n = 18	P. Raven LA	*H. Lewis* in 1956 LA	La Panza Range, San Luis Obispo County
	n = 18	P. Raven LA	*H. Lewis* in 1956 LA	San Juan Canyon, San Luis Obispo County, California
	n = 18	P. Raven LA	*H. Lewis* in 1956 LA	Temblor Grade, Kern County, Calif.
sibirica (L.) Howell	n = 12	W. H. Lewis ASTC	*W. H. Lewis 5367* SMU	Near Sechelt, British Columbia, Canada
RANUNCULACEAE				
Delphinium *virescens* Nutt.	n = 8	R. C. Jackson KANU	*McGregor 14282* KANU	Douglas County, Kansas
Trautvetteria *grandis* Nutt.	n = 8	R. Ornduff DUKE	*Ornduff 6262* UC	Multorpor Mountain, Clackamas County, Oregon
MAGNOLIACEAE				
Michelia **fuscata* Blume	n = 19	P. Raven LA	*Raven 14026* UC	Cultivated, Los Angeles, Calif.
SAXIFRAGACEAE				
Bolandra *oregana* S. Wats.	n = 7	R. Ornduff DUKE	*Ornduff 6240* UC	Elowah Falls, McCord Creek, Multnomah County, Oregon

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
THYMELAEACEAE				
Daphne genkwa Sieb. & Zucc.	n = 9	L. Nevling, Jr., A	*Nevling 105* AAH	Cultivated, Arnold Arboretum, Weston, Mass.
Daphne giraldii Nitsche	n = 9	L. Nevling, Jr., A	*Nevling 106* AAH	Cultivated, Arnold Arboretum, Weston, Mass.
LENNOACEAE				
Ammobroma sonorae Torr. ex. Gray	$2n = 18_{II}$	D. M. Moore LA	*J. Feldner* in 1961, UCLA	5.5 mi. W. of Glamis, Imperial County, California
PRIMULACEAE				
Hottonia inflata Ell.	n = 11	O. T. Solbrig GH	*C. Wood 9426* GH, UC	Middlesex Fells Reservation, Middlesex County, Massachusetts
POLEMONIACEAE				
Phlox oklahomensis Wherry	2n = 14	R. C. Jackson KANU	*Marsh* KANU	Cowley County, Kansas
VERBENACEAE				
Verbena bipinnatifolia Nutt.	n = 15	O. T. Solbrig GH	*Solbrig 3168* GH, UC	10 mi. N.E. of Santa Fe, New Mexico
	n = 15	O. T. Solbrig GH	*Solbrig 3175* GH, UC	32 mi. S. of Carizozo, New Mexico
	n = 15	O. T. Solbrig GH	*Solbrig 3181* GH, UC	28 mi. N. of Pecos, Texas
	n = 15	O. T. Solbrig GH	*Solbrig 3206* GH, UC	48 mi. S. of Alpine, Texas
	n = 15	O. T. Solbrig GH	*Solbrig 3213* GH, UC	11 mi. W. of Van Horn, Texas
perennis Wooton	n = 7	O. T. Solbrig GH	*Solbrig 3186* GH, UC	17 mi. S. of Fort Stockton, Texas
plicata Greene	n = 7	O. T. Solbrig GH	*Solbrig 3179* GH, UC	28 mi. N. of Pecos, Texas
wrightii Gray	n = 10	O. T. Solbrig GH	*Solbrig 3187* GH, UC	20 mi. S. of Fort Stockton, Texas
SCROPHULARIACEAE				
Mimulus brevipes Benth.	n = 8	B. B. Mukherjee, R. K. Vickery, Jr., UT	*C. Hubbs* in 1949 *54804* UT	Mount Palomar, San Diego County, California
PLANTAGINACEAE				
Plantago insularis Eastw.	$2n = 4_{II}$	D. M. Moore LA	*Raven, Davis, Moore 14763* RSA, JEPS	San Felipe, Baja California, Mexico
heterophylla Nutt.	2n = 22	D. M. Moore LA	*Raven, Blakley, Ornduff 14919* RSA	Santa Rosa Island, Santa Barbara County, California

Species	Number	Counted by	Collection	Locality
COMPOSITAE				
Bidens *polylepis* Blake	n = 12	R. C. Jackson KANU	*Jackson 2955* KANU	Douglas County, Kansas
Boltonia *latisquama* Gray var. *latisquama*	n = 9	R. C. Jackson KANU	*Jackson 2953* KANU	Douglas County, Kansas
latisquama Gray var. *recognita* Fern. & Grisc.	n = 18	R. C. Jackson KANU	*McGregor 15865* KANU	Harvey County, Kansas
Cacalia *atriplicifolium* L.	n = 25	R. C. Jackson KANU	*McGregor 15964* KANU	Anderson County, Kansas
Eupatorium *perfoliatum* L.	n = 10	R. C. Jackson KANU	*McGregor 15815* KANU	Cherokee County, Kansas
Grindelia *lanceolata Nutt.*	n = 6	R. C. Jackson KANU	*McGregor 16007* KANU	Taney County, Missouri
Helenium *tenuifolium* Nutt.	n = 15	R. C. Jackson KANU	*McGregor 15811* KANU	Cherokee County, Kansas
nudiflorum Nutt.	n = 14	R. C. Jackson KANU	*McGregor 15814* KANU	Cherokee County, Kansas
Heterotheca *latifolia* Buckl. var. *McGregoris* Wagenkn.	n = 9	R. C. Jackson KANU	*McGregor 15849* KANU	McPherson County, Kansas
Rudbeckia *missouriensis* Englm.	n = 19	R. C. Jackson KANU	*McGregor 16001* KANU	Taney County, Missouri
Senecio *obovatus* Muhl.	n = 22	R. C. Jackson KANU	*McGregor 14283* KANU	Douglas County, Kansas

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* Prepared slide available.

[1] Symbols for institutions are those listed by Lanjouw and Stafleu, Index Herbariorum, Part I. Fourth edition, 1959, Utrecht.

REVIEW

The Little Hill, a chronicle of the flora on a half acre at the Green Camp, Ringwood, New Jersey. By ANNE OPHELIA TODD. CUAS 8, pp. 1–20. 1961. Cooper Union School of Art and Architecture, New York.

There appeared on my desk a thin publication of twenty pages and four colored plates, much like a brochure spelling out some urgent need. The format caught my eye and the text, in keeping, filled me with sheer delight as it recounted the botany of an unkempt patch of weed.

> The Hill has been cut over, burnt over, and trampled over;
> it has been flooded in the torrential downpours of
> northeasters, hurricanes, and near-hurricanes;
> and it has seemed to die in the droughts of many years.

But each spring fresh foliage erupts,
and each summer the growing goes on, from wild ginger to wild geranium
to purple aster; then all returns to leaf mold for the winter.
The Hill is romantic in the morning mist, harsh in the noonday sun,
rich and lush in the shadows at twilight,
and eerie in the dark of the moon.
To the average person it is just a patch of rank weeds,
thick matted and threatening.
To the appreciative eye it is literally a garden
of wild flowers, full of surprises and beauties of form and color,
more wonderful than a suburbanite's well nurtured backyard and often more
rewarding, because it survives without cost, backbreak, or frustration.

I read it and reread it and as I held it in my hand there came over me the sense of holding a priceless jewel. A professional botanist would have written three times as much and in his pompous style have said half as little. For there is recorded in simple poetic language the history of the area, a description of its physical setting, of its topography and its vegetation, its relation to the human occupants of the area today and in colonial and aboriginal times. Several years of faithful recording bring to light nearly 200 kinds of plants (exclusive of grasses and fungi), here presented in the form of a weekly almanac of blooming dates through spring, summer, and fall. The seasons begin with *Stellaria media* the first week in April and close with goldenrods and asters in September. Each week a new set of blooms appears. There is a list of the trees, of the edible plants and of the medicinal plants, the latter lists in an ethnological and colonial context.

These are only a few of the secrets the Hill is waiting to disclose
to any searching eye.
A plant census, carried on faithfully through several years,
revealed in our little half-acre more than 170 species of herbaceous plants,
a dozen kinds of trees, many dozens of grasses, and a few fungi.
For many people, each name will recall a floral acquaintance;
other readers, who have not yet had the pleasure of an introduction,
may find enjoyment in the poetry of the Latin names
and in the often quaint charm of the colloquial ones.

The text is in blank verse and the typography flawless. The color plates include *Smilacina racemosa, Rubus orarius* and *R. allegheniensis, Daucus carota, Verbascum thapsus* and *V. phlomoides*. The drawings are botanically accurate and lifelike and the color rendition is excellent.

In a footnote we learn that the author, Anne Ophelia Todd (Mrs. Raymond Dowden), is artist, amateur botanist, teacher and author. The publication, known as CUAS, is produced by the third year students of the Cooper Union School of Art and Architecture of New York City. We raise our glass high in congratulations to all concerned.—H. L. MASON, Department of Botany, University of California, Berkeley.

NOTES AND NEWS

WYOMING PINYON REVISITED. The center of pinyon (*Pinus edulis* Engelm.) distribution falls close to the geographical point, unique in the United States, where four states—Utah, Colorado, New Mexico, and Arizona—come together. Beyond these four states, pinyon extends eastward to touch Oklahoma, southward into Texas and northern Mexico, and westward to California. Older works on tree distribution, and maps copied from them, complete the symmetry of this geographic range by showing pinyon extending northward to southwestern Wyoming. However, a recent treatment of "The Gymnospermae of Wyoming" (C. L. Porter, 1957, Leaflet 28, Rocky Mountain Herbarium, University of Wyoming) upsets this unusual symmetry by stating that "reports of . . . Pinyon Pine occurring naturally in southern Wyoming are believed to be erroneous, a thorough search for this species having failed to turn it up closer than about twenty miles south of the border in Larimer County, Colorado, and Daggett County, Utah."

In defense of the early references to the occurrence of pinyon northward into Wyoming, the following observations from a 1960 field trip are noted.

1. Pinyon occurs along Sheep Creek, 5 miles south of the Wyoming border, near Manila, Utah (Sec. 1–2, T. 2 N., R. 19 E., Daggett County).

2. Along the Glades, a rock outcrop nearly paralleling the State border near longitude 109 degrees 30 minutes West, scattered pinyons occur on both sides of the border, and are numerous at Minnie's Gap (a break in the Glades) in Wyoming (Sec. 23, T. 12 N., R. 107 W., Sweetwater County).

3. Northward from Minnie's Gap pinyon occurs as a very minor element in the juniper stands. The most northerly pine found is four miles inside Wyoming and five miles east of the Green River (that is, four and one-half miles east of the future shoreline of Flaming Gorge Reservoir; southern boundary of Sec. 34, T. 13 N., R. 107 W., Sweetwater County). This pine is twenty-six inches in diameter at breast height and more than 200 years old, but too decayed for exact dating. Probably pinyons occur north of this old tree as well.

Specimens of native Wyoming *Pinus edulis* from Minnie's Gap (*Peterson 206–60*) have been sent to the Rocky Mountain Herbarium, Laramie, Wyoming, and to the United States Forest Service Herbarium, Washington, D.C. ROGER S. PETERSON, Rocky Mountain Forest and Range Experiment Station, United States Forest Service, Fort Collins, Colorado.

A CONTROVERSIAL TREATMENT OF THE POLEMONIACEAE. The treatment of the Polemoniaceae in Part 4 of the "Vascular Plants of the Pacific Northwest" (Hitchcock, Cronquist, Ownbey, and Thompson, 1959) evokes criticism on the part of an emulator of Polemon, the bellicose philosopher. From numerous cases of disagreement, a few of major importance may be selected for attention.

Eriastrum wilcoxii, reduced to varietal status under the endemic *E. sparsiflorum.* The architecture, leaf-, calyx-, and corolla-characters of these are deemed too dissimilar to justify this. What is really needed is the separation of the comprehensive *E. wilcoxii* into its multiple subspecies or varieties.

Gilia attenuata, submerged in subjective ("taxonomic") synonymy in *G. aggregata.* The corolla-characters of the two are so distinctive, corresponding to pollination by different organisms, that they surely merit some nomenclatural recognition.

Gilia inconspicua, sinuata, etc., brought together in a chaotic assemblage. The thorough morphologic studies by the Grants deserve more respectful consideration than this, supplemented as they are by cytotaxonomic work, one of the best presently available means of throwing light on otherwise obscure inter-relationships.

Leptodactylon pungens segregates, reduced to subjective synonymy under one comprehensive species. These are so distinctive in morphology, ecology, and range that they need recognition at some level.

Phlox bryoides, reduced to subjective synonymy under *P. muscoides.* These are so unlike as to call for at least subspecies segregation.

Phlox douglasii, reduced to subjective synonymy under *P. caespitosa.* This is a serious misunderstanding. Judging by their types, as recognized by the systematists of a century, they are wholly unrelated. *Phlox douglasii* has thin dark green acicular leaves covered by long gland-tipped hairs. *Phlox caespitosa* has thickish pale green linear-oblong leaves bearing coarse glandless cilia; its only glandularity consists in a few hairs on the inflorescence-herbage. No intergrades between them are known. They are surely about as distinct species as can exist among the Microphloxes.

The type locality of *P. caespitosa* has been inferred from the label to lie at the mouth of the Flathead River, but McKelvey finds Wyeth on its collection-date to have been at Flathead Post, latitude 47° 35 'N., longitude 115° 12½' W.* The elevation of the "high hills" thereabouts approaches 6000 feet. Taxon *caespitosa,* then, is the ecad of moderate elevations, while taxon *pulvinata* is the ecad of high country. They do not differ in any major respect, and intergrade completely. If any reduction to subjective synonymy is considered desirable, taxon *pulvinata* is the one needing suppression.

Phlox lanata, reduced to subjective synonymy under *P. hoodii.* This intergrades, however, not with *P. hoodii* but with *P. bryoides,* and the plants at some stations—*e.g.,* Double Springs Pass, Idaho—can not be certainly assigned to one or the other.

Phlox longifolia, interpreted as a grossly comprehensive species, with a host of subjective synonyms. Field study shows that most of these submerged taxa occur so frequently in pure stands and under specialized ecologic or geographic conditions as to merit some degree of nomenclatorial recognition.

Phlox missoulensis, a striking endemic, reduced to varietal status under the wholly unrelated *P. kelseyi.* The latter is a succulent marsh plant with pale, coarsely ciliate leaves, its glandularity, if any, limited to the inflorescence-herbage. The endemic has thin, deep-green leaves, bearing copious long glandular hairs, and grows in dry rocky situations. If it must be reduced in status, then *P. douglasii* would be its closest earlier-named relative. However, students of plant geography, ecology, evolution, etc., find endemics of much interest, and these should be emphasized, not obscured by association with more or less (or un-)related taxa.

Phlox mollis, another endemic, reduced to subjective synonymy under the markedly dissimilar *P. viscida.* As its name implies, the latter is one of the most glandular phloxes known; it has multiflorous inflorescences and is accordingly assignable to Brand's subgenus *Macrophlox.* The endemic has the flowers solitary or in 3's, and so fits into his subgenus *Microphlox.* Its indument is utterly different, consisting of copious woolly hairs on the stems and lower side of leaves, indeed resembling *P. lanata.* Most specimens of *P. mollis* in herbaria have indefinite localities, but in addition to the type station, there is one at Lewis Peak, Washington (latitude 46° 3½' N., longitude 117° 59½' W.).

Phlox scleranthifolia, reduced to subjective synonymy under *P. hoodii.* In habit and measurements, except for the slightly narrower leaves, it agrees instead with *P. diffusa.*

Last but not least, comes *Polemonium.* In passing, it should be emphasized that *P. occidentale* was named by Greene provisionally only, and under the current Code of Nomenclature is not valid. However, it is the treatment of *P. pulcherrimum* for which special criticism is called. Many of the taxa made subjective synonyms of this are only remotely related. And what can be gained by classing as merely varietally distinct two taxa as dissimilar as those figured on page 144 as var. *pulcherrimum* and var. *calycinum*? (The latter, by the way, is not the same as *P. calycinum* Eastwood, a Californian endemic). If all the low-growing, simply-pinnate leaved, rotate-campanulate flowered members of the genus are deemed one species, then its name should be *Polemonium reptans* L.

To make "species" so comprehensive that they include multiple discordant elements releases collectors and herbarium curators from having to examine their specimens closely, but is not the way to advance our understanding of a family as complex as the Polemoniaceae. EDGAR T. WHERRY, Botanical Laboratory, University of Pennsylvania, Philadelphia.

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*A stupid reviewer of my book on *Phlox* held that my giving latitudes and longitudes made localities difficult to find. Actually the reverse is true: their positions can be ascertained by measurement in any atlas, however few place-names or political boundaries it may show. [The book on *Phlox* above referred to is "The Genus Phlox," Morris Arboretum Monograph III, 1955. Obtainable for $4.00, 9414 Meadowbrook Ave., Philadelphia 18, Penna.—Ed.]

CNEORIDIUM DUMOSUM (NUTTALL) HOOKER F. COLLECTED MARCH 26, 1960, AT AN ELEVATION OF ABOUT 1450 METERS ON CERRO QUEMAZÓN, 15 MILES SOUTH OF BAHÍA DE LOS ANGELES, BAJA CALIFORNIA, MÉXICO, APPARENTLY FOR A SOUTHEASTWARD RANGE EXTENSION OF SOME 140 MILES.

I got it there then (*8068*).

I wish to express my sincere thanks to the San Diego Museum of Natural History and particularly to its director, Dr. George E. Lindsay, for making possible the trip on which this interesting specimen was collected; to my companion of the trip, Mr. Glen Ives, then staff artist of the Museum but functioning on the trip as collector of birds and mammals, for much help and encouragement during the field work; to Señor Ricardo Daggett of Bahía de los Angeles, majordomo of the Vermilion Sea Field Station of the San Diego Museum of Natural History, for help in planning and arranging the trip; and to Señor Pepe Smith and his 14-year-old son Favian, both of Bahía de los Angeles, who packed us into the mountains, for many courtesies extended. I am very grateful to Miss Anita Carter, Principal Herbarium Botanist of the University of California, Berkeley, for graciously verifying my determination of the specimen. I also wish to extend my thanks to the editor of the publications of the San Diego Society of Natural History for his many helpful suggestions during the compilation and processing of the data and the writing of the manuscript; to Dr. Helen K. Sharsmith, Señora Herbarium Botanist of the University of California, Berkeley, for her valuable suggestions on expanding the discussion and making the title more precise; to Mrs. Jerry Heller of the Museum staff for her very careful and accurate typing and retyping of the manuscript; and to Mrs. Rosemarie Fiebig of the Museum staff for taking the final manuscript to the post office for mailing. I must also express my deep gratitude to all my former mentors, to whose excellent instruction and training must ultimately be attributed any merit that this unworthy contribution may possess, although, needless to say, any errors are my own: in particular, I would name Professor Ira L. Wiggins and the late Professor LeRoy Abrams, of Stanford University; Professor Robert T. Clausen, of Cornell University; and Professors Lincoln Constance, Herbert L.Mason, and G. Ledyard Stebbins, of the University of California, Berkeley. Last but not least, I cannot fail to mention my deep indebtedness to my parents, without whose early cooperation this work would never have been possible.—REID MORAN, Museum of Natural History, San Diego, California.

PUBLICATIONS OF MARCUS E. JONES AVAILABLE.—Recent correspondence with Mrs. C. A. Broaddus, a daughter of the noted western botanist, Marcus E. Jones, reveals that several of her father's botanical contributions are still available to those interested in purchasing them. These papers are of considerable historical as well as botanical interest and have been virtually unattainable from bookdealers in the past few years. The following works are in print: Ferns of the West (1882); Contributions to Western Botany, nos. 7, 8, 9, 13, 14, 15, 16, 17 and 18; Montana Botany Notes (1910); and Astralagus, Revision of the North American Species (1923). Correspondence regarding these publications should be directed to Mrs. C. A. Broaddus, P.O. Box A-1, Carmel, California.—ROBERT ORNDUFF, Duke University, Durham, North Carolina.

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Classified entries: Chromosome numbers, Reviews. New scientific names are in boldface type. Un-annotated taxa in floral lists are omitted from Index.

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